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COMPREHENSIVE REVIEW

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Population dynamics of *Listeria* spp., *Salmonella* spp., and *Escherichia coli* on fresh produce: A scoping review

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Abstract

Collation of the current scope of literature related to population dynamics (i.e., growth, die-off, survival) of foodborne pathogens on fresh produce can aid in informing future research directions and help stakeholders identify relevant research literature. A scoping review was conducted to gather and synthesize literature that investigates population dynamics of pathogenic and non-pathogenic *Listeria* spp., *Salmonella* spp., and *Escherichia coli* on whole unprocessed fresh produce (defined as produce not having undergone chopping, cutting, homogenization, irradiation, or pasteurization). Literature sources were identified using an exhaustive search of research and industry reports published prior to September 23, 2021, followed by screening for relevance based on strict, a priori eligibility criteria. A total of 277 studies that met all eligibility criteria were subjected to an in-depth qualitative review of various factors (e.g., produce commodities, study settings, inoculation methodologies) that affect population dynamics. Included studies represent investigations of population dynamics on produce before (i.e., pre-harvest; $n = 143$) and after (i.e., post-harvest; $n = 144$) harvest. Several knowledge gaps were identified, including the limited representation of (i) pre-harvest studies that investigated population dynamics of *Listeria* spp. on produce ($n = 13$, 9% of pre-harvest studies), (ii) pre-harvest studies that were carried out on non-sprouts produce types grown using hydroponic cultivation practices ($n = 7$, 5% of pre-harvest studies), and (iii) post-harvest studies that reported the relative humidity conditions under which experiments were carried out ($n = 56$, 39% of post-harvest studies). These and other knowledge gaps summarized in this scoping review represent areas of research that can be investigated in future studies.

KEYWORDS

E. coli, fresh produce, fruit, *Listeria*, population dynamics, post-harvest, pre-harvest, *Salmonella*, vegetables

1 | INTRODUCTION

Global trends in increased fresh produce production and consumption have highlighted the role of fresh produce as a source of foodborne illness outbreaks and cases (Balali et al., 2020; Berger et al., 2010; Painter et al., 2013; Sivapalasingam et al., 2004). Second only to norovirus, bacterial pathogens represent the most common etiological agents associated with fresh produce foodborne illness outbreaks in the European Union and the United States (Callejón et al., 2015) and are considered a high-priority food safety concern among stakeholders in the produce supply chain (Van Boxstael et al., 2013). In particular, the bacterial pathogens *Listeria monocytogenes*, *Salmonella enterica*, and pathogenic *Escherichia coli* were associated with 83 out of 85 multistate fresh produce outbreaks between 2010 and 2017 in the United States (Carstens et al., 2019).

L. monocytogenes, *S. enterica*, and pathogenic *E. coli* can contaminate fresh produce at multiple stages throughout the produce supply chain (Machado-Moreira et al., 2019), and as there is no definitive kill step between harvest and consumption of fresh produce (Weller et al., 2016), alternative control strategies or interventions are needed to control the survival and potential proliferation of these pathogens. A control strategy that has been proposed is the use of established time-dependent metrics of die-off or growth suppression of bacterial pathogens on fresh produce. An example of this is described in the Food Safety Modernization Act (FSMA) Produce Safety Rule's (PSR) agricultural water standard that was proposed in 2021 (U.S. Food & Drug Administration, 2021), which states that if the quality of any agricultural water source is deemed unacceptable based on water quality assessments, then growers can choose to wait at least 4 days from water application to harvest to allow for microbial die-off, assuming a 0.5 $\log_{10}$ die-off per day; this metric was determined based on population dynamics data taken from nine studies that measured die-off of several foodborne pathogens on fresh produce at the pre-harvest stage of the supply chain (Snellman et al., 2014). It should be noted that concerns have been raised that the limited number of studies used to establish this metric might limit its applicability across different produce types and growing conditions (Wall et al., 2019). This highlights a need for more comprehensive assessments (e.g., meta-analyses) of population dynamics data to better inform future time-dependent metrics for controlling foodborne pathogens on fresh produce. However, as available literature evaluating the population dynamics of bacterial pathogens on fresh produce is highly complex and heterogenous in nature, it can be challenging to identify areas where enough literature is available to warrant such meta-analyses.

Thus, we conducted a scoping review to elucidate the current scope of available literature that evaluates the population dynamics of pathogenic and non-pathogenic *Listeria* spp., *Salmonella* spp., and *E. coli* (referred to henceforth as *Listeria* spp., *Salmonella* spp., and *E. coli*) on whole fresh produce at both pre- and post-harvest stages of the supply chain. The specific goals of this scoping review were (i) to assess the scope of information available on the population dynamics (i.e., growth, die-off, survival) of *Listeria* spp., *Salmonella* spp., and *E. coli* on whole fresh produce; (ii) to assess the scope of information available on factors (e.g., produce commodities, study settings, experimental storage conditions, inoculation methodologies) that may affect these population dynamics; and (iii) to determine areas requiring additional research relating to the population dynamics of *Listeria* spp., *Salmonella* spp., and *E. coli* on whole fresh produce.

Unlike systematic reviews, which are guided by precise questions and generally focus on evaluating data of methodologically similar studies to enable recommendations on a narrow topic, scoping reviews are guided by broader questions and focus on describing data among studies that use diverse methodologies to enable the identification of knowledge gaps (Munn et al., 2018; Peterson et al., 2017). The data presented in this scoping review thus provide a broad overview of key factors and methodological characteristics pertaining to population dynamics studies on fresh produce, which can guide future in-depth evaluations (e.g., meta-analyses) and primary research pursuits.

2 | MATERIALS AND METHODS

This scoping review closely adheres to the reporting guidelines that are outlined in the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) Extension for Scoping Reviews (Tricco et al., 2018), which provides a template to maximize a review's transparency, replicability, and comprehensiveness while minimizing bias. A protocol for this review was registered with the Center for Open Science's Open Science Framework (osf.io) on May 9, 2019, and an updated protocol was registered on September 19, 2021. The protocols are available at https://osf.io/ayb67 and https://osf.io/76rqf. The review team was composed of experts in the field (MW, RI), research librarians (KAW, SSM), doctoral students (SB, AB) and one postdoctoral fellow (MP). Study screening and selection were carried out by SB and AB, as well as several other graduate students (SS, ZW, CBN, RL), postdoctoral fellows (DW, FEA), and one staff scientist (SRR).

2.1 | Research question and definitions

This review aims to identify and describe peer-reviewed and gray literature relevant to the research question "What is the available information and how complete is the information on the population dynamics of *Listeria* spp., *Salmonella* spp., and *E. coli* on unprocessed produce, and what approaches were used in the studies that collected this information?" and utilizes the following definitions:

Produce: We define produce as (i) all raw produce commodities explicitly listed as covered under the FSMA PSR (CFR 112.1 (b) (1)) (U.S. Food & Drug Administration, 2015) and (ii) any additional raw produce commodities identified as relevant in the *Draft Guidance for Industry: Standards for the Growing, Harvesting, Packing, and Holding of Produce for Human Consumption* (U.S. Food & Drug Administration, 2018). These include: almonds, apples, ackee, apricots, apriums, aronia, arrowhead, arrowroot, artichokes-globe-type, Asian pears, atemoya, avocados, babacos, bananas, Belgian endive, blackberries, blueberries, boysenberries, Brazil nuts, broad beans, broccoli, brussels sprouts, burdock, butterbur, cabbages, cactus, Chinese cabbages (bok choy, mustard, and napa), cantaloupes, carambolas, carrots, cauliflower, celeriac, celery, chayote fruit, cherries (sweet), chestnuts, chicory (roots and tops), chipilin, citrus (such as clementine, grapefruit, lemons, limes, mandarin, oranges, tangerines, tangors, and uniq fruit), cowpea beans, crabapple, cress-garden, cucumbers, curly endive, currants, dandelion leaves, dragon fruit, fennel-Florence, fiddlehead, garlic, genip, ginkgo nut, gooseberries, grapes, green beans, guavas, herbs (such as basil, chives, cilantro, oregano, and parsley), honeydew, huckleberries, Jerusalem artichokes, kale, kiwifruit, kohlrabi, komatsuna, kumquats, lavender, leek, lettuce, longan, loroco, lotus root, lychees, macadamia nuts, mangos, other melons (such as canary, crenshaw and Persian), microgreens, mulberries, mushrooms, mustard greens, nasturtiums, nectarines, onions, papayas, parsnips, passion fruit, peaches, pears, peas, peas-pigeon, peppers, persimmon, pine nuts, pineapples, plantains, plums, plumcots, pomegranate, pomelo, quince, radishes, ramp, raspberries, rhubarb, rutabagas, salsify, scallions, shallots, snow peas, soursop, spinach, sprouts, strawberries, squash blossoms, summer squash (such as patty pan, yellow and zucchini), swamp cabbage, sweetsop, Swiss chard, tamarillo, taro, tea, ti plant, tomatoes, turmeric, turnips (roots and tops), ulluko, walnuts, watercress, watermelons, yams.

Unprocessed produce: We define unprocessed produce as a raw agricultural commodity that is subject to the FSMA PSR (U.S. Food & Drug Administration, 2015, 2018). Unprocessed produce can have undergone hydrocooling, refrigeration, leaf/stem/husk removal, washing, and other steps to remove foreign objects from the produce. This category also includes produce still in the field prior to harvest.

Processed produce: We define processed produce as a raw agricultural commodity that has been subjected to an activity such as chopping, cooking, cutting, homogenization, irradiation, or pasteurization. Processed produce is not subject to the FSMA PSR (U.S. Food & Drug Administration, 2015, 2018).

2.2 | Search strategy and information sources

A comprehensive search was developed and executed for Medline (PubMed) using search terms related to population dynamics, *E. coli*, *Listeria*, *Salmonella*, and produce. The search was translated for and run in the Centre for Agriculture and Biosciences International (CAB) Abstracts and Global Health (Clarivate Analytics), AGRICOLA (EBSCO), Food Science and Technology Abstracts (Clarivate Analytics), ProQuest Dissertations and Theses Global (ProQuest), Scopus (Elsevier), and Web of Science Core Collection (Clarivate Analytics). All seven databases were searched to capture records available through September 23, 2021. This was achieved through (i) a primary search performed with no date, language, or source format restrictions on June 2, 2019, followed by (ii) a re-run of the primary search performed on September 23, 2021 (covering June 2019 to September 2021) to identify any new literature published after the primary search. Full search details, including search terms and syntax for each database search, can be found in Appendix A in the Supporting Information.

Additionally, a search of relevant gray literature sources, which represent sources not typically indexed in major bibliographic databases (Pappas & Williams, 2011), was also conducted to explore emerging trends and developments in studies of population dynamics of *Listeria* spp., *Salmonella* spp., and *E. coli* on fresh produce. As is common with scoping reviews, date restrictions (i.e., studies published between 2011 and 2021) were placed on gray literature searches to obtain a manageable collection of current gray literature sources. Gray literature sources were manually searched between September 14 and 20, 2021, from repositories including The Center for Produce Safety (CPS) Final Reports of Funded Research Projects (https://www.centerforproducesafety.org/funded-research-projects.php) published between 2011 and 2021; United States Food and Drug Administration (FDA) Guidance Documents Food and Beverage Reports (https://www.fda.gov/regulatory-information/search-fda-guidance-documents#guidancesearch) published between 2011 and 2021; and all publications of the

FDA Center for Food Safety and Applied Nutrition (https://www.fda.gov/food/science-research-food), spanning 2016–2021 (see Appendix A in the Supporting Information). Evidence syntheses (e.g., systematic reviews and meta-analyses) were not eligible for inclusion, but references from otherwise eligible reviews were evaluated for inclusion.

2.3 | Citation management

All references returned from initial database searches were imported or manually entered into EndNote X9 citation management software (endnote.com), where records were de-duplicated using the method described by Bramer et al. (2016). Records were then imported into Covidence screening software (covidence.org), where additional duplicates were identified and removed. All references returned from the updated database and gray literature searches were imported or manually entered into EndNote X9 and were immediately imported into Covidence software where duplicate records were identified and removed. All remaining records were considered for inclusion.

2.4 | Eligibility criteria and study selection

To be considered eligible for inclusion in this review, a study needed to (i) investigate *Listeria* spp., *Salmonella* spp., and/or *E. coli,* (ii) investigate microbial population dynamics on at least one produce commodity (see Section 2.1), (iii) investigate microbial population dynamics such that no antimicrobial agents were applied to produce following inoculation or contamination, (iv) investigate microbial population dynamics on unprocessed produce (see Section 2.1), and (v) be published in English. Studies were excluded if they did not satisfy all inclusion criteria.

The title and abstract of each record were screened for eligibility against the pre-determined inclusion criteria by two independent reviewers. Records that were not eliminated at this stage were then evaluated by two independent reviewers (including SB, AB, SRR, SS, ZW, DW, CBN, FEA, and RL) at the full-text level. If the reviewers determined that a given record did not meet the inclusion criteria at the full-text review stage, the reason for exclusion was documented. For both title and abstract screening and full-text review stages, any conflicts between the two independent researchers were resolved either by a consensus between the two reviewers or by a third "tie-breaker" independent reviewer.

The number of sources included at each stage of retrieval, screening, and data extraction, as well as reasons for exclusion at the full-text review stage, are indicated in the PRISMA diagram (Figure 1). As prescribed for scoping reviews (Arksey & O'Malley, 2005; Peters et al., 2015; Tricco et al., 2018), risk of source bias was not evaluated during consideration for inclusion, and a formal assessment of the methodological quality of studies was not performed prior to or during data extraction.

2.5 | Data extraction and summarization

Once the final list of full texts to be included in the scoping review was compiled, a list of relevant data categories was developed to guide data extraction. The key pieces of data that were extracted were organized into a survey format in Qualtrics (qualtrics.com). Key data characteristics extracted by two reviewers (SB, MP) included the type of reference (e.g., peer-reviewed journal article, industry report, thesis/dissertation), year of publication, experimental design elements (e.g., presence of control group), materials and methods pertaining to bacterial inoculation, recovery, and enumeration/detection, stage in the produce supply chain (i.e., pre- or post-harvest), bacterial strain characteristics (e.g., serovar, antibiotic resistance phenotypes), produce commodities evaluated, study setting (e.g., field, greenhouse), environmental factors monitored or collected (e.g., weather conditions), experimental temperature and relative humidity (RH) conditions, and type of population dynamics outcomes that were observed (i.e., growth, die-off, survival). Upon independently extracting data from 81 articles (representing ~30% of the included articles), the reviewers (SB and MP) met to discuss the results and clarify any differences or uncertainties. The characteristics of each additional full-text article (n = 196) were then extracted by one of the two reviewers. All raw data extracted from full texts are available on GitHub (https://github.com/sjb375/scoping_review). Descriptive analysis of relevant data was performed in R (4.0.2).

