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Recent advances in the use of bacterial probiotics in animal production

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Review Article

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Abstract

Animal husbandry is increasingly under pressure to meet world food demand. Thus, strategies are sought to ensure this productivity increment. The objective of this review was to gather advances in the use of bacterial probiotics in animal production. Lactobacilli correspond to the most used bacterial group, with several beneficial effects already reported and described, as well as the *Enterococcus* and *Pediococcus* genera – being the latter expressively used in aquaculture. Research on the *Bifidobacterium* genus is mostly focused on human health, which demonstrates great effects on blood biochemical parameters. Such results sustain the possibility of expanding its use in veterinary medicine. Other groups commonly assessed for human medicine but with prospective expansion to animal health are the genera *Leuconostoc* and *Streptococcus*, which have been demonstrating interesting effects on the prevention of viral diseases, and in dentistry, respectively. Although bacteria from the genera *Bacillus* and *Lactococcus* also have great potential for use in animal production, a complete characterization of the candidate strain must be previously made, due to the existence of pathogenic and/or spoilage variants. It is noteworthy that a growing number of studies have investigated the genus *Propionibacterium*, but still in very early stages. However, the hitherto excellent results endorse its application. In this way, in addition to the fact that bacterial probiotics represent a promising approach to promote productivity increase in animal production, the application of other strains than the traditionally employed genera may allow the exploitation of novel mechanisms and enlighten unexplored possibilities.

Introduction

The world population has grown rapidly in the past few decades, and this increase puts huge pressure on the food production chain to meet the demand. As the intensive production system guarantees a high yield per unit of land, it has been applied all over the world. However, the high density of animals, the confinement conditions, and practices such as the indiscriminate use of antibiotic growth promoters may promote the spread of illnesses in the animal production environment, despite the association with the antimicrobial resistance crisis. Therefore, alternatives are being sought to, not only assure productivity, maintain food quality and safety, and improve animal welfare (Ritchie *et al.*, 2020; Evangelista and Luciano, 2021; Evangelista *et al.*, 2021*a*).

For this purpose, the use of probiotics figures as one of the main biotechnological approaches in all types of commercial animal production. They are constituted by live microorganisms that confer health benefits to the host when consumed, exerting, for instance, bioprotective activity towards pathogenic bacteria through different mechanisms, including competitive exclusion and the production and excretion of antimicrobial substances (Corrêa *et al.*, 2019; Martín and Langella, 2019; Danielski *et al.*, 2022).

Lactic acid bacteria are the most used group of probiotics, along with specific strains of *Escherichia coli*, species of *Bacillus*, and yeast strains from the genus *Saccharomyces* (Fijan, 2014; Danielski *et al.*, 2022). Besides promoting animal health, probiotics can also improve zootechnical indexes (productive parameters), such as growth rate, final weight, and feed conversion ratio (Jatobá *et al.*, 2018; Bordin *et al.*, 2021). In addition, it has been shown that they may also present immunomodulatory effects, balancing inflammatory responses and acting in both innate and adaptive immune cells (Yahfoufi *et al.*, 2018).

Several effects attributed to the use of probiotics do not have their mechanism completely elucidated, such as immunomodulation and the improvement of zootechnical indices. Although the beneficial effect achieved is known, what causes this effect is not yet fully determined (Wang *et al.*, 2018*a*). The main mechanism of action of probiotics is competitive exclusion, occupying binding sites that are limited in the host, in addition to the consumption of available nutrients (Corrêa *et al.*, 2019). Some authors consider that the beneficial effects are caused by the interaction between intestinal cells or mucus with bacterial surface-associated proteins and other non-covalently surface-bound proteins, involved in stress tolerance, survival within the host digestive tract, and modulation of intestinal inflammation (do Carmo *et al.*, 2018). Other factors involved in the interaction between intestinal cells and probiotics, influencing host response, are tight adherence pili, sortase-dependent pili, fibronectin, or collagen-binding proteins (Abdelhamid *et al.*, 2019).

Authors postulate that the anti-inflammatory action of probiotics is modulated by the increase in the expression of interleukin-10 (IL-10), which may even play a role in reducing metabolic disorders because IL-10 has the potential to regulate insulin sensitivity. Other beneficial effects mentioned are the reduction of systemic blood pressure by the production of peptides that inhibit the activity of angiotensin I-converting enzymes (Zoumpopoulou *et al.*, 2018); the potential to promote the expression of host defence peptides (Wang *et al.*, 2018*b*); and the improvement of serum lipid levels, explained by the competition between the host and the probiotic for nutrients from the diet, such as fatty acids, resulting in decreased absorption by the host, which, consequently, decreases weight gain, body fat mass, and hepatic lipid accumulation (Jang *et al.*, 2019). Research into the mechanisms of action of probiotics is still required, and strategies such as bioinformatics and advanced molecular techniques are an option for a complete understanding of the mechanisms underlying the beneficial effects of probiotics.

As research on probiotics has been expanding in recent years, this review gathers the latest advances in the use of bacterial probiotics in animal production, while identifying gaps in the existing knowledge, both on the bacterial species used and on the use in different types of animal production.

Methodology

A literature review was planned to investigate the use of probiotics in animal production. Search strategies were applied in the online databases PubMed, Scopus, and Google Scholar, using the following descriptors: [(*Bacterial species or genus*) AND (probiotic* OR bioprotection OR preservative* OR bioprotective* OR biopreservation OR biopreservative*)]. The search collected original research and review articles written in English and published since 2016. Interventional studies were included in this review. Duplicate articles, reports, commentaries, letters to the editor, and publication types other than journal articles were excluded from the analysis. Previously published reviews were included as reference sources. Older studies were used for bacteria that showed probiotic potential, but no published articles in the area in recent years were found.