3 | RESULTS AND DISCUSSION

3.1 | Attributes of records identified and studies included

Of the 16,502 records that were imported into Covidence for title and abstract screening, 15,826 were excluded based on irrelevance to the scoping review objective (Figure 1). The remaining 676 records were subjected to full-text screening, in which an additional 399 records were found to not meet inclusion criteria and were subsequently excluded; reasons for exclusion of these records

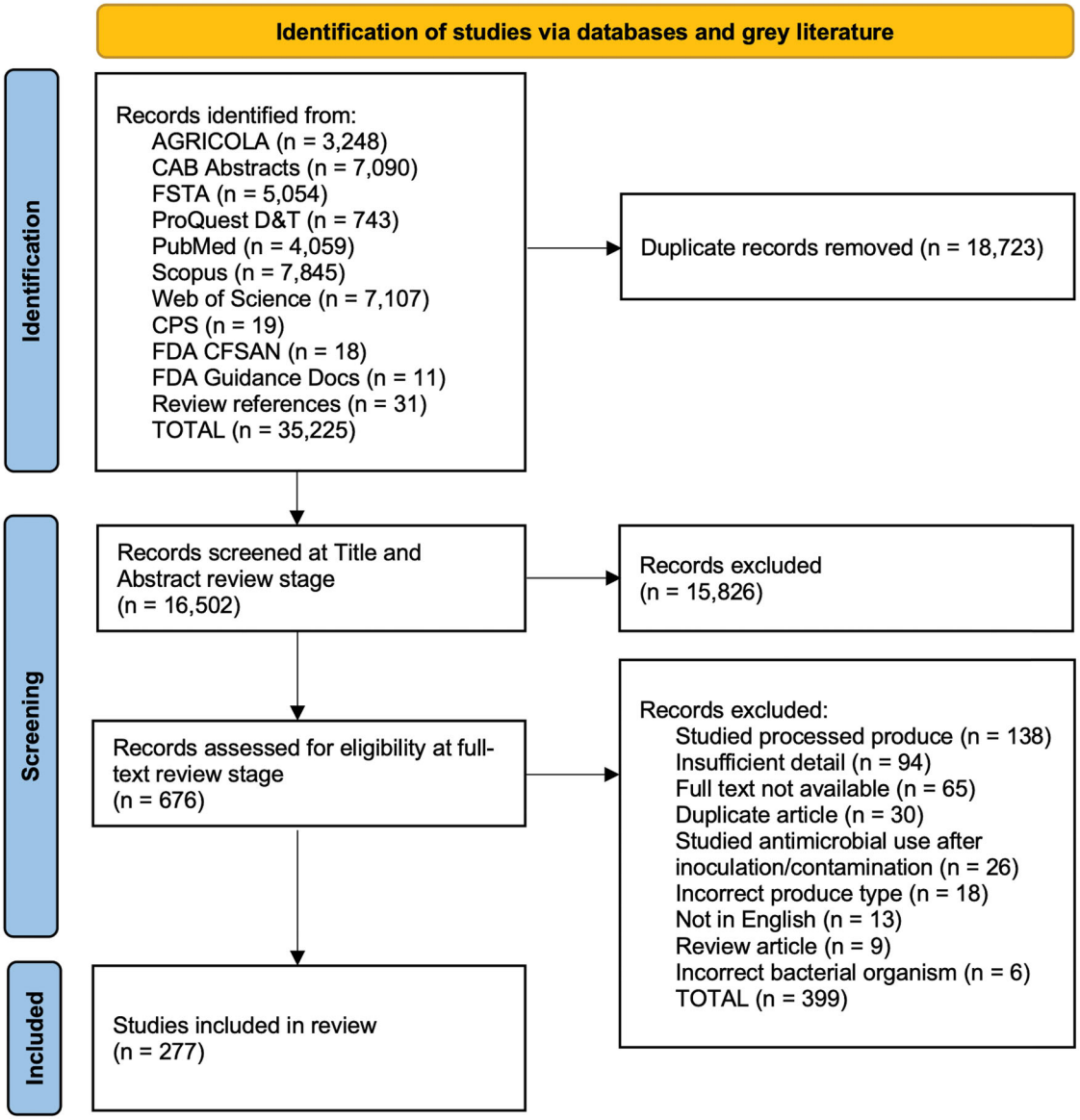

FIGURE 1 Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flow diagram. Number of records found at each stage of retrieval, screening, and data extraction (numbers represent combination of results from original and updated search; see Materials and Methods for details). Adapted from: Page et al. (2021).

are provided in Figure 1. A total of 277 studies met all inclusion criteria; a bibliography of references for all included studies is provided in Appendix B in the Supporting Information. Most included studies represented publications in peer-reviewed journals (85%), followed by theses and dissertations (11%), and finally CPS Final Reports and Funded Research Projects (4%). The majority (n = 186, 67%) of included studies were published between 2011 and 2021 (Figure 2), demonstrating a trend of increasing numbers of population dynamics studies on unprocessed whole fresh produce (henceforth referred to as produce) being published in recent years. Key takeaways described in subsequent sections of this scoping review (i.e., Sections 3.2–3.6) are also summarized in Supplementary Table S1.

3.2 | Key experimental design elements of included studies: Independent experimental trial replicates and presence of a control group

A total of 166 (60%) studies reported carrying out independent experimental trial replicates. For the remaining studies (n = 111, 40%), the number of independent experimental trial replicates was either not provided or could not

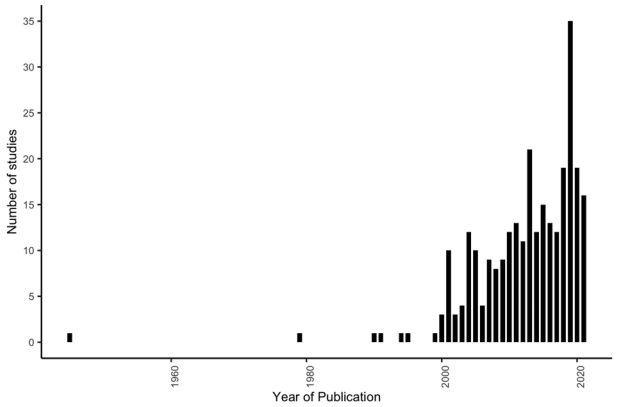

FIGURE 2 Studies included in this scoping review ($n = 277$) by year of publication.

be reliably extracted from full texts (both were reported as "not able to extract"). Overall, among the 166 studies that reported carrying out independent experimental trial replicates, the majority reported either two ($n = 81$) or three ($n = 74$) replicate trials being carried out. The relatively low number of studies that reported carrying out experimental trial replicates is in agreement with the notion that replication tends to be less common in studies that investigate temporal population dynamics in environmental microbiology-related fields (Lennon, 2011). Another key outcome revealed from this analysis was the inconsistency in the language used to report the number of independent experimental replicates that were carried out in included studies. For example, some studies would report that "samples were analyzed in triplicate," which could be interpreted to mean there were three biological replicates per treatment, or that three replicate trials were carried out; such studies were reported here as "not able to extract." Prosser (2010) reported a similar difficulty with distinguishing true independent experimental replicates from biological or technical replicates in articles published in environmental microbiology-focused journals. Thus, ambiguous descriptions regarding the number of independent experimental trial replicates conducted in a given study is a documented problem in environmental microbiology fields, and future studies should prioritize reporting clearer descriptions of the number of independent experimental trial replicates that are being carried out as a part of their investigations.

Among included studies, 274 (99%) were categorized as controlled experimental trials, where the bacterial target organism (i.e., *Listeria* spp., *Salmonella* spp., or *E. coli*) was inoculated onto produce; the remaining three studies (Castro-Ibáñez et al., 2015; Fu et al., 2008; Stewart et al., 2001) were categorized as observational studies. Castro-Ibáñez et al. (2015) assessed population dynamics of *Listeria* spp., *Salmonella* spp., and *E. coli* on lettuce in the field over a 7-week period after a naturally occurring flooding event, and Stewart et al. (2001) and Fu et al. (2008) investigated population dynamics of *Salmonella* on alfalfa sprouts obtained from seed lots associated with salmonellosis outbreaks.

Of the 274 studies that represented controlled experimental trials, a total of 146 (53%) reported including a control group of produce that was not inoculated with the bacterial target organism (i.e., either *Listeria* spp., *Salmonella* spp., or *E. coli*) while being subjected to the same conditions as inoculated produce in population dynamics experiments. For the remaining studies ($n = 128$, 47%), control group information was either not provided or could not be reliably extracted from full texts. These results suggest that there is either an issue of studies not including uninoculated control groups in experimental designs or an issue of studies not reporting this experimental design element in full texts. We hypothesize it is more likely the latter case, as it is well known that naturally occurring *Listeria* spp., *Salmonella* spp., and *E. coli* can be present on produce (de Oliveira Elias et al., 2019; Reddy et al., 2016), as well as in environments associated with the production of produce (Chapin et al., 2014; Sharma et al., 2020; Strawn et al., 2013; Townsend et al., 2021). Therefore, these findings highlight the need for future produce population dynamics studies to more clearly indicate the incorporation of uninoculated control groups as a study design element.

3.3 | Key methodological aspects of included studies: Inoculation, recovery, and enumeration/detection procedures used

Materials and methods pertaining to the (i) inoculation (including buffers used to prepare inocula, cocktail versus individual bacterial strain inoculum preparations, inoculation methods used, and the concentrations of bacterial inoculum suspensions), (ii) recovery, and (iii) enumeration/detection (including methods used to enumerate or detect recovered bacteria and base plating media used for classical culture-based enumeration/detection) were extracted from all included studies and are presented below in Sections 3.3.1–3.3.7.

3.3.1 | Buffers used for inoculum preparation

A total of 248 (90%) studies reported the buffers used to prepare bacterial inoculum suspensions. For the remaining studies ($n = 29$, 10%), the type of buffer used was either not provided or could not be reliably extracted from full texts (both cases were reported as "not able to extract") or was categorized as "not applicable" in the

case of observational studies (see Section 3.2). The types of buffers used to prepare inoculum suspensions represented four distinct categories: (i) rich media known to support bacterial growth, (ii) nutrient-poor buffers that minimally support bacterial growth, (iii) organic matter slurries (e.g., slurries of fecal or composted fecal matter), and (iv) low-moisture inoculum preparations (e.g., sand or soil matrix; Table 1). Across all bacterial types, the most frequently reported buffers represented category (ii) ($n = 126$, $n = 117$, and $n = 53$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by category (iii) ($n = 19$, $n = 11$, and $n = 3$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively). Buffers representing category (i) ($n = 7$, $n = 6$, and $n = 1$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively) and category (iv) ($n = 4$, $n = 1$, and $n = 1$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively) were less frequently reported. These data indicate that a limited number of studies used low-moisture inoculum preparations (i.e., category iv). This represents a key knowledge gap in the literature, as low-moisture matrices (e.g., dust) have been reported to facilitate the dispersal of bacterial pathogens (Kumar et al., 2017), as well as potentially support enhanced survival of bacteria on produce when compared to high-moisture matrices (Oni et al., 2015). Thus, the use of low-moisture inoculum preparations may be valuable in future population dynamics studies, particularly if contamination events through low-moisture fomites are likely for a given commodity.

One key aspect of preparing an inoculum that can be challenging is for the inoculum to both mimic natural inoculation routes and the physiological state of the inoculum expected under natural conditions. This could potentially be achieved through preparing inocula in organic matter slurries (i.e., category iii). Included studies reported using a variety of organic matter slurries to prepare bacterial inocula, including slurries made with fecal matter or composted fecal matter, tomato serum, sewage, or 5% horse serum. As fecal matter, composted fecal matter, tomato serum, and sewage all represent potential vehicles of natural contamination (Alegbeleye et al., 2018; Tokarskyy & Schneider, 2019), and 5% horse serum has a high organic load that may be representative of fecal matter or other environmental matrices (Beuchat et al., 2001; Knudsen et al., 2001), use of these slurries may facilitate the physiological state of inocula expected under natural conditions. However, it is important to note that, except for 5% horse serum, organic matter slurries are often "non-standardized" and can vary considerably with respect to their physicochemical properties and organic loads. Importantly, previous studies have reported that physicochemical properties, such as turbidity (López-Gálvez et al., 2018) and pH (Harrand et al., 2021), can influence the physiological state of bacterial inocula. Therefore, future studies should aim for improved reporting of the physicochemical properties of organic matter slurries and other non-standardized buffers (e.g., irrigation water), as this information may yield valuable insights about how the physiological state of a bacterial inoculum can impact population dynamics outcomes on produce.

3.3.2 | Cocktail versus individual strain inoculum preparation

A total of 163 (59%) studies reported inoculating produce with inoculum suspensions that were prepared using an individual strain (referred to as "individual strain inoculum preparations"), and 122 (44%) studies reported using inoculum suspensions that were prepared using more than one strain in each inoculum suspension (referred to as "cocktail inoculum preparations"). For the remaining studies ($n = 8$, 3%), the distinction of individual strain versus cocktail inoculum preparation was either not provided or could not be reliably extracted from full texts (both cases were reported as "not able to extract") or was categorized as "not applicable" in the case of observational studies (see Section 3.2). For *E. coli* and *Salmonella* spp., individual strain inoculum preparations ($n = 86$ and $n = 92$, respectively) were reported more frequently than cocktail inoculum preparations ($n = 67$ and $n = 65$, respectively; Table 1). Conversely, for studies that investigated population dynamics of *Listeria* spp., cocktail inoculum preparations ($n = 40$) were reported more frequently than individual strain inoculum preparations ($n = 23$), possibly because cocktails are more frequently used in post-harvest studies (which represent the majority of *Listeria* spp. studies; see Section 3.5).

Both cocktail and individual strain inoculum preparations have merit in population dynamics investigations. The use of cocktail inoculum preparations makes it easier to identify worst-case scenarios (e.g., specific strains that show enhanced survival) but limits the ability to calculate specific growth parameters (e.g., lag phase duration, μmax). Conversely, the use of individual strain inoculum preparations provides the data needed to calculate strain-specific growth parameters, which are essential for modeling efforts. To address the shortcoming of using cocktails, some included studies used molecular assays (e.g., polymerase chain reaction [PCR]) to differentiate the strains included in cocktail inoculum suspensions. For example, one study (Belias et al., 2020) performed PCR with strain-specific primers to differentiate the three *E. coli* strains in their cocktail inoculum preparation, and another (Ryser, 2021) tagged the eight *L. monocytogenes* strains in their cocktail inoculum preparation with unique barcodes and performed PCR with barcode-specific primers to

TABLE 1 Summary of the materials and methods pertaining to the (i) inoculation (including buffers used to prepare inocula, cocktail versus individual bacterial strain inoculum preparations, inoculation methods used, and the concentrations of bacterial inoculum suspensions), (ii) recovery, and (iii) enumeration/detection (including methods used to enumerate or detect recovered bacteria and base plating media used for enumeration or detection) that were extracted from included studies investigating population dynamics of *Listeria* spp., *Salmonella* spp., and *E. coli* on produce.

***Listeria* spp. ($n = 60$)**	***Salmonella* spp. ($n = 150$)**	***E. coli* ($n = 148$)**
Buffers used to prepare inocula (number of studies)		
Rich media that can support bacterial growth: (total: 1)	Rich media that can support bacterial growth: (total: 7)	Rich media that can support bacterial growth: (total: 6)
Brain heart infusion broth (1)	Buffered peptone water (4)	Buffered peptone water (4)
	Tryptic soy broth (2)	Brain heart infusion broth (1)
	Lysogeny broth (LB)[a] (1)	LB (1)
Nutrient-poor buffers that minimally support bacterial growth: (total: 53)	Nutrient-poor buffers that minimally support bacterial growth: (total: 126)	Nutrient-poor buffers that minimally support bacterial growth: (total: 117)
Water[b] (16)	Water (43)	Water (44)
0.1% peptone water (16)	0.1% peptone water (40)	0.1% peptone water (33)
Phosphate-buffered saline (7)	Phosphate-buffered saline (24)	Phosphate-buffered saline (18)
Saline solution[c] (4)	Saline solution (7)	Butterfield's phosphate buffer (6)
Butterfield's phosphate buffer (4)	Potassium phosphate buffer (6)	Saline solution (6)
Maximum recovery diluent (3)	Butterfield's phosphate buffer (2)	Potassium phosphate buffer (4)
Potassium phosphate buffer (3)	Maximum recovery diluent (1)	Maximum recovery diluent (3)
	Quarter strength ringer solution (1)	Phosphate buffer (2)
	Sodium phosphate buffer (1)	Quarter strength ringer solution (1)
	10 mM $MgCl_2$ (1)	
Organic matter slurries: (total: 3)	Organic matter slurries: (total: 11)	Organic matter slurries: (total: 19)
Fecal/composted fecal matter (2)	Fecal/composted fecal matter (7)	Fecal/composted fecal matter (17)
5% horse serum (1)	5% horse serum (2)	Sewage (1)
	Sewage (1)	5% horse serum (1)
	Tomato serum (1)	
Low-moisture inoculum preparations: (total: 1)	Low-moisture inoculum preparations: (total: 4)	Low-moisture inoculum preparations: (total: 1)
Sand matrix (1)	Soil matrix (2)	Soil matrix (1)
	Sand matrix (1)	
	Chalk matrix (1)	
Not able to extract[d] (6)	Not able to extract (13)	Not able to extract (12)
Not applicable[e] (1)	Not applicable (3)	Not applicable (1)
Cocktail versus individual strain inoculum preparation (number of studies)		
Individual strain preparations (23)	Individual strain preparations (92)	Individual strain preparations (86)
Cocktail preparations (40)	Cocktail preparations (65)	Cocktail preparations (67)
Not able to extract (1)	Not able to extract (1)	Not able to extract (5)
Not applicable (1)	Not applicable (3)	Not applicable (1)
Inoculation methods used (number of studies)		
Direct application methods where inoculum was directly applied to produce surface (e.g., dip, spot, or spray inoculation) (57)	Direct application methods where inoculum was directly applied to produce surface (e.g., dip, spot, or spray inoculation) (139)	Direct application methods where inoculum was directly applied to produce surface (e.g., dip, spot, or spray inoculation) (127)

(Continues)

TABLE 1 (Continued)

***Listeria* spp. ($n = 60$)**	***Salmonella* spp. ($n = 150$)**	***E. coli* ($n = 148$)**
Indirect application methods where inoculum was not directly applied to produce surface (e.g., furrow/drip line irrigation or inoculation with an inoculum suspension directly into soil/soil amendment) (4)	Indirect application methods where inoculum was not directly applied to produce surface (e.g., furrow/drip line irrigation or inoculation with an inoculum suspension directly into soil/soil amendment) (7)	Indirect application methods where inoculum was not directly applied to produce surface (e.g., furrow/drip line irrigation or inoculation with an inoculum suspension directly into soil/soil amendment) (23)
Not able to extract (2)	Not able to extract (5)	Not able to extract (7)
Not applicable (1)	Not applicable (3)	Not applicable (1)
Concentration of bacterial inoculum suspensions used[f] (number of studies)		
6–7 log CFU/mL (14)	5–6 log CFU/mL (30)	7–8 log CFU/mL (36)
5–6 log CFU/mL (13)	7–8 log CFU/mL (22)	6–7 log CFU/mL (31)
7–8 log CFU/mL (11)	6–7 log CFU/mL (20)	5–6 log CFU/mL (28)
4–5 log CFU/mL (9)	4–5 log CFU/mL (19)	8–9 log CFU/mL (20)
3–4 log CFU/mL (8)	8–9 log CFU/mL (16)	4–5 log CFU/mL (18)
8–9 log CFU/mL (8)	3–4 log CFU/mL (12)	3–4 log CFU/mL (14)
9–10 log CFU/mL (4)	9–10 log CFU/mL (11)	2–3 log CFU/mL (8)
11–12 log CFU/mL (4)	10–11 log CFU/mL (7)	9–10 log CFU/mL (7)
2–3 log CFU/mL (2)	2–3 log CFU/mL (5)	11–12 log CFU/mL (2)
10–11 log CFU/mL (2)	11–12 log CFU/mL (4)	0–1 log CFU/mL (1)
	1–2 log CFU/mL (1)	10–11 log CFU/mL (1)
Not able to extract (17)	Not able to extract (44)	Not able to extract (37)
Not applicable (1)	Not applicable (3)	Not applicable (1)
Recovery procedures (number of studies)		
Manual methods that do not compromise the structural integrity of produce (e.g., hand massaging, rubbing, shaking) (15)	Manual methods that do not compromise the structural integrity of produce (e.g., hand massaging, rubbing, shaking) (59)	Manual methods that do not compromise the structural integrity of produce (e.g., hand massaging, rubbing, shaking) (46)
Mechanical methods that result in minimal damage to the structural integrity of produce (e.g., vortexing, sonication) (5)	Mechanical methods that result in minimal damage to the structural integrity of produce (e.g., vortexing, sonication) (15)	Mechanical methods that result in minimal damage to the structural integrity of produce (e.g., vortexing, sonication) (8)
Mechanical methods that result in substantial damage to the structural integrity of produce (e.g., stomaching, homogenization, pummeling, maceration) (42)	Mechanical methods that result in substantial damage to the structural integrity of produce (e.g., stomaching, homogenization, pummeling, maceration) (83)	Mechanical methods that result in substantial damage to the structural integrity of produce (e.g., stomaching, homogenization, pummeling, maceration) (92)
		Pulsification (3)
Not able to extract (6)	Not able to extract (8)	Not able to extract (9)
Enumeration or detection methods used (number of studies)		
Classical culture-based enumeration methods: (total: 65)	Classical culture-based enumeration methods: (total: 154)	Classical culture-based enumeration methods: (total: 159)
Direct plating (59)	Direct plating (138)	Direct plating (133)
Most probable number assay (6)	Most probable number assay (10)	Most probable number assay (13)
	Filter plating[g] (6)	Filter plating (11)
		Colilert quanti-tray assay (2)
Culture-independent enumeration methods: (total: 3)	Culture-independent enumeration methods: (total: 4)	Culture-independent enumeration methods: (total: 9)
Microscopy assay (e.g., direct viable count) (2)	qPCR assay (3)	qPCR assay (6)

(Continues)

TABLE 1 (Continued)

***Listeria* spp. ($n = 60$)**	***Salmonella* spp. ($n = 150$)**	***E. coli* ($n = 148$)**
qPCR assay (1)	Microscopy assay (e.g., direct viable count) (1)	Microscopy assay (e.g., direct viable count) (3)
Classical culture-based detection methods: (total: 17)	Classical culture-based detection methods: (total: 42)	Classical culture-based detection methods: (total: 55)
Sample enrichment followed by streaking on agar (17)	Sample enrichment followed by streaking on agar (42)	Sample enrichment followed by streaking on agar (54)
		Sample enrichment followed by IDEXX Colilert test (1)
Culture-based rapid detection methods: (total: 3)	Culture-based rapid detection methods: (total: 7)	Culture-based rapid detection methods: (total: 6)
Sample enrichment followed by an immunological-based assay (e.g., lateral flow immunoassay) (2)	Sample enrichment followed by a nucleic acid-based assay (e.g., PCR) (5)	Sample enrichment followed by a nucleic acid-based assay (e.g., PCR) (4)
Sample enrichment followed by a nucleic acid-based assay (e.g., PCR) (1)	Sample enrichment followed by an immunological-based assay (e.g., lateral flow immunoassay) (2)	Sample enrichment followed by an immunological-based assay (e.g., lateral flow immunoassay) (2)
	Not able to extract (4)	Not able to extract (3)
Base plating media used in classical culture-based enumeration/detection (number of studies)		
Non-selective base media: (total: 20)	Non-selective base media: (total: 77)	Non-selective base media: (total: 78)
Tryptic soy agar (17)	Tryptic soy agar (55)	Tryptic soy agar (66)
Lysogeny agar (LA)[h] (1)	LA (12)	LA (10)
Plate count agar (1)	Brain heart infusion agar (7)	Brain heart infusion agar (1)
Tryptose phosphate agar (1)	Nutrient agar (2)	Plate count agar (1)
	Plate count agar (1)	
Selective base media: (total: 57)	Selective base media: (total: 104)	Selective base media: (total: 98)
Modified Oxford agar (15)	Xylose lysine deoxycholate agar (47)	Sorbitol MacConkey agar (39)
Oxford agar (12)	Bismuth sulfite agar (20)	CHROMagar O157 (18)
CHROMagar *Listeria* (7)	Xylose lysine tergitol-4 agar (14)	MacConkey agar (13)
Agar *Listeria* according to Ottaviani and Agosti (6)	Hektoen enteric agar (13)	CHROMagar *E. coli*/coliform (6)
Polymyxin acriflavine lithium chloride ceftazidime aesculin mannitol agar (6)	Salmonella-Shigella agar (4)	Petrifilm *E. coli*/coliform (6)
Listeria selective agar (3)	CHROMagar *Salmonella* (3)	Eosin-methylene blue agar (5)
Rapid L. mono agar (3)	Rappaport Vassiliadis agar (2)	Chromocult agar (2)
Modified Vogel Johnson agar (2)	Triple sugar iron agar (1)	Membrane fecal coliform agar (2)
Brilliance *Listeria* agar (1)		Tryptone bile x-glucuronide agar (2)
Harlequin agar (1)		Violet red bile dextrose agar (2)
Listeria monocytogenes chromogenic plating medium (1)		BCM O157:H7 agar (1)
		Brilliant green agar (1)
		SD-39 agar (1)
Combination of selective and non-selective base media: (total: 3)	Combination of selective and non-selective base media: (total: 7)	Combination of selective and non-selective base media: (total: 3)
Tryptic soy agar overlaid with modified Oxford agar (2)	Nutrient agar overlaid with xylose lysine deoxycholate agar (2)	Sorbitol MacConkey agar overlaid with tryptic soy agar (2)

(Continues)

TABLE 1 (Continued)

Listeria spp. ($n = 60$)	*Salmonella* spp. ($n = 150$)	*E. coli* ($n = 148$)
Tryptic soy agar overlaid with Oxford agar (1)	Tryptic soy agar overlaid with xylose lysine deoxycholate agar (2)	Tryptic soy agar overlaid with sorbitol MacConkey agar (1)
	Xylose lysine deoxycholate agar overlaid with tryptic soy agar (2)	
	Brain heart infusion agar overlaid with xylose lysine deoxycholate agar (1)	
Not able to extract (1)	Not able to extract (8)	Not able to extract (6)
	No classical culture-based methods performed (1)	No classical culture-based methods performed (1)

Note: Note that each given study may have used multiple methods pertaining to inoculation, recovery, and enumeration/detection.

[a]The terms "Luria-Bertani broth," "Luria broth," and "Lennox broth" are frequently used interchangeably to refer to lysogeny broth (LB, containing 1% Tryptone, 0.5% Yeast extract, and 1% NaCl) in scientific literature (Bertani, 2004). Therefore, to ensure accurate reporting, LB and its derivatives (i.e., Lennox broth [0.5% NaCl] and Luria broth [0.05% NaCl]) were reported together here.

[b]Includes distilled, deionized, deoxygenated, or natural irrigation water.

[c]Includes 0.9% saline, 0.85% saline, or studies that reported using saline solution but did not specify the saline concentration.

[d]Refers to the number of studies in which relevant data were not able to be extracted because the information was either not provided or could not be reliably extracted from full texts.

[e]Refers to observational studies in which inoculation methodologies were not applicable as bacterial targets were not inoculated onto produce.

[f]If inoculum suspension concentration of exactly "7 log CFU/mL" was reported in the full-text of a given study, the concentration range of "7–8 log CFU/mL" was reported here.

[g]Refers to enumeration assays in which rinsate/washate is first filtered through a 0.45-μm filter, followed by plating of the filter on agar.

[h]The terms "Luria-Bertani agar," "Luria agar," and "Lennox agar" are frequently used interchangeably to refer to lysogeny agar (LA, containing 1% tryptone, 0.5% yeast extract, 1% NaCl, and 1.5% agar) in the scientific literature (Bertani, 2004). Therefore, to ensure accurate reporting, LA and its derivatives (i.e., Lennox broth [0.5% NaCl] and Luria broth [0.05% NaCl]) were reported together here.

differentiate strains. Future studies can take advantage of these molecular techniques to characterize strain-specific population dynamics outcomes on produce inoculated with cocktails.

3.3.3 | Inoculation methods used

A total of 262 (95%) studies reported the inoculation methodology that was used to inoculate produce with target bacterial strains. For the remaining studies ($n = 15$, 5%), the inoculation methodology used was either not provided or could not be reliably extracted from full texts (both cases were reported as "not able to extract") or was categorized as "not applicable" in the case of observational studies (see Section 3.2). Inoculation methodologies were categorized as either direct application methods, where inocula were directly applied to the produce surface (e.g., dip, spot, or spray inoculation) or indirect application methods, where inocula were not directly applied to the produce surface (e.g., furrow/drip line irrigation or inoculation with an inoculum suspension directly into soil/soil amendment; Table 1). Across all bacterial types, direct application methods were reported more frequently ($n = 139$, $n = 127$, and $n = 57$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively) than indirect application methods ($n = 23$, $n = 7$, and $n = 4$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively).

Different inoculation methods represent different naturally occurring contamination routes of bacterial organisms on produce. For example, direct application methods can mimic the contamination of produce through overhead irrigation, rain splash events, cross-contamination from equipment, co-mingling, or washing practices (Alegbeleye et al., 2018; Cevallos-Cevallos et al., 2012; Machado-Moreira et al., 2019). Similarly, indirect application methods can mimic the contamination of produce through furrow/drip irrigation or the application of contaminated manures or composts that do not come in direct contact with the edible portion of a crop (Alegbeleye et al., 2018). As all the aforementioned represent possible contamination routes of produce with *Listeria* spp., *Salmonella* spp., or *E. coli*, the limited representation of studies that reported using indirect application methods to inoculate produce highlights a knowledge gap that can be explored in future population dynamics studies.

3.3.4 | Inoculum concentrations

A total of 197 (71%) studies reported the concentrations of inoculum suspensions (e.g., colony-forming units/mL

[CFU/mL]) used to inoculate produce. For the remaining studies (n = 80, 29%), information related to the concentrations of prepared inoculum suspensions was either not provided or could not be reliably extracted from full texts (both cases were reported as "not able to extract") or was categorized as "not applicable" in the case of observational studies (see Section 3.2). Of the 197 studies that reported inoculum suspension concentrations used, the concentration range most frequently reported across all bacterial types was 7–8 log CFU/mL (n = 57), followed by 6–7 log CFU/mL (n = 49) and 5–6 log CFU/mL (n = 47). While the most reported inoculum suspension concentration range for *E. coli* followed the same pattern (see Table 1), for *Salmonella* spp., the most reported concentration range used was 5–6 log CFU/mL (n = 30), followed by 7–8 log CFU/mL (n = 22) and 6–7 log CFU/mL (n = 20), and for *Listeria* spp., the most reported concentration range used was 6–7 log CFU/mL (n = 14), followed by 5–6 log CFU/mL (n = 13) and 7–8 log CFU/mL (n = 11; Table 1).