A three-stage screening (title, abstract, and full text) and data extraction were performed. Mendeley software (Mendeley Desktop for Windows v. 1.80.3) was used for the management and screening of the searched results.

Although *E. coli* strains considered safe have been used as probiotics for decades, recent research indicates that their use may pose risks to the consumer (Massip *et al.*, 2019; Nougayrède *et al.*, 2021). The authors understand that probiotic *E. coli* requires a more specific and in-depth approach, which requires the elaboration of a specific review on the subject. Therefore, it was decided to keep the species out of those included in the study.

Lactobacilli as probiotics

In 2020, Zheng *et al.* (2020) reclassified the former *Lactobacillus* genus into 25 new genera, in addition to uniting the *Lactobacillaceae* and *Leuconostocaceae* families, in order to solve taxonomic inconsistencies. The former *Lactobacillus* genus comprised of 261 species, including Gram-positive, fermentative, facultatively anaerobic, and non-spore-forming microorganisms. In this review, we use the generic term 'Lactobacilli' to designate all organisms formerly classified as *Lactobacillaceae*, and adopt the reclassified taxonomy to refer to Lactobacilli species. After the three-stage screening, 12 studies were included in the review.

Lactobacilli are the most explored bacteria for probiotic and/or bioprotective purposes, presenting numerous previously described positive effects in animal health and zootechnical indexes (Evangelista *et al.*, 2021*b*). It can be inferred that Lactobacilli use as a feed supplement is a viable option for many species, in different dosages, varying from 5 to 9.6 log CFU (colony-forming units)/g or ml (Liu *et al.*, 2017*a*, 2017*b*), applied directly in feed (Phuoc and Jamikorn, 2016), drinking water (Qin *et al.*, 2018), and milk (Shen *et al.*, 2020) (Table 1).

The results of the use of Lactobacilli probiotics in animal feeding include an increase in daily weight gain and better feed conversion ratio; improvement of the immune profile, such as the enhanced proliferation of immune cells in the blood; and changes in the gastrointestinal microbiology, with reduction of pathogenic bacteria population (Wang *et al.*, 2018*a*; Saleh *et al.*, 2020; Shen *et al.*, 2020) (Table 1).

Research on Lactobacilli is at an advanced level, with extensive *in vitro* characterization of several species in addition to *in vivo* studies with different production animals and methods of administration. Consequently, there is a current vast application of these microorganisms in animal production. However, some controversial issues have been raised through the years, such as the possible development of adaptation and pathogen resistance, to be further discussed in this review. Thus, it is essential to exploit different technologies to address the problem from different approaches, increasing our range of options to improve the sanitary quality of herds and, consequently, of the produced food.

Among the Lactobacilli, the species *Lacticaseibacillus rhamnosus*, *Lactiplantibacillus plantarum*, *Lacticaseibacillus casei*, and *Lactobacillus acidophilus* stand out as the most used for probiotic purposes, for almost all animal species. Referring to human health, Lactobacilli are also the most famous probiotics used, mainly in dairy products.

Use of genus *Bifidobacterium* as probiotics in animal production

Bacteria of the genus *Bifidobacterium* are commonly applied as probiotics in human diets, although research on their use for production animals is still scarce. The genus is composed of Gram-positive, anaerobic, non-spore-forming, and non-motile bacteria (Duranti *et al.*, 2020). After the three-stage screening, five studies were included in the review.

Bifidobacterium use in rodent models has demonstrated that these bacteria induce changes in the gut microbiota, in addition to attenuation of endothelial dysfunction, and decrease in blood pressure in low-renin hypertension (Robles-Vera *et al.*, 2020). Its effects as a psychobiotic have also been observed, reducing depressive-like behaviour in the forced swimming test of mice (Yunes *et al.*, 2020).

Table 1. Use of Lactobacilli in animal production to improve zootechnical indexes and health parameters

Bacteria	Animal	Dosage	Effects	Reference
L. acidophilus	New Zealand White rabbits, 28-day-old	7 log CFU g^{-1} of feed	Increase in body weight, digestibility coefficients of dry matter, organic matter, crude protein, neutral detergent fibre, and gross energy; Increase in intestinal Lactobacilli populations, and decrease in intestinal coliform populations	Phuoc and Jamikorn (2016)
	Chicken, 15-day-old	8.48 log CFU g^{-1} of feed	Increase in body weight, in digestibility coefficients of dry matter, crude protein, and crude fibre, and plasma high-density-lipoprotein cholesterol	Saleh *et al.* (2020)
L. casei	Newborn piglets, Duroc × landrace × Yorkshire	9–9.6 log CFU per animal	Decrease in mortality and diarrhoea indexes, and improvement of the average daily gain and slaughter weight	Liu *et al.* (2017*b*)
	New Zealand White rabbits, 5-day-old	8.7 log CFU ml^{-1} of milk	Reduction of *E. coli* and *Shigella* spp. population	Shen *et al.* (2020)
Lactobacillus johnsonii	Male chicks, 1-day-old, Cobb 500	5–6 log CFU g^{-1} of feed	Decrease of abdominal fat and feed conversion ratio, and increase of final weight, daily weight gain, and breast percentage	Liu *et al.* (2017*a*)
	Male chicks, 1-day-old, Cobb 500	5–6 log CFU g^{-1} of feed	Increase in antioxidant abilities; in the serum levels of IMs, IL-2, and IFN-γ; and in the CD3+CD4+T-lymphocyte percentage in peripheral blood	Wang *et al.* (2018*a*)
Lacticaseibacillus paracasei paracasei	Chicken, 1-day-old, Dagu × Xianju	6 log UFC ml^{-1} of feed	Increase in weight gain and in the metabolic pathway functions, and improvement of the intestinal microflora	Xu *et al.* (2019)
L. plantarum	Male chicken, 1-day-old, Arbor Acres	8 log CFU g^{-1} of feed	Reduced mortality, crypt depth, and serum levels of diamine oxidase, and higher levels of acetic acid and total short-chain fatty acids	Ding *et al.* (2019)
	Male chicken, 5 and 30-day-old, ISA 15	9 log CFU per animal	Increase in animal food intake and weight gain	Benbara *et al.* (2020)
L. rhamnosus, *L. plantarum, L. casei,* and *L. acidophilus*	Larval zebrafish	6 log UFC ml^{-1} of water in tanks	Higher final body weight, decrease in mortality rates, and enhancement of immunity	Qin *et al.* (2018)
Ligilactobacillus salivarius	Male chicken	9 log CFU g^{-1} of feed	Reduction of coliforms population	Castillo *et al.* (2018)
L. plantarum and *Lactiplantibacillus pentosus*	Bullfrog tadpoles, 15-day-old	7.16–7.42 log CFU g^{-1} of feed	Increase of final weight gain and feed conversion ratio	Pereira *et al.* (2017)