The concentration of an inoculum suspension, which may also be correlated with the level of bacteria on or near produce (in the case of indirect application methods, see Section 3.3.3), can impact population dynamics outcomes. In most cases, the use of inoculum suspensions with high bacterial concentrations (i.e., the 7–8 log CFU/mL reported in 57 studies) could result in unrealistically high initial pathogen loads on produce; bacterial pathogen levels on naturally contaminated produce have previously been reported to typically be < 3 log CFU/g (de Oliveira Elias et al., 2019; Ding et al., 2013). Importantly, using unrealistically high initial pathogen loads could result in population dynamics outcomes that are not relevant to the "real world", as supported by studies that have observed that different inoculation levels of the same bacterial suspensions can result in different population dynamics outcomes (e.g., growth versus die-off), even on the same produce commodities stored under the same conditions (Blessington, 2011; Song et al., 2019). Moreover, Igo et al. (2022) showed that high initial cell concentrations on produce can significantly impact the growth rates of *L. monocytogenes*, with increasing initial cell concentrations being associated with lower growth rates. Therefore, ensuring that the level of bacteria used for direct or indirect application onto produce is representative of naturally occurring contamination levels can be important for drawing real-world relevant conclusions. While investigations of population dynamics in the context of "worst-case scenario" contamination events with bacterial pathogens at high levels are not unwarranted and thus should not be discouraged, they are currently overrepresented in the scope of included studies. These findings highlight a key knowledge gap that can be explored in future studies.

3.3.5 | Recovery procedures used

A total of 263 (95%) studies reported the recovery procedure that was used to recover target bacterial organisms from produce surfaces. For the remaining studies (n = 14, 5%), recovery procedures used were either not provided or could not be reliably extracted from full texts. Recovery procedures reported represented four distinct categories: (i) manual recovery methods that do not compromise the structural integrity of produce (e.g., hand massaging, rubbing, shaking), (ii) mechanical recovery methods that result in minimal damage to the structural integrity of produce (e.g., sonication, vortexing), (iii) mechanical recovery methods that result in substantial damage to the structural integrity of produce (e.g., stomaching, homogenization, pummeling, maceration), and (iv) pulsification (Table 1). Across all bacterial types, the most frequently reported recovery method category was category (iii) (n = 92, n = 83, and n = 42 for *E. coli, Salmonella* spp., and *Listeria* spp., respectively), followed by category (i) (n = 59, n = 46, and n = 15 for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively) and category (ii) (n = 15, n = 8, and n = 5 for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively). Additionally, three studies that investigated population dynamics of *E. coli* reported using the mechanical recovery method of (iv) pulsification to facilitate bacterial recovery (Table 1). While pulsification has been reported to not result in the maceration of spinach (Gutiérrez-Rodríguez et al., 2019), this method may show differential damage to food matrices depending on product types (Cook et al., 2006; Fung et al., 1997), and thus was classified separately from categories (i) to (iii).

Our data indicate that a variety of recovery methodologies were used to recover bacteria from produce, which can ultimately influence enumeration or detection outcomes. For example, one study (Kim et al., 2012) showed that pummeling (representing category iii) resulted in higher recovery of bacterial populations from iceberg lettuce, cucumber, and green pepper, compared to sonication (representing category ii) and hand-shaking (representing category i). While these results might be taken to suggest that category (iii) recovery methods should be utilized exclusively to maximize bacterial recovery, this is not consistent across all produce commodities. For example, for relatively acidic produce (e.g., tomatoes), pummeling has been shown to result in less recovery of bacterial populations, compared to sonication and hand-shaking (Kim et al., 2012). Moreover, substantial damage to the structural integrity of brassica-type vegetables (e.g., broccoli, cauliflower, kale) through recovery methods represented in category (iii) could result in the release of isothiocyanates (Hanschen et al., 2014), which can inactivate

bacterial cells (Sanz-Puig et al., 2015). For example, Redding et al. (2023) reported > 2 log die-off of *L. monocytogenes* in sterile cauliflower juice, extracted via a mechanical homogenization procedure, after 24-h incubation at 37°C. However, it should be noted that this same study reported that the antilisterial activity of sterile cauliflower juice was reduced when diluted two-fold in water. Thus, care should be taken to evaluate how the release of potential antimicrobial compounds due to damage to produce structural integrity can impact bacterial recovery, and to ensure adequate dilution of such antimicrobial compounds when developing recovery procedures.

3.3.6 | Enumeration and detection methods used

A total of 273 (99%) studies reported the method used to enumerate/detect target bacterial organisms on produce in population dynamics experiments. For the remaining studies ($n = 4$, 1%), enumeration/detection methodologies were either not provided or could not be reliably extracted from full texts. Reported enumeration or detection methods represented four distinct categories: (i) classical culture-based enumeration methods (e.g., direct plate count, most probable number assay), (ii) culture-independent enumeration methods (e.g., quantitative polymerase chain reaction [qPCR]), (iii) classical culture-based detection methods (e.g., sample enrichment followed by streaking on agar), and (iv) culture-based rapid detection methods (e.g., sample enrichment followed by a nucleic acid-based assay or an immunological-based assay; Table 1). Among enumeration methods reported, category (i) classical culture-based enumeration methods were reported more frequently across all bacterial types ($n = 159$, $n = 154$, and $n = 65$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively), compared to category (ii) culture-independent enumeration methods ($n = 9$, $n = 4$, and $n = 3$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively). Similarly, among detection methods that were reported, category (iii) classical culture-based detection methods were reported more frequently across all bacterial types ($n = 55$, $n = 42$, and $n = 17$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively), compared to category (iv) culture-based rapid detection methods ($n = 7$, $n = 6$, and $n = 3$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively; Table 1).

It is not surprising that most population dynamics studies reported using classical culture-based enumeration/detection methods, given the common historical use, relative simplicity, and often relatively high sensitivity of these methods (Gracias & McKillip, 2004). Nevertheless, advances in molecular biology and biochemistry have made culture-based rapid detection methods and culture-independent enumeration methods more accessible (Giraffa & Neviani, 2001; Law et al., 2015), and, in certain scenarios, these methods offer distinct advantages, compared to classical culture-based methods. For example, culture-based rapid detection methods can be more time-efficient, compared to classical culture-based detection methods (Law et al., 2015). However, as one study (Lopez-Velasco et al., 2015) reported that culture-based rapid detection methods showed reduced sensitivity for detecting bacterial targets inoculated on produce in a field setting compared to produce inoculated in a laboratory setting, culture-based rapid detection methods may underestimate the prevalence of bacterial targets on produce in certain experimental settings.

Additionally, specific culture-independent enumeration methodologies (e.g., propidium monoazide qPCR) can be advantageous for quantifying viable but non-culturable (VBNC) cells that are unable to be cultured on traditional culture media (Ding et al., 2022). Induction of a VBNC state has been reported in bacterial cells subjected to stressors such as low temperatures (Pinto et al., 2011), desiccation (Se et al., 2021), and exposure to sanitizers (Afari et al., 2019; Truchado et al., 2021); all of which represent relevant stressors that bacteria can be exposed to throughout the produce supply chain. As some reports have indicated that cells in a VBNC state can maintain virulence potential and may be resuscitated under in vivo conditions (Highmore et al., 2018; Makino et al., 2000), bacterial organisms in a VBNC state may pose a food safety risk that warrants consideration in population dynamics investigations on produce. Thus, if the food safety relevance of VNBC cells can be confirmed, future studies that quantify bacterial organisms in a VNBC state on produce may be valuable.

3.3.7 | Base plating media used for classical culture-based enumeration/detection

A total of 266 (96%) studies reported the base plating media (e.g., tryptic soy agar, modified Oxford agar, etc.) that was used to enumerate/detect *Listeria* spp., *Salmonella* spp., or *E. coli* from produce using classical culture-based methods. For the remaining studies ($n = 11$, 4%), the base plating media used was either not provided or could not be reliably extracted from full texts (both cases were reported as "not able to extract"). The types of base plating media used to enumerate/detect target bacteria represented three distinct categories: (i) non-selective base media (this category includes instances where a non-selective base media was supplemented with an antibiotic in order to recover challenge strains with antimicrobial resistance markers), (ii) selective base media, and (iii) a combination of non-selective and selective base media (e.g., overlaying

non-selective base media over selective base media; Table 1). Across all bacterial types, the most reported base plating media category was category (ii) ($n = 104$, $n = 98$, and $n = 57$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by category (i) ($n = 78$, $n = 77$, and $n = 20$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively; Table 1).

Our data indicate that a substantial number of studies used selective media, which may underestimate bacterial numbers, particularly if bacterial cells are in a physiological state described as "injured." For example, recovery of injured cells has been shown to be reduced on selective media compared to non-selective media (Wu, 2008), and thus any population dynamics outcomes of die-off evaluated through plating on selective media would likely be overestimated compared to those evaluated on non-selective media. However, the use of selective media is often necessary for classical culture-based enumeration/detection of bacterial organisms on produce, which can have background microbiota levels ranging from < 1 to 9 log CFU/g (Allen et al., 2013; Korir et al., 2016; Seow et al., 2012; G. Zhang et al., 2018). While addressing this trade-off between enumeration/detection of injured bacterial cells in samples with high levels of background microbiota represents a substantial challenge, overlay approaches, such as those represented in category (iii), as well as culture-independent enumeration methods (see Section 3.3.6), can help to obtain more accurate population dynamics outcomes on produce.

While the findings reported here provide important high-level data regarding the type of base media used for plating, several other aspects of plating media can influence population dynamics outcomes. For example, media additives such as chromogenic substrates (e.g., 5-bromo-4-chloro-3-indolyl-β-D-glucopyranoside), which support the differentiation of bacterial targets from background microbiota (Guo et al., 2016), or reactive oxygen species scavengers (e.g., sodium pyruvate), which can promote recovery of injured cells (Valero et al., 2017), can also influence enumeration/detection outcomes. Thus, the literature compiled here can be used in future studies to further explore information on how plating media can influence the enumeration/detection of (i) bacterial targets in complex produce matrices and (ii) injured bacterial targets on produce.

3.4 | Key aspects of pre-harvest studies

Studies in which the population dynamics of *Listeria* spp., *Salmonella* spp., or *E. coli* were evaluated on produce before it was harvested are collectively referred to here as "pre-harvest studies." Pre-harvest studies represented a total of 143 (52%) included studies; 133 of these studies reported investigating only pre-harvest population dynamics on produce, and 10 of these studies reported investigating both pre-harvest and post-harvest population dynamics on produce. The bacterial target investigated most in pre-harvest studies was *E. coli* ($n = 93$), followed by *Salmonella* spp. ($n = 69$) and *Listeria* spp. ($n = 13$). Importantly, the underrepresentation of pre-harvest studies investigating population dynamics of *Listeria* spp. is notable. While several historic listeriosis outbreaks associated with produce have been traced back to contamination in post-harvest environments (e.g., processing facilities, packing houses; Angelo et al., 2017; Jackson et al., 2015; McCollum et al., 2013), a recent *L. monocytogenes* outbreak associated with lettuce linked to contaminated harvest equipment has underscored the potential for *L. monocytogenes* to contaminate produce in pre-harvest environments as well (Gartley et al., 2022). This further emphasizes the critical need for more studies that investigate the population dynamics of *Listeria* spp. on produce at the pre-harvest stage of the supply chain.

In Sections 3.4.1 through 3.4.5, we describe key characteristics that were extracted from pre-harvest studies including: (i) bacterial strains used (including subtyping classifications, attenuated or non-pathogenic status, antimicrobial resistance phenotype(s), and isolation source(s)), (ii) produce commodities evaluated, (iii) settings in which produce was grown, (iv) environmental conditions that were monitored or collected, and (v) geographic locations where produce was grown.

3.4.1 | Pre-harvest studies: Bacterial strain characteristics

Species and subtyping classifications

For *Listeria* spp., a total of 10 (77%) pre-harvest studies reported using *L. monocytogenes* strains, and four (30%) studies reported using *L. innocua* strains. Among the 10 pre-harvest studies that reported using *L. monocytogenes* strains, subtypes reported represented eight distinct serovars (i.e., 1/2a, 1/2b, 1/2c, 4a, 4b, 4c, 4d, and 4e; Table 2). The three most reported serovars were 1/2b ($n = 7$), 1/2a ($n = 6$), and 4b ($n = 5$), while the remaining serovars were reported in fewer than three studies. For *Salmonella* spp., a total of 66 (96%) pre-harvest studies reported using *S. enterica* subsp. *enterica* strains and one study also reported using a strain of *S. enterica* subsp. *arizonae*; the remaining three studies did not report the *Salmonella* species or subspecies that were evaluated (these studies represented observational studies; see Section 3.2). A total of 43 distinct serovars of *S. enterica* subsp. *enterica* were represented in pre-harvest studies (Table 2). The three

TABLE 2 Bacterial strain characteristics that were reported for bacterial strains used in pre-harvest studies (including serovars represented, attenuated or non-pathogenic status of strains, antimicrobial resistance phenotypes, and isolation sources).

***Listeria* spp. (*n* = 13)**	***Salmonella* spp. (*n* = 69)**	***E. coli* (*n* = 93)**
Serovars represented (number of studies)		
L. monocytogenes	*S. enterica* subsp. *enterica*	O157:H7 (68)
1/2b (7)	Typhimurium (32)	O26:H11 (5)
1/2a (6)	Newport (20)	Serogroup O157 (4)
4b (5)	Enteritidis (16)	O104:H4 (3)
1/2c (2)	Thompson (8)	OR:H48:K- (2)
4a (1)	Stanley (7)	O103:H2 (2)
4c (1)	Montevideo (6)	O111:NM (1)
4d (1)	Anatum (5)	O145:NM (1)
4e (1)	Cubana (5)	O157:H12 (1)
No serogroup or serovar provided (3)	Poona (5)	Serogroup O8 (1)
	Senftenberg (5)	Serogroup O13 (1)
L. innocua (4)	Saintpaul (4)	Serogroup O45 (1)
	Baildon (3)	Serogroup O111 (1)
	Infantis (3)	Serogroup O145 (1)
	Mbandaka (3)	No serogroup or serovar provided (29)
	Agona (2)	
	Braenderup (2)	
	Derby (2)	
	Javiana (2)	
	Michigan (2)	
	Schwarzengrund (2)	
	Tennessee (2)	
	Typhi (2)	
	Bareilly (1)	
	Berta (1)	
	Canada (1)	
	Chingola (1)	
	Hadar (1)	
	Hartford (1)	
	Havana (1)	
	Heidelberg (1)	
	Litchfield (1)	
	Liverpool (1)	
	Luciana (1)	
	Muenchen (1)	
	Negev (1)	
	Newington (1)	
	Ohio (1)	
	Oranienburg (1)	
	Reading (1)	
	Rubislaw (1)	
	Sofia (1)	
	Uganda (1)	
	Weltevreden (1)	

(Continues)

TABLE 2 (Continued)