Intravenous treatment with probiotic *Bifidobacterium bifidum* (100 μl containing 10^8 CFU) reportedly caused antigen-specific responses, resulting in (1) elevation of IL-12 and interferon (IFN)-γ (pro-inflammatory cytokines), (2) lymphocyte proliferative responses, (3) CD8+ cytolytic effects in the spleen, (4) significantly enhanced expression of IL-6 (pro-inflammatory cytokine and anti-inflammatory myokine) in the tumour microenvironment, (5) antitumour responses, and (6) inhibition of tumour growth in tumour-bearing mice (Abdolalipour *et al*., 2020). *Bifidobacterium longum infantis*, orally administered, demonstrated the potential to reduce intestinal colonization by pathogens (*Salmonella* and *E. coli*) and to stimulate a local immune response in a weaned piglet model (Barba-Vidal *et al*., 2017).

Reduction of visceral fat accumulation and improvement in glucose tolerance have been observed during treatment using *Bifidobacterium animalis lactis* in 5-week-old male C57BL/6J mice. Also, the levels of acetate and glucagon-like peptide-1 had increased in both gut and plasma, indicating that the bacteria can mitigate metabolic disorders by modulating gut microbiota, leading to an elevation of short-chain fatty acids (Aoki *et al*., 2017), suggesting improved digestibility.

There is a wide possibility of the use of *Bifidobacterium* to promote beneficial effects in animal production; however, few studies have explored them to date. Several strains of *Bifidobacterium* are used as probiotics and supplements for human consumption, and there is huge potential for their application in animal production. To enable their use, further research must focus on *in vivo* model studies that evaluate the positive effects of this genus on animal health and performance, just as it has been done with Lactobacilli for many years.

Enterococcus as probiotics for farm animals

The genus *Enterococcus* is widely used as a probiotic in animal production. They are Gram-positive bacteria with an ovoid shape, forming neither spores nor capsules, but some species may be capable of movement by a flagellum (Růžičková *et al*., 2020). After the three-stage screening, nine studies were included in this review.

Among the probiotic species, *Enterococcus faecium* stands out as the most studied bacteria, regarded in 77.8% of the *Enterococcus* research articles gathered for this review ($n = 7$). With lower incidence, *Enterococcus faecalis* ($n = 1$), and

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Enterococcus durans ($n = 1$) are also present in the literature. The bacterial concentration assessed in these studies varied between 8.54 and 9.83 log CFU g^{-1} or ml (Hanczakowska *et al.*, 2017; Wang *et al.*, 2020), which has been administered in feed (Sato *et al.*, 2019), drinking water (Ognik *et al.*, 2019), or through a Ringer solution (Lauková *et al.*, 2017*b*) (Table 2).

The observed effects summarized in Table 2 include improvement in important zootechnical indexes, such as feed conversion ratio and daily weight gain, and in biochemical parameters, such as serum concentration of immunoglobulins (IMs) – which supports the immunomodulatory potential of enterococci. Another observed effect was the decrease of pathogenic microorganisms in the host gut (Liu *et al.*, 2017*b*; Ognik *et al.*, 2019; Wang *et al.*, 2021).

The *Enterococcus* genus is comprised of 14 species, three of which are extensively characterized: *E. faecium*, *E. faecalis*, and *E. durans*. Studies using other *Enterococcus* species as probiotic agents – e.g. *Enterococcus casseliflavus* and *Enterococcus raffinosus* (Divya *et al.*, 2012; Liang *et al.*, 2022) – may also be promising due to previously favourable results, thus requiring *in vitro* characterization studies and further *in vivo* evaluations to allow successful applications in the future.

The vast use of *Lactococcus* in aquaculture

Bacteria of the *Lactococcus* genus, especially *Lactococcus lactis*, are largely used as probiotics, majorly in aquaculture, for the great success observed in research and commercial applications. They are Gram-positive, facultatively anaerobic, catalase-negative, motile, do not constitute cytochrome and do not form spores (Yerlikaya, 2019). After the three-stage screening, 11 studies were included in this review.

In the studies evaluated in this review, *L. lactis* was administered through supplementation in feed, in doses between 6 and 10 log CFU g^{-1} (Sun *et al.*, 2018). The possibility of combinations of *Lactococcus* with bacteria of other genera – *Pediococcus acidilactici*, for instance (Soltani *et al.*, 2019) – to enhance results is also noteworthy (Table 3).

The use of this group as a probiotic feed supplement can improve zootechnical indexes and intestinal health, also showing immunomodulatory effects, in addition to combating important pathogens in aquaculture, such as *Vibrio harveyi* (Adel *et al.*, 2017*a*; Ghasemzadeh *et al.*, 2018; Won *et al.*, 2020) (Table 3). Furthermore, strains of *L. lactis* are potential producers of antimicrobial peptides, such as nisin (Corrêa *et al.*, 2019), and thus can provide additional mechanisms for pathogen control in animal production.

It is worth noting that, although *L. lactis* is widely used as a probiotic in aquaculture, certain species of *Lactococcus* may present pathogenic or deteriorating characteristics, such as *Lactococcus garvieae*, associated with *Lactococcosis* and high mortality rates in fish farming (Halimi *et al.*, 2020). Thus, a thorough characterization of potential new probiotic strains must be carried out with caution, including genotypic tests to avoid the introduction of harmful bacteria to production systems, causing economic and animal welfare losses.

Leuconostoc: a potential probiotic for farm animals

The use of the genus *Leuconostoc* is already well characterized in human and animal models. The bacteria exhibit Gram-positive, facultatively anaerobic, non-spore-forming and catalase-negative characteristics (Sharma and Chandra, 2018). After the three-stage screening, six studies were included in this review.

Bae *et al.* (2018) observed that *Leuconostoc mesenteroides* administration increased the length and rates of survival of mice infected with human seasonal and avian influenza viruses. In the study conducted by Traisaeng *et al.* (2020), *L. mesenteroides* increased insulin secretion in MIN6 cell culture and in streptozotocin-induced diabetic mice; while Le and Yang (2019) described a strong cholesterol-lowering activity of the species. In addition, Yi *et al.* (2017) reported that *L. mesenteroides* had shown remarkable resistance to lead and a capacity to remove this heavy metal.

Bacteria of the *Leuconostoc* genus are still underutilized in animal production, yet one particular species has been showing interesting properties for this use. Chang-Liao *et al.* (2020) showed that the intracellular extracts of *L. mesenteroides* exerted *in vitro* prophylactic, therapeutic, and direct inhibitory effects against porcine epidemic diarrhoea virus in a Vero cell culture model. The expression levels of type-I IFN-dependent genes – including myxovirus resistance 1 (MX1) and IFN-stimulated gene 15 – had significantly increased after treatment with the extracts. In the study of Seo *et al.* (2012), *L. mesenteroides* exhibited antiviral activity against low-pathogenic avian influenza virus (H9N2) both *in vitro* and *in vivo*, respectively in Madin–Darby canine kidney cell line and in specific-pathogen-free chickens.

L. mesenteroides strains have a peculiar ability to prevent viral infections, a characteristic not yet described in common probiotics genera/species, which represents a promising unexplored field of research in animal science, considering the beneficial effects achieved in human health. Like *Bifidobacterium*, the use of *Leuconostoc* shows unexplored potential, with the need for greater investment and attention from the scientific community. Among the needs for its application in animal production, *in vitro* tests to evaluate its survival in the gastrointestinal tract of production animals and *in vivo* tests to determine health and zootechnical effects are warranted.

Pediococcus in aquaculture

Pediococci are coccoidal or ovoid, Gram-positive, non-motile, non-spore-forming and anaerobic to microaerophilic. Most species are catalase- and oxidase-negative, although *Pediococcus pentosaceus* has been reported to possess pseudo-catalase activity (Wade *et al.*, 2019). After the three-stage screening, 12 studies were included in this review. The use of *Pediococcus* in animal production is also well characterized, especially in aquaculture, corresponding to 58.3% of the gathered articles ($n = 7$). Among them, *P. acidilactici* stands out, having been surveyed in 66.7% of the studies ($n = 8$).

Pediococcus-based probiotics were supplemented mainly through feeding, in concentrations between 6 and 10 log CFU g^{-1} (Mikulski *et al.*, 2020; Yu *et al.*, 2020). It is noteworthy that, like the *Leuconostoc* strains, *P. acidilactici* also demonstrates antiviral action through the modulation of genes associated with the immune system (Jaramillo-Torres *et al.*, 2019) (Table 4).

In order to make the most of their abilities and beneficial activities, *Pediococcus* strains should be thoroughly characterized and evaluated for application as probiotics in animal production. Likewise, different supplementation strategies and combinations with other species may also be assessed, posing great gaps to be filled by researchers in this field.

Table 2. Use of *Enterococcus* in animal production to improve zootechnical indexes and health parameters

Bacteria	Animal	Dosage	Effects	Reference
E. durans	Rabbit, 5-week-old, from both sexes	8.7 log CFU per animal per day	Decrease in coliforms and *Eimeria* oocysts, and increase in phagocytic activity; Reduction in glutathione-peroxidase (oxidative stress indicative)	Lauková *et al.* (2017*a*)
E. faecalis	Newborn piglets, Duroc × landrace × Yorkshire	Oral administration of a solution at 9.0–9.6 log CFU ml^{-1}	Increase in average daily gain, and decrease in diarrhoea and mortality rates	Liu *et al.* (2017*b*)
E. faecium	Horse, both sexes, 6–29-year-old	9 log CFU per animal per day	Increase in phagocytic, cellulolytic, amylolytic, xylanolytic, inulolytic, and pectinolytic activities	Lauková *et al.* (2020)
	Chicken, 1-day-old, Cobb 500	200 μl of a 9 log CFU ml^{-1} Ringer solution	Increase in phagocytic activity and decrease in the *Campylobacter* population; Biochemical parameters maintained at reference levels	Laukova *et al.* (2017*b*)
	Broiler chicken, 1-day-old, Arbor Acres	9.83 log CFU g^{-1} of feed	Increase in *Alistipes*, *Eubacterium*, *Rikenella*, and *Ruminococcaceae* populations, and decrease in *Faecalibacterium*, *Escherichia*, and *Shigella* populations; Increase in the population of short-chain fatty acid-producing bacteria, improvement of intestinal absorption of phosphorus and bone-forming metabolic activities, and decrease in phosphorus excretion	Wang *et al.* (2020)
	Pig, 30-day-old, landrace × large white × Duroc	9.01 log CFU g^{-1} of feed	Increase in body weight	Sato *et al.* (2019)
	Piglet, landrace	8.54 log CFU g^{-1} of feed	Increase in body weight and short-chain fatty acid concentration in intestines; Strong antibacterial activity against *E. coli* and *Clostridium perfringens*	Hanczakowska *et al.* (2017)
	Broiler breeder, 48-week-old, Arbor Acres	8.78 log CFU kg^{-1} of feed	Improvement in egg weight and concentration of follicle-stimulating hormone in the serum, and decrease in *Bacteroidetes* population	Wang *et al.* (2021)
	Chicken, 1-day-old, Ross 308	9.52–9.82 log CFU l^{-1} of drinking water	Increase in body weight, lysozyme activity, and in content of IgA in blood serum; and decrease in feed conversion ratio and in the content of IL-6 in blood serum	Ognik *et al.* (2019)