***Listeria* spp. (*n* = 13)**	***Salmonella* spp. (*n* = 69)**	***E. coli* (*n* = 93)**
	No serovar provided (2)	
	S. enterica subsp. *arizonae* (1)	
	Salmonella spp.: no species provided[a] (3)	
Attenuated or non-pathogenic status of strains (number of studies)		
Studies that reported using attenuated or non-pathogenic strains (4)	Studies that reported using attenuated or non-pathogenic strains (16)	Studies that reported using attenuated or non-pathogenic strains (37)
Strains used:	Strains used:	Strains used:
L. innocua CIP 80-12 (2)	*S.* Typhimurium χ3985 (10)	*E. coli* O157:H7 ATCC 700728 (9)
L. innocua LiP60 (2)	*S.* Typhimurium LT2 (3)	*E. coli* TVS 354 (5)
L. innocua CECT-910 (1)	S. Typhimurium MHM112 (3)	*E. coli* O157:H7 ATCC 43888 (4)
L. innocua: No strain information provided (1)	*S.* Newport 17*Δtolc*::*aph* (2)	*E. coli* O157:H7 MD56 (4)
		E. coli O157:H7 MD58 (4)
		E. coli O157:H7 B6914 (3)
		E. coli TVS 353 (3)
		E. coli TVS 355 (3)
		E. coli ATCC 25922 (2)
		E. coli K12 (2)
		E. coli MW416 (2)
		E. coli MW423 (2)
		E. coli MW425 (2)
		E. coli O157:H7 NCTC 12900 (2)
		E. coli ATCC 8739 (1)
		E. coli ATCC 11775 (1)
		E. coli ATCC 23716 (1)
		E. coli O157:H7 MB3885 (1)
		E. coli O157:H7 pTVS 154 (1)
		E. coli O157:H7 pTVS 155 (1)
		E. coli O157:H7 3704 (1)
		E. coli P1 (1)
		E. coli P8 (1)
		E. coli P14 (1)
		E. coli PM3823 (1)
		E. coli PM3954 (1)
		E. coli W778 (1)
		No strain information provided (4)
Studies that did not report using attenuated or non-pathogenic strains (9)	Studies that did not report using attenuated or non-pathogenic strains (53)	Studies that did not report using attenuated or non-pathogenic strains (56)
Antimicrobial resistance phenotypes (number of studies)		
Erythromycin (1)	Rifampicin (16)	Rifampicin (27)
Nalidixic acid (1)	Ampicillin (13)	Ampicillin (26)
Streptomycin (1)	Kanamycin (11)	Nalidixic acid (13)
	Nalidixic acid (7)	Kanamycin (9)
	Streptomycin (4)	Streptomycin (6)
	Gentamicin (2)	Chloramphenicol (2)
	Chloramphenicol (1)	Gentamicin (2)

(Continues)

TABLE 2 (Continued)

Listeria spp. ($n = 13$)	*Salmonella* spp. ($n = 69$)	*E. coli* ($n = 93$)
	Tetracycline (1)	Ciprofloxacin (1)
		Erythromycin (1)
		Spectinomycin (1)
Not able to extract[b] (10)	Not able to extract (25)	Not able to extract (24)
Isolation source (number of studies)		
Non-human outbreak-associated strains (7)	Non-human outbreak-associated strains (26)	Non-human outbreak-associated strains (35)
Strains associated with a non-produce-associated human outbreak (1)	Strains associated with a produce-associated human outbreak (19)	Strains associated with a produce-associated human outbreak (22)
		Strains associated with a non-produce-associated human outbreak (1)
Not able to extract (6)	Not able to extract (36)	Not able to extract (51)

Note: Note that for each given study multiple serovars, attenuated or non-pathogenic strains used, antimicrobial resistance phenotypes, and isolation sources may have been reported.

[a]Refers to three observational studies in which strains of *Salmonella* spp. were not inoculated onto produce.

[b]Refers to the number of studies in which relevant data were not able to be extracted because the information was either not provided or could not be reliably extracted from full texts.

most reported serovars of *S. enterica* subsp. *enterica* were Typhimurium ($n = 32$), Newport ($n = 20$), and Enteritidis ($n = 16$), and all remaining serovars were represented in fewer than eight studies. For *E. coli*, 14 distinct subtypes, reported to either serogroup level only (i.e., O8, O13, O45, O111, O145, and O157) or to serovar level (i.e., OR:H48:K-, O26:H11, O103:H2, O104:H4, O111:NM, O145:NM, O157:H7, and O157:H12), were represented among pre-harvest studies (Table 2). The three most reported serogroups or serovars were serovar O157:H7 ($n = 68$), serovar O26:H11 ($n = 5$), and serogroup O157 ($n = 4$), and all remaining serogroups and serovars were reported in fewer than four studies (Table 2).

Our data indicate that certain serovars were overrepresented in pre-harvest studies, most notably *E. coli* O157:H7, which was reported to be used in 73% of *E. coli* studies. *E. coli* O157:H7 represents one serovar of Shiga toxin-producing *E. coli* (STEC), a category of pathogenic *E. coli* that are of notable public health concern, particularly as a subset of STEC (referred to as enterohemorrhagic *E. coli* [EHEC]) can cause a severe disease known as hemolytic uremic syndrome (HUS) in humans (Meng et al., 2012). While *E. coli* O157:H7 remains a major public health concern, particularly in the United States where it represents the primary cause of HUS (Banatvala et al., 2001) and has been implicated in several high-profile fresh produce outbreaks (Irvin et al., 2021; Wendel et al., 2009), several other non-O157 STEC and EHEC also represent hazards relevant to produce safety (Smith et al., 2014). For example, among multistate fresh produce outbreaks of pathogenic *E. coli* in the United States between 2010 and 2017, a slight majority (13/23) of outbreaks were attributed to *E. coli* O157:H7, while the other 10 outbreaks were attributed to non-O157:H7 STEC including serogroups O26, O111, O121, and O145 and serovar O157:NM (Carstens et al., 2019). This highlights a need for more studies that investigate population dynamics of non-O157 STEC and EHEC on produce.

For *Listeria* spp. and *Salmonella* spp., the serovars most frequently reported in pre-harvest studies are also highly relevant to produce safety. For example, the three most reported serovars of *Listeria* spp. (i.e., *L. monocytogenes* 1/2b, 1/2a, and 4b) represent serovars that have been frequently isolated from environmental samples throughout the produce supply chain (Townsend et al., 2021; Y. Zhang et al., 2007) and are commonly associated with human listeriosis cases (Kathariou, 2002; Tappero et al., 1995). Similarly, *S.* Enteritidis and *S.* Newport, the second and third most frequently reported *Salmonella* serovars used in pre-harvest studies, respectively, were reported as the causative agents for 16/49 (33%) single-etiology multistate salmonellosis outbreaks in the United States between 2010 and 2017 (Carstens et al., 2019).

Attenuated or non-pathogenic status of strains used

During the data extraction phase, if the phrase "non-pathogenic," "attenuated," "avirulent," "non-virulent," or "surrogate of [a pathogenic organism]" was used in the

full text of a given study to describe a bacterial strain, then we reported that the study used "attenuated or non-pathogenic strains" to perform population dynamics experiments. For pre-harvest studies, attenuated or non-pathogenic strains were most frequently reported to be used in studies investigating population dynamics of *E. coli* ($n = 37$), followed by *Salmonella* spp. ($n = 16$) and *Listeria* spp. ($n = 4$; Table 2). For *Listeria* spp., three distinct strains of *L. innocua* were represented among pre-harvest studies, with the two most frequently reported strains including *L. innocua* CIP 80-12 ($n = 2$) and *L. innocua* LiP60 ($n = 2$). For *Salmonella* spp., four distinct attenuated or non-pathogenic strains of *S. enterica* were represented among pre-harvest studies; the strain most frequently reported was *S.* Typhimurium χ3985 ($n = 10$). For *E. coli*, 27 distinct attenuated or non-pathogenic strains of *E. coli* were represented among pre-harvest studies; the strain most frequently reported was *E. coli* O157:H7 ATCC 700728 ($n = 9$), which is considered attenuated as it lacks both *stx1* and *stx2* genes and is classified as a biosafety level 1 (BSL-1) organism (Moyne et al., 2020).

Using attenuated or non-pathogenic strains in pre-harvest studies is particularly important because these strains can be used for studies investigating population dynamics of relevant organisms (i.e., *Listeria* spp., *Salmonella* spp., and *E. coli*) in non-contained settings (e.g., fields) with a reduced risk of causing human exposure and illness. However, the selection of appropriate attenuated or non-pathogenic strains can be challenging, particularly for studies that seek to use attenuated or non-pathogenic strains to define population dynamics parameters for a pathogen under specific conditions (e.g., survival on a specific produce type, such as baby spinach cultivar 'Whale,' under specific conditions, such as drought stress). For example, while *L. innocua* CIP 80-12 and *L. innocua* LiP60 were reported to show similar survival on parsley in a pre-harvest setting when compared to *L. monocytogenes* (Dreux et al., 2007), it may still be important to further validate the suitability of these strains as surrogates for *L. monocytogenes* for different produce types grown in a pre-harvest setting. Additionally, while *S.* Typhimurium χ3985 has been reported to show comparable persistence with pathogenic *S.* Typhimurium in infected live chickens (J. O. Hassan & Curtiss, 1990), we could not identify empirical evidence in the literature indicating its suitability as a surrogate for pathogenic *Salmonella* in produce population dynamics studies. Thus, investigators should carefully consider the suitability of attenuated or non-pathogenic strains as reliable surrogates for their specific pre-harvest population dynamics studies.

Interestingly, we also observed that, except for *E. coli*, pre-harvest investigations used a limited diversity of strains with attenuated or non-pathogenic status. The finding that only four attenuated or non-pathogenic strains of *S.* Typhimurium and *S.* Newport were used among 16 pre-harvest studies (Table 2) may represent a particular challenge as a number of different *Salmonella* serovars have been linked to produce related outbreaks (Carstens et al., 2019; Hanning et al., 2009). This highlights a potential need to increase the diversity of bacterial strains with attenuated or non-pathogenic status that are available for and used in pre-harvest studies, particularly for *Salmonella*.

Antimicrobial resistance phenotypes

A total of 96 (67%) pre-harvest studies reported using bacterial strains that showed phenotypic resistance to at least one antimicrobial. For the remaining pre-harvest studies ($n = 47$, 33%), information pertaining to the antimicrobial resistance phenotype(s) of bacterial strains was not either provided or could not be reliably extracted from full texts. Overall, 10, eight, and three distinct antimicrobial resistance phenotypes were represented among strains of *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively (Table 2). The most frequently reported antimicrobial resistances among *E. coli* and *Salmonella* spp. were against rifampicin ($n = 27$ and $n = 16$, respectively) and ampicillin ($n = 26$ and $n = 13$, respectively). For *Listeria* spp., strains were reported to be resistant to erythromycin and streptomycin (both $n = 1$). Additionally, while the majority of *Listeria* spp. show intrinsic resistance to nalidixic acid (Beerens & Tahon-Castel, 1966), only one pre-harvest study specifically reported that *Listeria* spp. strains used showed phenotypic resistance to nalidixic acid.

Our data indicate that resistance to rifampicin represented the most frequently reported antimicrobial resistance phenotype present in bacterial strains used in pre-harvest studies. This may be due in part to the relative ease of selecting for bacterial strains with rifampicin resistance through culture-based adaptation protocols (e.g., exposure to increasing concentrations of rifampicin; Katz & Hershberg, 2013), as well as the observation that these mutations can remain stable in bacterial strains over time (Glandorf et al., 1992). However, it should be noted that phenotypic rifampicin resistance, as well as other antimicrobial resistance phenotypes, can incur fitness costs that may impact population dynamics outcomes on produce (Compeau et al., 1988). For example, Reynolds (2000) reported that *E. coli* strains carrying *rpoB* mutations, which conferred phenotypic rifampicin resistance, showed reduced fitness and transcription efficiency compared to their wild-type counterparts under in vitro growing conditions. Therefore, while antimicrobial resistance phenotypes can aid in the selective enumeration and detection of bacterial targets on produce, care should be taken to evaluate how antimicrobial resistance phenotypes may impact

growth and survival and hence population dynamics outcomes.

Isolation source of strains used

A total of 65 (45%) pre-harvest studies reported the isolation source(s) of bacterial strains that were used in population dynamics experiments. For the remaining pre-harvest studies (n = 78 55%), information pertaining to the isolation source(s) of bacterial strains was either not provided or could not be reliably extracted from full texts. Bacterial strains with reported isolation source information in pre-harvest studies were categorized into three distinct groups: (i) non-human outbreak-associated strains, (ii) strains associated with a produce-associated human outbreak, and (iii) strains associated with a non-produce-associated human outbreak (Table 2). Across all bacterial types, the most frequently reported isolation source category among pre-harvest studies was category (i) (n = 35, n = 26, and n = 7 for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively). In addition, a relatively high number of pre-harvest studies also reported using strains representing category (ii) (n = 22 and n = 19 for *E. coli* and *Salmonella* spp., respectively), while only two studies (*E. coli* and *Listeria* spp., both n = 1) reported using strains representing category (iii).

Overall, less than 50% of pre-harvest studies provided information related to the isolation source(s) of bacterial strains used. This points to a need for improved data reporting on the characteristics and sources for strains used in these types of studies, as well as more stringent insistence from reviewers and editors for authors to include this information. Notably, the high frequency of pre-harvest studies that reported using bacterial strains associated with produce outbreaks may better represent the population dynamics outcomes of strains that are known to cause foodborne illness and are potentially more adapted to survival and persistence on produce commodities compared to strains that are not associated with produce outbreaks (Burris et al., 2020).

While bacterial isolation sources have traditionally been considered meaningful and important (as strains with specific phenotypes or adaptations may be found in different environments), recent molecular advances (e.g., whole-genome sequencing [WGS], transcriptomics) can provide better resolution for whether an isolate obtained from a given environment may or may not carry specific phenotypic advantages or adaptations. For example, providing WGS data for a given strain can allow for the assessment of whether a strain is representative of other strains for a given source environment (e.g., soil, irrigation water) and shows genomics characteristics that suggest phenotypic advantages (e.g., presence of stress response genes that are functional and do not show truncations or premature stop codons). Therefore, future population dynamics studies could benefit from providing higher-resolution molecular data associated with strains.

3.4.2 | Pre-harvest studies: Produce commodities

As expected, based on the literature search algorithm, produce commodities evaluated were provided in all (n = 143) pre-harvest studies. The three most frequently investigated produce commodities in pre-harvest studies included lettuce, spinach, and sprouts for *E. coli* (n = 55, n = 19, and n = 10, respectively), lettuce, sprouts, and spinach for *Salmonella* spp. (n = 25, n = 15, and n = 9, respectively), and lettuce, sprouts, and parsley for *Listeria* spp. (n = 4 for all; Figure 3). As lettuce represents a produce commodity that has been previously associated with several high-profile outbreaks (Gajraj et al., 2012; Irvin et al., 2021), it is unsurprising that, across all bacterial types, pre-harvest studies most frequently reported investigating population dynamics on this produce commodity.

Notably, out of 146 possible produce commodities included in inclusion criteria for this scoping review (see Section 2.1), only 18, 17, and six were represented among pre-harvest studies for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively (Figure 3). Recently, a risk-ranking model developed by FDA to inform FSMA's Food Traceability List (section 204 (d) (2)) identified several key food commodities as "high-risk" based on the evaluation of multiple criteria, including factors such as the likelihood of contamination and growth potential, for hazards such as pathogenic STEC, *L. monocytogenes*, and *Salmonella* spp. (FDA Food Traceability Rule Workgroup, 2022). Several produce commodities explicitly highlighted in the Food Traceability List, including leafy greens such as chicory and watercress, and tropical tree fruits such as guava, lychee, and papaya, were notably absent from all studies included in this scoping review (U.S. Food & Drug Administration, 2022). Therefore, future studies should consider increasing the diversity of produce commodities investigated in population dynamics studies, particularly for produce commodities identified as high risk for bacterial pathogen growth or contamination.