From the data presented, it is possible to observe the great importance of the use of *Pediococcus* in aquaculture. In this way, other branches of animal husbandry can explore this effectiveness in their production systems, in order to promote an increase in productivity through a sustainable approach.

Streptococcus strains have great potential for animal probiotic application

The use of probiotic *Streptococcus* species remains unexplored in animal production; however, it has been widely investigated in human health. The genus is composed of Gram-positive, non-spore-forming, facultatively anaerobic bacteria whose members include potent probiotics as well as animal and human pathogens (Patel and Gupta, 2018). After the three-stage screening, three studies were included in the review.

Esteban-Fernández *et al.* (2019) described a strong inhibitory action of *Streptococcus dentisani* supernatant against periodontal pathogens, such as *Porphyromonas gingivalis* and *Fusobacterium nucleatum*. The oral probiotic strongly increased the secretion of an anti-inflammatory cytokine, IL-10, and significantly reduced IFN-γ expression.

Humphreys and McBain (2019) reported that *Streptococcus salivarius* significantly reduced viable counts of potentially pathogenic streptococci and staphylococci in pharyngeal microbiota. Also, Bidossi *et al.* (2018) reported that *S. salivarius* and *Streptococcus oralis* can inhibit the biofilm formation capacity of certain pathogens, including *Staphylococcus aureus*, *S. epidermidis*, *S. pneumoniae*, *S. pyogenes*, *Propionibacterium acnes*, and *Moraxella catarrhalis*, and even disperse their preformed biofilms. Diffusible molecules secreted by the two streptococci and a decrease in the pH of the culture medium were implied mechanisms of the anti-biofilm activity.

As observed, the use of *Streptococcus* is widely characterized for the promotion of human health, mainly in the field of dentistry, which substantiates its possibility of application in animal production for different purposes. However, due to the existence of pathogenic species, such as *S. pneumoniae* and *S. pyogenes*, it is extremely important to fully characterize the microorganisms before their use.

Bacillus as probiotic agent

The probiotic use of *Bacillus*, mainly *Bacillus subtilis*, has been widely described in the most varied animal production systems, from aquaculture to sheep farming. The *Bacillus* genus is comprised of Gram-positive, obligate aerobes or facultative anaerobes, and spore-forming rods. Due to their ability to form endospores, they are able to survive in different niches including extreme environmental conditions (Tiwari *et al.*, 2019). After the three-stage screening, 21 studies were included in this review.

Studies with *B. subtilis* and associations comprise 71.4% of the articles gathered in this review for this genus ($n = 15$). Bacterial concentration varied between 3 and 10.4 log CFU g^{-1} or ml (Deng *et al.*, 2018; Abdel-Moneim *et al.*, 2020) applied to feed (Deng *et al.*, 2021) or drinking water (Tarnecki *et al.*, 2019),

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Table 3. Use of *Lactococcus* in animal production to improve zootechnical indexes and health parameters

Bacteria	Animal	Dosage	Effects	Reference
L. lactis	Olive flounder	9 log CFU g^{-1} of feed	Increase in citrulline, tricarboxylic acid cycle intermediates, short-chain fatty acids, vitamins, and taurine concentrations, linked to growth promotion	Nguyen *et al.* (2018)
			Promotion of protection against streptococcosis caused by *Streptococcus parauberis* through competitive exclusion and the increase of innate immune responses; Significantly higher specific growth rate and feed conversion ratio	Nguyen *et al.* (2017)
	Cyprinus carpio	8.7 log CFU g^{-1} of feed	Increase in weight gain and specific growth rate; Up-regulation of protein levels of pro-inflammatory (tumour necrosis factor (TNF)-α, IL-1β, IL-6, IL-12) and anti-inflammatory (IL-10, transforming growth factor-β) cytokines; Greater resistance to *Aeromonas hydrophila* challenge	Feng *et al.* (2019)
	Cromileptes altivelis	6–10 log CFU g^{-1} of feed	Increase in per cent weight gain and survival rates following injection with *V. harveyi*; Enhancement of the respiratory burst activity of head kidney macrophages, superoxide dismutase, acid phosphatase, and lysozyme activities of serum; Improvement of survival rate, and up-regulation of expression of a broad spectrum of immunity	Sun *et al.* (2018)
	Artemia sp., 4-day-old	8.48 log CFU ml^{-1} of artificial seawater in flasks	Inhibition of proliferation of pathogens, such as *Edwardsiella tarda*, in fish seedling production	Taoka *et al.* (2017)
	Litopenaeus vannamei	8 log CFU g^{-1} of feed	Increase in growth rate and superoxide dismutase activity; Healthier intestinal histology and improvement of immune-related gene expression	Won *et al.* (2020)
	Seriola dumerili	10.3 log CFU g^{-1} of feed	The growth performance of fish in the treated group was significantly higher than those in the control group, and five amino acids (aspartate, sarcosine, taurine, alanine, and arginine) in the gut content and 13 of 21 amino acids in the edible parts of fish in the treated group were significantly higher than those in the control group	Linh *et al.* (2018)
	Mugil cephalus	8.18–8.78 CFU g^{-1} of feed	Increase in growth parameters and survival rate; Greater resistance to *L. garvieae* challenge	Ghasemzadeh *et al.* (2018)
L. lactis lactis	*L. vannamei*	6–8 log CFU g^{-1} of feed	Increase in growth rate, survival, and body protein level; Improvement in cellulose, lipase, amylase, and protease activities; Greater resistance to *Vibrio anguillarum* challenge	Adel *et al.* (2017*a*)
	Nile tilapia	8 log CFU g^{-1} of feed	Increase in growth rate and feed utilization, in gut microvilli length and density, and in the expression of TNF-α, IFN-γ, and IL-1β in intestine and liver; Greater resistance to *Streptococcus agalactiae* challenge	Xia *et al.* (2018)
L. lactis[a]	Caspian roach larva	7–10 log CFU g^{-1} of feed	Increase of growth performance, enzymatic activity, and short-chain fatty acid production	Soltani *et al.* (2019)

[a]Analysis performed in combination with *P. acidilactici* at 7–10 log CFU g^{-1} of feed.

resulting in improved zootechnical indexes, including weight gain and feed conversion ratio, and also immunomodulatory effects, such as stimulation of anti-inflammatory cytokine production (Du *et al*., 2018; Keerqin *et al*., 2021) (Table 5).

This genus is especially interesting for commercial use due to its spore-formation ability, which may facilitate product development (Elisashvili *et al*., 2019). However, there are pathogenic and toxigenic species within the *Bacillus* genus, such as *Bacillus cereus*, classified in hazard group 2 due to the ability of some strains to produce toxins that may be fatal (e.g. cereulide) (Andersson *et al*., 2007; Advisory Committee on Dangerous Pathogens, 2013).

Beyond *B. subtilis*, several species of this genus demonstrate great potential for probiotic use – e.g. *Bacillus amyloliquefaciens* (Wealleans *et al*., 2017), *Bacillus licheniformis* (Zhao *et al*., 2020), *Bacillus megaterium* (Deng *et al*., 2021), *Bacillus pumilus* (Elsabagh *et al*., 2018), and *Bacillus toyonensis* (Roos *et al*., 2018), which may suggest a wide range of directions for future research.

Can *Propionibacterium* be an effective probiotic?

The use of the genus *Propionibacterium* has not yet been fully investigated as a probiotic agent for animal production or human health. *Propionibacterium* are Gram-positive, non-motile, non-spore-forming, catalase-positive bacilli. They are recognized as either anaerobic or relatively anaerobic bacteria (Piwowarek *et al*., 2018). After the three-stage screening, two studies were included in the review.

Although not widely used as a probiotic, Nair *et al*. (2019, 2021) described the bioprotective effects of *Propionibacterium freudenreichii freudenreichii* against multidrug-resistant

Table 4. Use of *Pediococcus* in animal production to improve zootechnical indexes and health parameters

Bacteria	Animal	Dosage	Effects	Reference
Pediococcus parvulus	*Danio rerio*	Larvae immersion in a 7.7 log CFU ml^{-1} solution	Competition with the pathogen *V. anguillarum*	Pérez-Ramos *et al.* (2018)
P. acidilactici	Juvenile *Rutilus kutum*	9.0–9.48 log CFU g^{-1} of feed	Increase in weight gain, specific growth rate, and survival rate	Valipour *et al.* (2018)
	Pig, 28-day-old, Duroc × landrace × large white	9.72 log CFU g^{-1} of feed	Increase in average daily gain and IL-10 serum levels; Decrease in IL-1 β, IL-6, and IFN-γ serum levels; Stimulation of production of acetic and propionic acids in caecal digesta	Wang *et al.* (2019)
	Broiler chicken, male, 420-day-old, Ross 308	8 log CFU g^{-1} of feed	Increase in villi height and crypt depth; Greater resistance to *Salmonella* Typhimurium challenge	Jazi *et al.* (2018)
	Chicken, male, 1-day-old, Lohmann brown	6 log CFU g^{-1} of feed	Increase in body weight, average daily gain, and serum total protein; Increase in the length of duodenum, and ileum; Increase in the weight of the spleen, duodenum, jejunum, and ileum	Yu *et al.* (2020)
	31-week-old Hy-line brown hens	10 log CFU g^{-1} of feed	Increase in egg weight, relative eggshell weight, eggshell thickness, and feed conversion ratio; Authors suggest that the low-energy diet promoted a probiotic response to optimize energy utilization	Mikulski *et al.* (2020)
	Pig, female, HD K-75 (Hampshire × local)	9.0–9.3 log CFU g^{-1} of feed	Improvement in growth performance, feed intake, digestibility of crude protein, nitrogen retention, triglyceride, cholesterol serum levels, dressing percentage, and vital organ weight; Decrease in serum glucose	Joysowal *et al.* (2018)
	Atlantic salmon	6.07 log CFU g^{-1} of feed	Increase in antiviral response (*mx*-1 and *tlr*3 gene expression)	Jaramillo-Torres *et al.* (2019)
P. acidilactici[a]	Caspian roach larva	7–10 log CFU g^{-1} of feed	Increase of growth performance, enzymatic activity, and short-chain fatty acid production	Soltani *et al.* (2019)
P. pentosaceus	*L. vannamei*	6–8 log CFU g^{-1} of feed	Increase in final body weight, final length, weight gain, survival rate, protease and amylase activities, Lactobacilli and *Bacillus* intestinal count, total haemocyte counts, and lysozyme activity; Greater resistance to *V. anguillarum* challenge	Adel *et al.* (2017*b*)
	C. carpio	7–9 log CFU g^{-1} of feed	Increase in final body weight, weight gain, specific growth rate, digestive enzymes activities, total viable heterotrophic aerobic bacteria population, red blood cells, white blood cells, haemoglobin, and haematocrit	Ahmadifar *et al.* (2020)
	Juvenile *Scylla paramamosain*	9 log CFU g^{-1} of feed	Increase in weight gain, specific growth rate, and serum enzyme activities of phenoloxidase and lysozyme; Greater resistance to *Vibrio parahaemolyticus* challenge	Yang *et al.* (2019)

[a]Analysis performed in combination with *L. lactis* at 7–10 log CFU g^{-1} of feed.