3.4.3 | Pre-harvest studies: Study setting

All (n = 143) pre-harvest studies reported the setting in which population dynamics experiments were carried out. The types of settings represented in pre-harvest studies included studies carried out in field (e.g., open fields, screenhouses), greenhouse, growth chamber, and

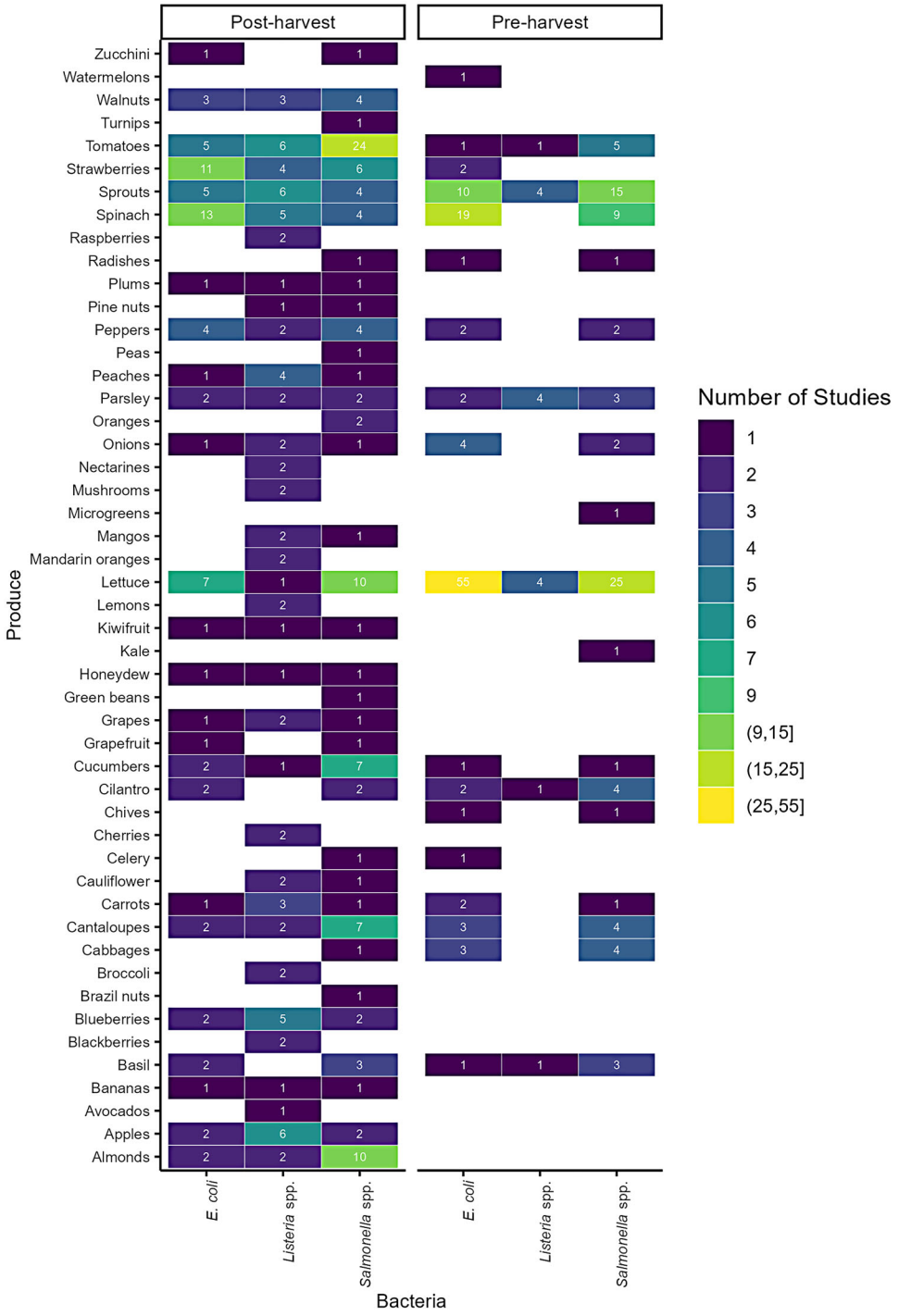

FIGURE 3 Heatmap showing the number of produce commodities evaluated for *E. coli*, *Listeria* spp., and *Salmonella* spp. population dynamics in pre- and post-harvest studies. Blank (white) boxes indicates that no studies with a given combination of bacterial type and produce commodity were conducted.

laboratory settings. Information related to cultivation practices used to grow produce (e.g., soil vs. hydroponic cultivation) was also extracted and reported here. For *E. coli* and *Listeria* spp., the majority of pre-harvest studies were reported to be carried out in a field setting ($n = 41$ and $n = 5$, respectively), while for *Salmonella* spp., the majority of pre-harvest studies were reported to be carried out in a growth chamber setting ($n = 28$; Table 3). Produce grown in field, greenhouse, or growth chamber settings was more frequently reported to be grown using soil cultivation practices ($n = 86$, $n = 53$, and $n = 11$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively) than hydroponic cultivation practices ($n = 5$ and $n = 4$ for *Salmonella* spp. and *E. coli*, respectively).

TABLE 3 Key characteristics reported for pre-harvest population dynamics studies, including the study setting (i.e., field, greenhouse, growth chamber, and laboratory setting), cultivation practices used (i.e., soil and hydroponic cultivation), and environmental conditions that were monitored or collected (i.e., weather conditions, soil physicochemical properties, and irrigation water physicochemical properties).

***Listeria* spp. (*n* = 13)**	***Salmonella* spp. (*n* = 69)**	***E. coli* (*n* = 93)**
Study setting		
Field: (total: 5)	Field: (total: 21)	Field: (total: 41)
Soil cultivation (5)	Soil cultivation (21)	Soil cultivation (41)
Greenhouse: (total: 4)	Greenhouse: (total: 9)	Greenhouse: (total: 16)
Soil cultivation (4)	Soil cultivation (9)	Soil cultivation (14)
		Hydroponic cultivation (2)
Growth chamber: (total: 2)	Growth chamber: (total: 28)	Growth chamber: (total: 33)
Soil cultivation (2)	Soil cultivation (23)	Soil cultivation (31)
	Hydroponic cultivation (5)	Hydroponic cultivation (2)
Laboratory setting: (total: 4)	Laboratory setting: (total: 17)	Laboratory setting: (total: 12)
Hydroponic cultivation (4)	Hydroponic cultivation (15)	Hydroponic cultivation (10)
	Soil cultivation (2)	Soil cultivation (2)
Environmental conditions collected or monitored		
Weather conditions: (total: 25)	Weather conditions: (total: 117)	Weather conditions: (total: 210)
Ambient temperature (12)	Ambient temperature (56)	Ambient temperature (80)
Humidity (7)	Humidity (37)	Humidity (62)
Precipitation (3)	Precipitation (9)	Precipitation (27)
Evapotranspiration (1)	Solar radiation (5)	Wind gust or speed (9)
Photosynthetically active radiation (1)	Photosynthetically active radiation (3)	Solar radiation (8)
Solar radiation (1)	Evapotranspiration (2)	Evapotranspiration (6)
	Wind gust or speed (2)	UV radiation (5)
	CO_2 level (1)	Leaf wetness (4)
	Solar light intensity (1)	Wind direction (4)
	Total radiation (1)	CO_2 level (1)
		Photosynthetically active radiation (1)
		Quantum radiation (1)
		Solar hours (1)
		Total radiation (1)
Soil and soil amendment physicochemical properties: (total: 1)	Soil and soil amendment physicochemical properties: (total: 7)	Soil and soil amendment physicochemical properties: (total: 24)
Moisture content (1)	Moisture content (4)	Temperature (8)
	pH (3)	Moisture content (8)
		pH (6)
		Electrical conductivity (2)
	Irrigation water physicochemical properties: (total: 7)	Irrigation water physicochemical properties: (total: 11)
	Chemical oxygen demand (2)	pH (4)
	pH (2)	Electrical conductivity (3)
	Biological oxygen demand (1)	Biological oxygen demand (1)
	Electrical conductivity (1)	Chemical oxygen demand (1)

(Continues)

TABLE 3 (Continued)

Listeria spp. ($n = 13$)	*Salmonella* spp. ($n = 69$)	*E. coli* ($n = 93$)
	Turbidity (1)	Temperature (1)
		Turbidity (1)
Not able to extract[a] (1)	Not able to extract (10)	Not able to extract (10)

Note: Note that each given study may have investigated population dynamics on produce in multiple study settings and collected or monitored multiple environmental conditions.

[a]Refers to the number of studies in which relevant data were not able to be extracted because the information was either not provided or could not be reliably extracted from the full text.

It is important to note that all produce grown in a laboratory setting using hydroponic cultivation practices represented studies investigating population dynamics of sprouts, which are typically grown using hydroponic cultivation practices. Therefore, overall, there were a limited number of pre-harvest studies across all study settings (i.e., field, greenhouse, growth chamber, laboratory) that investigated population dynamics on non-sprouts produce commodities grown using hydroponic cultivation practices ($n = 7$). Additionally, no pre-harvest studies reported using aeroponic or aquaponic systems to grow produce. Given the increased food safety concerns that have been raised with respect to produce grown in controlled environment agriculture (CEA) settings using soil-less culture systems (Gómez et al., 2019), our findings here highlight a key area of research that can be explored in future pre-harvest population dynamics studies.

3.4.4 | Pre-harvest studies: Environmental conditions collected or monitored

A total of 126 (88%) pre-harvest studies reported specific environmental conditions that were collected/monitored alongside experiments that investigated population dynamics of *Listeria* spp., *Salmonella* spp., or *E. coli* on produce. For the remaining studies ($n = 17$, 12%), environmental conditions that were collected/monitored were either not provided or could not be reliably extracted from full texts. The types of reported environmental conditions collected/monitored represented three distinct categories: (i) weather conditions, (ii) soil and soil amendment physicochemical properties, and (iii) irrigation water physicochemical properties (Table 3). Across all bacterial types, weather conditions (representing category i) were the most frequently reported to be collected/monitored, specifically the conditions of ambient temperature ($n = 80$, $n = 56$, and $n = 12$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively) and humidity ($n = 62$, $n = 37$, and $n = 7$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively) (Table 3).

Compared to category (i), a limited number of studies reported collecting/monitoring environmental conditions representing category (ii) soil physicochemical properties ($n = 24$, $n = 7$, and $n = 1$ for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively) and category (iii) irrigation water physicochemical properties ($n = 11$ and $n = 7$ for *E. coli* and *Salmonella* spp., respectively). These findings highlight a key knowledge gap in pre-harvest studies, as soil, soil amendments, and irrigation water have all been highlighted as key vectors of pathogen contamination of produce (Alegbeleye et al., 2018). Specifically, several previous reports have shown that the survival of pathogens in soil and soil amendments can be influenced by factors such as moisture content and temperature (Sharma et al., 2016; Underthun et al., 2017), and the survival of pathogens in irrigation water can be influenced by factors such as pH, temperature, and turbidity (Murphy et al., 2022; Sharma et al., 2020; Weller et al., 2020). Therefore, more intensive reporting of these key characteristics can provide better insight into population dynamics outcomes on produce in pre-harvest studies.

3.4.5 | Pre-harvest studies: Geographic location information

A total of 50 (35%) pre-harvest studies that were carried out in field study settings reported the geographic location where a given study was carried out. Additionally, seven (5%) pre-harvest studies that were carried out in a growth chamber ($n = 6$) or a greenhouse ($n = 1$) reported that weather conditions were simulated to represent a specific geographic location. Therefore, in total, 57 (40%) pre-harvest studies reported either the geographic location where a given population dynamics study took place or the geographic location that was simulated with regard to weather patterns (such information for both cases is collectively referred to here as "geographic location information"). For the remaining studies ($n = 86$, 60%), geographic location information was not provided or could not be reliably extracted from full texts. Among the

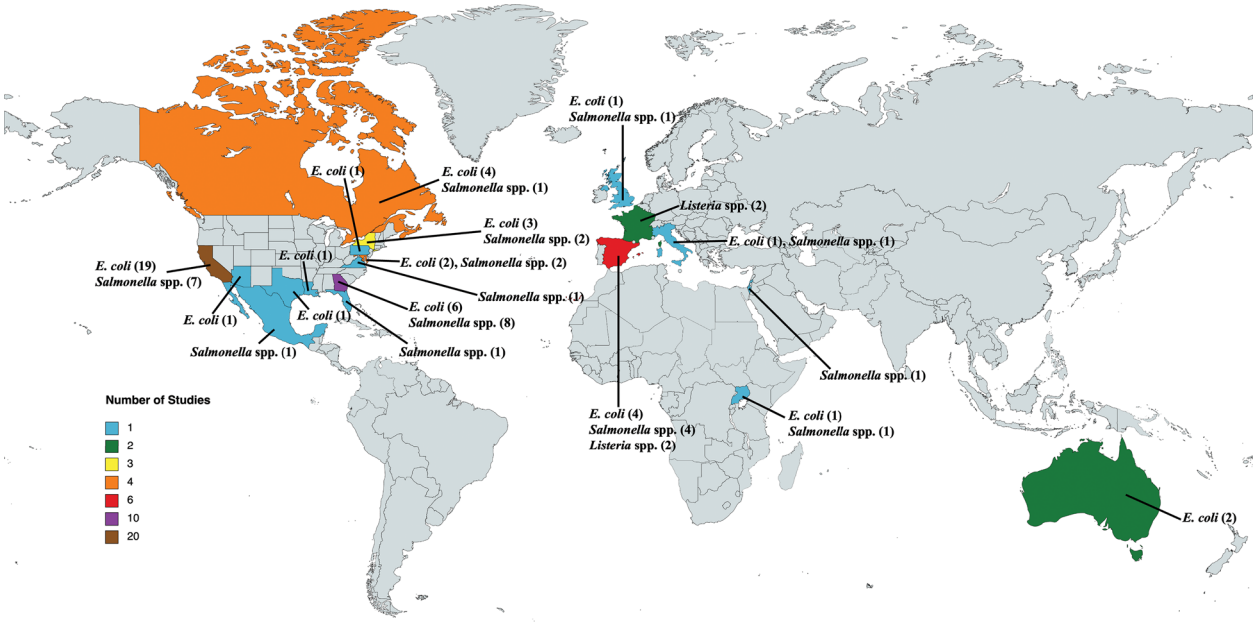

FIGURE 4 Number of studies reporting specific geographic location (country and US state) information for pre-harvest population dynamics studies. Geographic locations represent either (i) geographic locations where studies were carried out in a field setting or (ii) geographic locations that weather conditions were simulated for in the case of studies carried out in greenhouses or growth chambers. The number of studies that evaluated population dynamics for each individual bacterial type (i.e., *E. coli*, *Listeria* spp., or *Salmonella* spp.) for a given country or US state are provided by text connected to arrows. For example, two pre-harvest studies evaluating *E. coli* on produce were reported in Australia.

57 studies that reported geographic location information, 41 took place in the United States, and 19 took place outside of the United States, including in Spain ($n = 6$), Canada ($n = 4$), France ($n = 2$), Australia ($n = 2$), Israel, Italy, Mexico, Uganda, and the United Kingdom (all $n = 1$; Figure 4). All studies that took place in the United States also reported the state in which the study was carried out; the top three US states reported included California ($n = 20$), Georgia ($n = 10$), and Maryland ($n = 4$). For all pre-harvest studies that provided geographic location information, *E. coli* was the most reported bacterial organism investigated (45 studies across seven countries and eight US states), followed by *Salmonella* spp. (31 studies across eight countries and six US states) and *Listeria* spp. (4 studies across two countries; Figure 4).