Salmonella Heidelberg in finishing turkeys, including reduction of caecal colonization and internal organ dissemination.

Hence, the research on *Propionibacterium* as probiotic agents has ample potential for growth. Due to the current limited use of *Propionibacterium* as a probiotic, the chance of adaptation and/or resistance of pathogenic bacteria is reduced, which may lead to the development of more efficient products.

Limits on the use of probiotics in animal production

Probiotics, although a viable and increasingly used option, can still promote some disadvantages to animal production (Table 6). After the three-stage screening, three studies were included in this review.

Some studies reviewing possible limitations to the use of probiotics are available in indexing databases, mainly reporting (1) worsening of dysbiosis in environments with a high degree of stress, (2) problems related to the dynamics of gastrointestinal microbial communities, (3) worsening of dysbiosis in immunocompromised groups, (4) excessive stimulation of the immune system, (5) increased costs related to production and storage of inputs and/or feed, and (5) sensory changes in the host. Some points also reported as problematic involved the different dose–response for each individual, in addition to the difference obtained in the effects, often observed in the same individual exposed to successive doses (Ayichew *et al.*, 2017; Evivie *et al.*, 2017; Amenyogbe *et al.*, 2020; Zommiti *et al.*, 2020).

However, it is worth mentioning that the results are still presented in a generic way. Several authors report the lack of depth in the safety of probiotics, mainly due to the lack of publications reporting negative results (Mehta, 2019) – only three articles reporting negative results were found for this review – which

Table 5. Use of *Bacillus* in animal production to improve zootechnical indexes and health parameters

Bacteria	Animal	Dosage	Effects	Reference
B. amyloliquefaciens	Broiler chicken, male, Ross 308	5.18 log CFU g^{-1} of feed	Increase in body weight, feed intake, ileal digestible energy, and ileal digestible fat and starch	Wealleans *et al.* (2017)
B. amyloliquefaciens and *B. subtilis*	Growth-retarded beef calves, 3–6-month-old	10.6 log CFU per animal per day	Increase in body weight gain, feed intake, feed conversion rate, and GH/IGF-1 levels; Decrease in *Anaeroplasma* and *Acholeplasma* populations, and increase of *Proteobacteria*, *Rhodospirillaceae*, *Campylobacterales*, and *Butyricimonas* (short-chain fatty acid-producers) populations	Du *et al.* (2018)
	Pig, 63-day-old, large white boar × (York × Dutch landrace) sow	8.78 log CFU g^{-1} of feed	Improvement in feed conversion ratio and average daily gain	van der Peet-Schwering *et al.* (2020)
B. licheniformis	Broiler chicken, male, 1-day-old, Ross 308	6 log CFU g^{-1} of feed	Improvement in the morphology of small intestine and liver; Enhancement of growth performance, and antioxidant capacity against *C. perfringens*-induced subclinical necrotic enteritis	Zhao *et al.* (2020)
	Sheep, 1-year-old, Dorper × thin-tailed han crossbred wethers	8.4–10.4 log CFU per animal per day	Increase in apparent digestibility of dry matter, organic matter, nitrogen, and neutral detergent fibre; Improved nitrogen utilization efficiency and energy metabolizability; Reduced methane emissions	Deng *et al.* (2018)
B. licheniformis and *B. amyloliquefaciens*	Larval *Centropomus undecimalis*	5.2 log CFU ml^{-1} of drinking water	Higher survival rate (2.5 times), faster growth, improvement in innate immune enzyme activities, and inhibition of opportunistic bacteria	Tarnecki *et al.* (2019)
B. megaterium	Lactating dairy cows, Holstein	8 log CFU g^{-1} of feed	Increase in the 4% fat-corrected milk production and improved nitrogen utilization	Deng *et al.* (2021)
B. subtilis	Broiler chicken, 1-day-old, Ross 308	8 log CFU g^{-1} of feed	Increase in weight gain and up-regulation of genes coding for tight junction proteins, cytokines, and Toll-like receptors; Increase in *Faecalibacterium*, *Oscillospira*, and *Butyricicoccus* populations; Decrease of *Ruminococcus*, Lactobacilli, and *Bacteroides* populations	Keerqin *et al.* (2021)
	Broiler chicken, 1-day-old, Arbor Acres	9 log spores kg^{-1} of feed	Increase in average body weight, average daily gain, villi height, and villi height to crypt depth ratio of the ileum; Increase in *Firmicutes*, *Christensenellaceae*, and *Caulobacteraceae* abundance and reduction of *Bacteroidetes*, *Vampirovibrio*, *Escherichia*, *Shigella*, and *Parabacteroides* populations in cecum	Ma *et al.* (2018)
	Broiler chicken, 100-day-old, Ross 308	8–9 log CFU kg^{-1} of feed	Greater resistance to *C. perfringens* in a necrotic enteritis challenge	Aljumaah *et al.* (2020)
	Pig, (Yorkshire × landrace) × Duroc	8–9 log CFU kg^{-1} of feed	Increase in average daily gain and lower incidence of diarrhoea; In association with essential oils, reduced fecal ammonia emission and blood urea nitrogen, and increased IgG concentration in serum	Tan *et al.* (2021)
	Broiler chicken, male, Cobb 500, 1-day-old	8 log CFU kg^{-1} of feed	Increase in final body weight gain and feed conversion ratio; High feed efficiency correlated with a significant increase in intestinal microvilli length; Increase in *Ruminococcus*, *Butyrivibrio*, *Lachnoclostridium*, and *Anaerostipes* populations	Jacquier *et al.* (2019)
	Laying hens, 36-week-old	9.9–10.2 log CFU g^{-1} of feed	Increase in shell thickness, eggshell quality and breaking strength; Decrease of plasma cholesterol and triglyceride, and increase in IgM concentration	Fathi *et al.* (2018)
	Quail, 1-day-old	3–9 log spores kg^{-1} of feed	Increase in live body weight and body weight gain, and decrease in feed-to-gain ratio; Increase in serum total protein and albumin levels, and decrease in concentrations of glucose, creatinine, urea-N, aspartate aminotransferase, and alanine aminotransferase; Elevated triiodothyronine and thyroxine activities; Increase in glutathione content and catalase activities, and decrease in lipid	Abdel-Moneim *et al.* (2020)