Our results indicate that there were a limited number of countries ($n = 10$) represented among pre-harvest studies that reported geographical location information. As all studies included in this scoping review had to be available in English (see Section 2.4), results reported here may be biased toward studies that are published in English-speaking countries and thus not truly representative of the scope of geographic locations where population dynamics investigations are carried out.

One key outcome of this analysis was that more than half (60%) of pre-harvest studies did not report the geographic location in which their population dynamics study was carried out or the geographic location that was simulated (relevant to studies carried out in a greenhouse or growth chamber setting). Of the 86 pre-harvest studies that did not report geographic location information, 23 evaluated population dynamics on sprouts, which are generally grown in indoor environments where geographic location is unlikely to influence population dynamics outcomes. The remaining 63 pre-harvest studies lacking reported geographic location information investigated pre-harvest population dynamics on crops that are not exclusively grown in an indoor setting; these studies were carried out in growth chambers ($n = 40$), greenhouses ($n = 18$), laboratories ($n = 4$), and open fields ($n = 2$). Importantly, geographic location and/or weather and climatic conditions associated with a specific geographic location are expected to substantially influence pre-harvest population dynamics outcomes (Alegbeleye et al., 2018; Liu et al., 2013). While population dynamics studies using static and/or highly standardized conditions (as possible in growth chambers, etc.) are valuable, our data suggest that a future focus on population dynamics studies that mimic more complex weather and climatic conditions (e.g., those typical for major produce growing regions) may be warranted.

3.5 | Key aspects of post-harvest studies

Studies in which the population dynamics of *Listeria* spp., *Salmonella* spp., or *E. coli* were evaluated on produce after it was harvested are collectively referred to here as "post-harvest studies." Post-harvest studies represented a total of 144 (52%) included studies; 134 of these studies reported investigating only post-harvest population dynamics on produce, and 10 of these studies reported investigating both post-harvest and pre-harvest population dynamics on produce. The bacterial target investigated most in post-harvest studies was *Salmonella* spp. ($n = 87$), followed by *E. coli* ($n = 61$) and *Listeria* spp. ($n = 49$).

In Sections 3.5.1 through 3.5.4, we describe key characteristics that were extracted from post-harvest studies including (i) bacterial strains used (including subtyping classifications, attenuated or non-pathogenic status, antimicrobial resistance phenotype(s), and isolation source(s)), (ii) produce commodities evaluated, (iii) experimental temperature conditions, and (iv) experimental RH conditions. Where appropriate, we also included a final paragraph in a given section where we briefly compare and contrast the characteristics reported in post-harvest studies to characteristics reported in pre-harvest studies (e.g., comparing serovars most commonly used in pre- and post-harvest studies).

3.5.1 | Post-harvest studies: Bacterial strain characteristics

Species and subtyping classifications

For *Listeria* spp., a total of 47 (96%) post-harvest studies reported using *L. monocytogenes* strains and four (8%) studies reported using *L. innocua* strains. Among the 47 post-harvest studies that reported using *L. monocytogenes* strains, 10 distinct subtypes, reported to either the serogroup level (i.e., PCR serogroups IIb, IIIa, and IV) or to serovar level (1/2a, 1/2b, 1a, 3a, 4a, 4b, 4bv1), were represented (Table 4). The three most reported serogroups or serovars of *L. monocytogenes* used in post-harvest studies were serovars 1/2a ($n = 15$), 4b ($n = 14$), and 1/2b ($n = 11$); all remaining serogroups and serovars were only reported to be used in one study. For *Salmonella* spp., all ($n = 87$, 100%) post-harvest studies reported using strains of *S. enterica* subsp. *enterica*, with a total of 36 distinct serovars represented (Table 4). The three most reported serovars of *S. enterica* subsp. *enterica* were Typhimurium ($n = 36$), Enteritidis ($n = 35$), and Montevideo ($n = 29$), and the remaining 33 serovars were reported to be used in fewer than 18 studies. For *E. coli*, eight distinct subtypes, reported to either serogroup level (i.e., O18, O92, O117, O157, O163, and O175) or to serovar level (i.e., O157:H7 and O1:K1:H7) were represented among post-harvest studies (Table 4). The most reported serovar of *E. coli* used in post-harvest studies was O157:H7 ($n = 48$); all other serogroups or serovars were only reported to be used in one study.

Overall, the most common *E. coli* and *Listeria* spp. serovars were similar across both pre- and post-harvest studies (see section 3.4.1: Species and subtyping classifications) and included *E. coli* O157:H7 and *L. monocytogenes* 1/2a, 1/2b, and 4b. However, while *S.* Typhimurium represented the most reported *Salmonella* serovar used in both pre- and post-harvest studies, several other *Salmonella* serovars were reported at varying frequencies between pre- and post-harvest studies. For example, *S.* Newport was more frequently reported in pre-harvest studies (20/69, 29%) compared to post-harvest studies (17/87, 20%), and *S.* Montevideo was more frequently reported in post-harvest studies (29/87, 33%) compared to pre-harvest studies (6/69, 9%; see Tables 2 and 4). It is possible that the occurrence of previous high-profile outbreaks of *S.* Newport, traced back to the pre-harvest environment (Greene et al., 2008), and *S.* Montevideo, traced back to the post-harvest environment (Hedberg et al., 1999), may have influenced decisions to use *S.* Newport and *S.* Montevideo in pre-harvest and post-harvest studies, respectively.

Interestingly, none of the six non-O157 STEC serogroups (i.e., O26, O45, O103, O111, O121, and O145), which account for 74% of non-O157 STEC-associated foodborne illness cases in the United States (Meng et al., 2012) were reported to be used in any post-harvest studies, while five (i.e., serogroups O26, O45, O103, O111, and O145) were represented among pre-harvest studies. Similarly, *E. coli* O104:H4, which was reported to be used in three pre-harvest studies, was not reported in any post-harvest studies. As *E. coli* O26, O45, O103, O111, O121, O145, and O104:H4 have been implicated in several multistate fresh produce outbreaks (Buchholz et al., 2011; Carstens et al., 2019), they are highly relevant to produce safety and should be considered for inclusion in future post-harvest population dynamics studies.

Attenuated or non-pathogenic status of strains used

Using the same definition of "attenuated or non-pathogenic status" as described for pre-harvest studies (see section 3.4.1: Attenuated or non-pathogenic status of strains used), post-harvest studies that used attenuated or non-pathogenic strains were most frequently reported for *E. coli* ($n = 8$), followed by *Salmonella* spp. ($n = 5$) and *Listeria* spp. ($n = 4$; Table 4). For *Listeria* spp., two distinct strains of *L. innocua* were represented among post-harvest studies, including *L. innocua* NCTC 11288 ($n = 1$) and *L. innocua* NRCC B33076 ($n = 1$). For *Salmonella* spp., three distinct attenuated or non-pathogenic strains of *S. enterica* were represented among post-harvest studies,

TABLE 4 Bacterial strain characteristics that were reported for bacterial strains used in post-harvest studies (including serovars represented, attenuated or non-pathogenic status of strains, antimicrobial resistance phenotypes, and isolation sources).

***Listeria* spp. (*n* = 49)**	***Salmonella* spp. (*n* = 87)**	***E. coli* (*n* = 61)**
Serovars represented (number of studies)		
L. monocytogenes	*S. enterica* subsp. *enterica*	O157:H7 (48)
1/2a (15)	Typhimurium (36)	O1:K1:H7 (1)
4b (14)	Enteritidis (35)	Serogroup O18 (1)
1/2b (11)	Montevideo (29)	Serogroup O92 (1)
1a (1)	Newport (17)	Serogroup O117 (1)
3a (1)	Saintpaul (15)	Serogroup O157 (1)
4a (1)	Poona (14)	Serogroup O163 (1)
4bv1 (1)	Agona (11)	Serogroup O175 (1)
PCR serogroup[a] IIb (1)	Michigan (11)	No serogroup or serovar provided (14)
PCR serogroup IIIa (1)	Gaminara (10)	
PCR serogroup IV (1)	Anatum (9)	
No serogroup or serovar provided (28)	Javiana (9)	
	Oranienburg (7)	
L. innocua (4)	Tennessee (6)	
	Thompson (6)	
	Braenderup (5)	
	Muenchen (5)	
	Rubislaw (5)	
	Hartford (4)	
	Stanley (4)	
	Mbandaka (3)	
	Typhi (3)	
	Baildon (2)	
	Litchfield (2)	
	Senftenberg (2)	
	Cubana (1)	
	Daytona (1)	
	Derby (1)	
	Dublin (1)	
	Hadar (1)	
	Infantis (1)	
	Kentucky (1)	
	Newington (1)	
	Gallinarum (1)	
	Reading (1)	
	Salford (1)	
	Sundsvall (1)	
	No serovar provided (2)	
Attenuated or non-pathogenic status of strains (number of studies)		
Studies that reported using attenuated or non-pathogenic strains (4)	Studies that reported using attenuated or non-pathogenic strains (5)	Studies that reported using attenuated or non-pathogenic strains (8)
Strains used:	Strains used:	Strains used:
L. innocua NCTC 11288 (1)	*S.* Typhimurium LT2 (2)	*E. coli* O157:H7 ATCC 43888 (2)

(Continues)

TABLE 4 (Continued)

***Listeria* spp. (*n* = 49)**	***Salmonella* spp. (*n* = 87)**	***E. coli* (*n* = 61)**
L. innocua NRCC B33076 (1)	S. Typhimurium MHM112 (2)	*E. coli* O157:H7 ATCC 700728 (1)
L. innocua: No strain information provided (2)	*S.* Newport 17*Δtolc*::*aph* (1)	*E. coli* O157:H7 CECT 5947 (1)
		E. coli O157:H7 NCTC 12900 (1)
		E. coli ATCC 15597 (1)
		E. coli ATCC 25922 (1)
		E. coli ATCC 35218 (1)
		E. coli ATCC 43896 (1)
		E. coli NRRL B-33314 (1)
		E. coli BAA-1427 (1)
		E. coli BAA-1428 (1)
		E. coli BAA-1430 (1)
		E. coli TVS 353 (1)
		E. coli TVS 354 (1)
		E. coli TVS 355 (1)
		No strain information provided (1)
Studies that did not report using attenuated or non-pathogenic strains (45)	Studies that did not report using attenuated or non-pathogenic strains (82)	Studies that did not report using attenuated or non-pathogenic strains (53)
Antimicrobial resistance phenotypes (number of studies)		
Rifampicin (12)	Rifampicin (30)	Rifampicin (29)
Nalidixic acid (8)	Nalidixic acid (18)	Nalidixic acid (10)
Streptomycin (1)	Kanamycin (5)	Kanamycin (5)
	Ampicillin (4)	Gentamicin (3)
	Gentamicin (2)	Ampicillin (2)
	Streptomycin (2)	Streptomycin (2)
	Tetracycline (1)	Amikacin (1)
		Amoxicillin (1)
		Chloramphenicol (1)
		Clavulanic acid (1)
		Colistin (1)
Not able to extract[b] (29)	Not able to extract (33)	Not able to extract (18)
Isolation source (number of studies)		
Non-human outbreak-associated strains (22)	Non-human outbreak-associated strains (38)	Non-human outbreak-associated strains (30)
Strains associated with a produce-associated human outbreak (19)	Strains associated with a produce-associated human outbreak (32)	Strains associated with a produce-associated human outbreak (19)
Strains associated with a non-produce-associated human outbreak (12)	Strains associated with a non-produce-associated human outbreak (16)	Strains associated with a non-produce-associated human outbreak (13)
Not able to extract (19)	Not able to extract (34)	Not able to extract (22)

Note: Note that for each given study multiple serovars, attenuated or non-pathogenic strains used, antimicrobial resistance phenotypes, and isolation sources may have been reported.

[a]Serogroup was identified by a PCR serogrouping assay (Doumith et al., 2004).

[b]Refers to the number of studies in which relevant data were not able to be extracted because the information was either not provided or could not be reliably extracted from full texts.

with the two most frequently reported strains including *S.* Typhimurium LT2 ($n = 2$) and *S.* Typhimurium MHM112 ($n = 2$). For *E. coli*, 15 distinct attenuated or non-pathogenic strains of *E. coli* were represented among post-harvest studies; the strain most frequently reported was *E. coli* O157:H7 ATCC 43888 ($n = 2$).

Our data indicate that fewer post-harvest studies reported using strains with attenuated or non-pathogenic status, compared to pre-harvest studies (see section 3.4.1: Attenuated or non-pathogenic status of strains used). This is unsurprising, as most post-harvest studies are carried out in contained settings (e.g., incubators in laboratories), which limits biosafety concerns. Regardless, strains with attenuated or non-pathogenic status may still be used in post-harvest studies to reduce exposure risks or to allow experiments to be conducted in BSL-1 laboratories. Notably, all attenuated or non-pathogenic *Salmonella* spp. strains used in post-harvest studies (Table 4) were also represented in pre-harvest studies (Table 2). This indicates that the lack of strain diversity associated with the use of attenuated or non-pathogenic *Salmonella* spp. strains represents an issue in both pre- and post-harvest studies.

Antimicrobial resistance phenotypes

A total of 80 (56%) post-harvest studies reported using bacterial strains that showed phenotypic resistance to at least one antimicrobial. For the remaining post-harvest studies ($n = 64$, 44%), information pertaining to the antimicrobial resistance phenotype(s) of bacterial strains was either not provided or could not be reliably extracted from full texts. Overall, 11, seven, and three distinct antimicrobial resistance phenotypes were represented among strains of *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively (Table 4). Across all bacterial types, antimicrobial resistance to rifampicin was most frequently reported ($n = 30$, $n = 29$, and $n = 12$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by resistance to nalidixic acid ($n = 18$, $n = 10$, $n = 8$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively).

Similar to pre-harvest studies (see section 3.4.1: Antimicrobial resistance phenotypes), rifampicin represented the most frequently reported antimicrobial resistance phenotype in post-harvest studies, while the second most reported antimicrobial resistance phenotype in pre-harvest studies (i.e., ampicillin, see Table 2) was only reported in a total of six post-harvest studies ($n = 4$ and $n = 2$ for *Salmonella* spp. and *E. coli*, respectively; Table 4). One might speculate that the relative infrequent use of ampicillin resistance as a selective marker in post-harvest studies could be due to the more frequent presence of ampicillin resistance among produce-associated microbiota (Al-Kharousi et al., 2019; S. A. Hassan et al., 2011). In particular, a previous study (Al-Kharousi et al., 2019) identified AmpC β-lactamases (enzymes conferring resistance to penicillins such as ampicillin) in produce types such as banana, cucumber, tomato, and watermelon, all of which represented produce commodities that were either only investigated in post-harvest studies or were investigated at higher frequency in post-harvest studies compared to pre-harvest studies (Figure 3).

Isolation source of strains used

A total of 85 (59%) post-harvest studies reported the isolation source(s) of bacterial strains that were used in population dynamics experiments. For the remaining post-harvest studies ($n = 59$, 41%), information pertaining to the isolation source(s) of bacterial strains was either not provided or could not be reliably extracted from full texts. Isolation sources of target bacterial strains used in post-harvest studies represented three distinct categories previously described for pre-harvest studies (see section 3.4.1: Isolation source of strains used). Across all bacterial types, the most frequently reported isolation source category was category (i) non-human outbreak-associated strains ($n = 38$, $n = 30$, $n = 22$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by category (ii) strains associated with a produce-associated human outbreak ($n = 32$, $n = 19$, and $n = 19$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively; Table 4).

While a larger number of post-harvest studies reported isolation source(s) of bacterial strains used in population dynamics experiments compared to pre-harvest studies (see section 3.4.1: Isolation source of strains used), reporting frequency of this information was still < 60% across both pre- and post-harvest studies. Regardless, as discussed in section 3.4.1, while isolation source has traditionally been provided to support that strains used might be more representative of potential strains that could contaminate produce under real-world scenarios, providing molecular data associated with strains (e.g., WGS, transcriptomics) represents a better future approach to define and describe strains used in both pre- and post-harvest population dynamics studies.

3.5.2 | Post-harvest studies: Produce commodities

In line with our search algorithm, produce commodities evaluated were provided in all ($n = 144$) post-harvest studies. The three most frequently investigated produce commodities in post-harvest studies included spinach, strawberries, and lettuce for *E. coli* ($n = 13$, $n = 11$, and $n = 7$, respectively), tomatoes, almonds, and lettuce for *Salmonella* spp. ($n = 24$, $n = 10$, and $n = 10$, respectively), and apples, sprouts, and tomatoes for *Listeria* spp.

($n = 6$ for all; Figure 3). Many of the most frequently investigated bacteria–produce pairs reported here have been associated with high-profile outbreaks in the past, such as *S. enterica* and tomatoes (Greene et al., 2008), pathogenic *E. coli* and spinach (Wendel et al., 2009), and *L. monocytogenes* and apples (Angelo et al., 2017). This represents a potential reason for the high frequency of studies that reported investigating population dynamics for these bacteria–produce pairs. It should be noted that this is a responsive rather than proactive approach to evaluating the risk associated with foodborne pathogens on produce. A more comprehensive approach might be to select produce commodities for population dynamics evaluations based on risks associated with intrinsic characteristics (e.g., water activity, pH, surface antimicrobial constituents) and production characteristics (e.g., seasonality, growing environment, and typical processing and ripening steps employed). This is supported by the observation that several produce commodities (e.g., chicory, watercress, guava, lychee, and papaya) deemed "high risk" by the risk ranking model that informed FSMA's Food Traceability List (FDA Food Traceability Rule Workgroup, 2022; U.S. Food & Drug Administration, 2022) were not investigated in any post-harvest studies, similar to what we observed for pre-harvest studies (see Section 3.4.2). These findings further highlight the need for risk-based strategies to inform the produce commodities that are investigated in future population dynamics studies at both pre- and post-harvest stages of the produce supply chain.

3.5.3 | Post-harvest studies: Experimental temperature conditions

A total of 141 (98%) post-harvest studies reported the experimental temperature conditions that were evaluated in population dynamics experiments on produce. For the remaining studies ($n = 3$, 2%), experimental temperature conditions were either not provided or could not be reliably extracted from full texts. Overall, a wide range of experimental temperature conditions were reported for post-harvest studies (i.e., 0 to 37°C). Across all bacterial types, the most frequently reported temperature range used for experiments was 2 to 4°C ($n = 44$, $n = 34$, and $n = 30$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by 23 to 25°C ($n = 42$, $n = 30$, and $n = 20$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively; Table 5).

The wide range of temperatures used for the storage of produce is likely reflective of the range of temperatures recommended for storing different varieties of produce throughout the post-harvest supply chain to prolong shelf life and preserve quality (Gross et al., 2016; University of California, Davis, 2017). However, produce is generally not recommended to be stored at temperatures exceeding 25°C (Gross et al., 2016). Importantly, while a fair number of studies reported evaluating population dynamics of *Listeria* spp., *Salmonella* spp., or *E. coli* on produce that was stored at temperatures exceeding 25°C ($n = 14$, $n = 8$, and $n = 7$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), all of these studies also evaluated at least one lower temperature range in their study designs (e.g., 2 to 4°C, 8 to 10°C, 20 to 22°C). Therefore, the inclusion of temperatures > 25°C likely represented a "worst-case scenario" of simulated storage conditions for produce.

3.5.4 | Post-harvest studies: Experimental RH conditions

A total of 56 (39%) post-harvest studies reported the experimental RH conditions that were evaluated in population dynamics experiments on produce. For the remaining studies ($n = 88$, 61%), experimental RH conditions were either not provided or could not be reliably extracted from full texts. Among the 56 post-harvest studies that reported experimental RH conditions used in population dynamics experiments, RH levels ranged from 20% to 100%. Across all bacterial types, the most frequently reported RH range used for experiments was 90% to 100% ($n = 16$, $n = 12$, and $n = 7$ for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by 80% to 90% for *E. coli* and *Listeria* spp. ($n = 8$ and $n = 6$, respectively) and 70% to 80% for *Salmonella* spp. ($n = 14$; Table 5).

Overall, a wide range of RH levels were reported in produce population dynamics studies. This is again reflective of the wide range of optimal RH levels for storing different produce commodities throughout the post-harvest produce supply chain (Gross et al., 2016; University of California, Davis, 2017). Therefore, the spread of experimental RH conditions reported here is likely representative of the different varieties of produce represented among included studies. Notably, experimental RH conditions were not able to be extracted for over half (61%) of post-harvest studies. As there is increasing evidence to suggest that RH conditions can significantly impact population dynamics outcomes of bacterial organisms on produce (Fonseca, 2009; Likotrafiti et al., 2013; Marik et al., 2019), this represents a knowledge gap that should be addressed in future post-harvest studies.

TABLE 5 Key characteristics reported for post-harvest population dynamics studies, including experimental temperature and relative humidity (RH) conditions evaluated in population dynamics experiments.

Experimental condition	*Listeria* spp. ($n = 49$)	*Salmonella* spp. ($n = 87$)	*E. coli* ($n = 61$)
Temperature range			
−1 to 1°C	6	2	3
2 to 4°C	30	44	34
5 to 7°C	10	14	17
8 to 10°C	16	15	12
11 to 13°C	9	7	5
14 to 16°C	6	7	10
17 to 19°C	4	2	2
20 to 22°C	11	30	9
23 to 25°C	20	42	30
> 25°C	7	14	8
Not able to extract[a]	0	2	1
RH range[b]			
20% to 30%	4	9	4
30% to 40%	5	7	7
40% to 50%	4	6	4
50% to 60%	2	4	3
60% to 70%	1	9	5
70% to 80%	3	14	1
80% to 90%	6	11	8
90% to 100%	7	16	12
Not able to extract	33	47	38

Note: Note that each given study may have evaluated multiple temperature ranges and RH ranges.

[a]Refers to the number of studies in which relevant data were not able to be extracted because the information was either not provided or could not be reliably extracted from full texts.

[b]If RH of exactly "60%" was reported in the full text of a given study, the RH range of "60%–70%" was reported here.

3.6 | Pre- and post-harvest population dynamics outcomes for *Listeria* spp., *Salmonella* spp., and *E. coli*

For each included study, the overall population dynamics outcome observed on produce (i.e., growth, survival, or die-off) was extracted. For the purpose of this analysis, "growth" was defined as > 1 log unit increase in the population of the bacterial target organism (i.e., *Listeria* spp., *Salmonella* spp., or *E. coli*) at the final evaluation point of the population dynamics experiment compared to initial levels on produce, "survival" was defined as ≤ 1 log unit change (either increase or decrease) in population of the bacterial target, and "die-off" was defined as a > 1 log unit decrease in the population of the bacterial target. Population dynamics outcomes of growth, survival, or die-off were only extracted from a given study if the populations of bacterial target organisms on produce at the beginning of the population dynamics experiment (e.g., day 0) and at the end of the population dynamics experiment were explicitly provided in the full text or tables. The purpose of this preliminary analysis was to identify (i) studies that may contain enough extractable quantitative data to warrant further consideration in evidence synthesis studies (e.g., meta-analyses) and (ii) high-level trends in population dynamics outcomes; we elected to not attempt to extract key attributes associated with particular population dynamics outcomes (e.g., environmental conditions associated with growth vs. survival). As such, the findings reported here provide both important initial data but also set the stage for future synthesis studies that can address additional questions.

3.6.1 | Population dynamics outcomes for pre-harvest studies

Population dynamics outcomes could be extracted from a total of 63 (44%) pre-harvest studies. For the remaining studies ($n = 80$, 55%), these outcomes were not able to be extracted as levels of the bacterial target organisms at the beginning and end of population dynamics

TABLE 6 Population dynamics outcomes of *Listeria* spp., *Salmonella* spp., and *E. coli* on produce for both pre-harvest and post-harvest studies.

Bacteria	Stage of supply chain (number of studies)	Number of studies reporting[a]			
		Growth	Survival	Die-off	NE
Listeria spp.	Pre-harvest (13)	3	1	4	7
	Post-harvest (49)	8	13	22	20
Salmonella spp.	Pre-harvest (69)	9	11	17	43
	Post-harvest (87)	12	20	37	42
E. coli	Pre-harvest (93)	7	9	37	49
	Post-harvest (61)	8	15	29	27

[a]Growth is defined as > 1 log unit increase in the population of the bacterial target organism (i.e., *Listeria* spp., *Salmonella* spp., or *E. coli*) at the final evaluation point of the population dynamics experiment compared to initial levels on produce; Survival is defined as ≤ 1 log unit change (either increase or decrease) in population of the bacterial target; Die-off is defined as a > 1 log unit decrease in the population of the bacterial target; NE, not able to extract. Refers to the number of studies in which the population dynamics outcomes of growth, survival, or die-off could not be extracted because populations of bacterial targets on produce at the beginning of the population dynamics experiment (e.g., Day 0) and/or at the end of the population dynamics experiment were not explicitly provided in full text or tables of included studies.

experiments were not explicitly provided in the full text or tables. For pre-harvest studies where population dynamics outcomes could be extracted, die-off was most the frequently reported population dynamics outcome across all bacterial types (n = 37, n = 17, and n = 4 for *E. coli*, *Salmonella* spp., and *Listeria* spp., respectively; Table 6). Survival was the second most frequently reported population dynamics outcome for *Salmonella* spp. and *E. coli* (n = 11 and n = 9, respectively), while growth was the second most frequently reported population dynamics outcome for *Listeria* spp. (n = 3). These data indicate that key quantitative data needed for extracting high-level population dynamics outcomes was absent from over 50% of pre-harvest studies. Importantly, this highlights a need for improved reporting of quantitative data in pre-harvest studies. These quantitative data are essential for conducting comprehensive systematic reviews with meta-analysis (Bown & Sutton, 2010), which, in turn, can support the establishment of time-dependent die-off rates of foodborne bacterial pathogens on produce at the pre-harvest stage of the supply chain.

It is also important to note that, while our preliminary analysis suggests a trend of bacterial die-off on produce being the most likely population dynamics outcome among pre-harvest studies, these findings may be biased. We hypothesize that studies may be more likely to explicitly report exact population changes (either in full text or tables) when larger changes are observed (i.e., changes of more than 1 log, which may be considered a more noteworthy biological outcome), compared to smaller changes (i.e., < 1 log). Therefore, the information extracted here should not be seen as confirming that foodborne bacterial pathogens are most likely to die off at the pre-harvest stage of the supply chain. Rather, future evidence synthesis studies, as well as possibly additional experiments, are important to establish whether pre-harvest die-off can represent an effective and reproducible control strategy to mitigate bacterial food safety hazards on produce.

3.6.2 | Population dynamics outcomes for post-harvest studies

Population dynamics outcomes could be extracted from a total of 82 (57%) post-harvest studies. For the remaining studies (n = 62, 43%), population dynamics outcomes were not able to be extracted as levels of the bacterial target organisms at the beginning and end of population dynamics experiments were not explicitly provided. For post-harvest studies where population dynamics outcomes could be extracted, die-off was most frequently reported across all bacterial types (n = 37, n = 29, and n = 22 for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively), followed by survival (n = 20, n = 15, and n = 13 for *Salmonella* spp., *E. coli*, and *Listeria* spp., respectively; Table 6).

Similar to pre-harvest studies (see Section 3.6.1), population dynamics outcomes were not able to be extracted from a high percentage (i.e., > 40%) of post-harvest studies. Therefore, while this scoping review identified a sizable body of literature that investigates produce population dynamics at both pre- and post-harvest stages of the supply chain, many of these studies might not be applicable for consideration for more in-depth evidence synthesis studies, given their limited reporting of key quantitative data. Overall, these findings underscore a critical need to establish improved standards for reporting quantitative data in produce population dynamics studies; such efforts will help provide more data that can be used to define time-dependent metrics for controlling foodborne

bacterial pathogens on produce at both the pre- and post-harvest stages of the supply chain.

4 | CONCLUSION

The collation of data included in this scoping review identified key knowledge gaps surrounding both study subjects investigated and factors assessed in population dynamics studies on produce, with two of the most notable knowledge gaps including the underrepresentation of studies that investigated (i) *Listeria* spp. population dynamics in a pre-harvest setting and (ii) population dynamics for produce grown in CEA settings using soil-less culture systems. Addressing such knowledge gaps will provide a more complete repertoire of the population dynamics of bacterial organisms on produce throughout the produce supply chain, which is essential for establishing time-dependent metrics that demonstrate the die-off or growth suppression of foodborne bacterial pathogens on fresh produce. In addition, this scoping review identified several incongruities in the materials and methods used in previous population dynamics investigations on produce. Such incongruities can hinder the ability of systematic evaluations (e.g., meta-analyses) to draw clear conclusions about population dynamics outcomes, and these conclusions are crucial for establishing time-dependent metrics that can be utilized to control foodborne bacterial pathogens on produce. Therefore, we urge the produce safety field to consider harmonizing study designs and methods that are used to carry out future population dynamics investigations of food safety relevant bacterial organisms on produce. Finally, for a large number of included studies, factors known to be relevant to bacterial population dynamics either were not provided or could not be reliably extracted from full texts. Poor reporting unnecessarily raises doubts about the rigor of conducted research and limits the reproducibility and synthesis of findings. Thus, it is urgent for the research community to establish and promote the use of reporting standards that will assure rigor and reproducibility of food safety research outcomes.

AUTHOR CONTRIBUTIONS

Samantha Bolten: Conceptualization; investigation; writing—original draft; methodology; validation; visualization; writing—review and editing; formal analysis; project administration; data curation; supervision. **Alexandra Belias**: Conceptualization; investigation; methodology; writing—review and editing; project administration; supervision. **Kelly A. Weigand**: Resources; investigation; writing—review and editing; writing—original draft; methodology; validation; project administration; data curation; supervision. **Magdalena Pajor**: Writing—review and editing; investigation; methodology. **Chenhao Qian**: Methodology; writing—review and editing; visualization; validation; software; formal analysis; data curation. **Renata Ivanek**: Conceptualization; funding acquisition; writing—review and editing; supervision. **Martin Wiedmann**: Funding acquisition; conceptualization; writing—review and editing; writing—original draft; supervision; resources; project administration; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors do not report any conflicts of interest.

DATA AVAILABILITY STATEMENT

All raw data extracted from included studies is available on GitHub (https://github.com/sjb375/scoping_review).

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SUPPORTING INFORMATION

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