(*Continued*)

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Table 5. (*Continued.*)

Bacteria	Animal	Dosage	Effects	Reference
			peroxidation; Increase in duodenal proteolytic, lipolytic, amylolytic activities, and nutrient digestibility	
	Broiler chicken, 1-day-old, Ross 308	5.08–7.3 log CFU g^{-1} of feed	Increase in performance efficiency factor, feed intake, and body weight, and decrease in feed conversion ratio; Greater resistance to *Salmonella* challenge	Abudabos *et al.* (2019)
	L. vannamei	9 log CFU kg^{-1} of feed	Increase in growth performance and feed utilization; Increase in apparent digestibility coefficients of dry matter, crude protein, amino acids, and crude lipids	Tsai *et al.* (2019)
	Broiler chicken, Ross 708, day of hatch	6.2 log CFU kg^{-1} of feed	Improvement of zootechnical performance and nutrient digestibility; Decrease in production costs	Reis *et al.* (2017)
	Anguilla japonica	7–8 log CFU g^{-1} of feed	Increase in average weight gain, feed efficiency, and protein efficiency ratio; High detection of non-specific enzymatic activities, including lysozyme, superoxide dismutase, and myeloperoxidase; Increase of intestine glyceraldehyde-3-phosphate dehydrogenase, heat shock protein 70 and 90, and IgM; Greater resistance to *Vibrio angulillarum* challenge	Lee *et al.* (2017)
B. subtilis and *B. amyloliquefaciens*	Laying hens and roosters, 1-day-old	5–7 log spores kg^{-1} of feed	Positively affected egg production, quality of sperm production, and quality and hatchery of eggs	Mazanko *et al.* (2018)
B. subtilis, *B. licheniformis*, and *B. pumilus*	*Oreochromis niloticus*	8.0–8.2 log CFU g^{-1} of feed	Increase in growth performance, feed conversion ratio, blood serum profiles, whole intestinal lengths, anterior and terminal intestinal villi heights, and anterior goblet cells count	Elsabagh *et al.* (2018)
B. toyonensis[a]	Sheep, 3-month-old	6 log CFU g^{-1} of feed	Increase in seroconversion against bovine alphaherpesvirus (BoHV)-5, and higher neutralizing antibodies titres to BoHV-5 after vaccination; Higher mRNA transcription levels of cytokines IL-10 and IL-17A in splenocytes	Roos *et al.* (2018)

[a]Analysis performed in combination with *Saccharomyces boulardii* at 7 log CFU g^{-1} of feed.

may reflect their undervaluation in high-impact journals. Although negative results do not generate the same scientific expectations as positive results, they still have importance, especially to guide new studies. Even with the issues mentioned, most researchers emphasized that probiotics remain one of the most viable options for reducing the use of antibiotics in animal production.

Table 6. Negative results reported on the research on probiotics in animal production

Bacteria	Animal	Effects	Reference
Lactobacilli	Roosters, white rook	Decrease of fertility when the Lactobacilli population in semen is greater than 6 log CFU ml^{-1}	Haines *et al.* (2015)
L. acidophilus	Roosters, white rook	Decrease of fertility in gavage animals with 7 log CFU ml^{-1} for 14 days	Kiess *et al.* (2016)
Bacillus	Broiler chicken	Insignificant effects on the percentage of abdominal fat and carcass quality in a dosage of 50–60 mg kg^{-1} of feed (8.9–9.1 CFU kg^{-1})	Hidayat *et al.* (2016)

Conclusions and future perspectives

The use of probiotics is extremely widespread in animal production, with the use of Lactobacilli, *Bacillus*, and *Pediococcus* well characterized and largely investigated in the literature, in addition to certain species such as *L. lactis* and *E. faecium*. The *Propionibacterium*, *Streptococcus*, *Bifidobacterium*, and *Leuconostoc* genera, as well as other species of *Lactococcus* and *Enterococcus*, still need to be assessed to validate the potential abilities observed in exploratory studies.

With the gradual increase in food production demand, it is expected that the use of probiotics will also grow considering their positive association with the production indexes and the prevention of certain infectious diseases both in human and animal health. As an example, the great impact of probiotics on weight gain and mortality reduction in herds, in addition to the control of important pathogens, such as *Salmonella* and *E. coli*. In addition, studies involving combined applications and synergisms show great possibilities, being an open field for new research.

Few studies go beyond the *in vitro* stage and present benefits in animal health and production; in this review, only 84 articles were selected after a three-stage screening. Research in the area is advanced enough to extend *in vitro* studies and *in vivo* validation methods for transforming scientific findings into commercially viable technological innovations. Furthermore, research on the mechanism of action of probiotics must advance. Newly available techniques allow novel approaches to ensure more safety and efficacy in the use of probiotics.

Future studies focused on the use of neglected bacteria and the use of knowledge built over the past few decades about probiotics used in human health must be used for the development of new strategies and products for animal production. Partnerships between research centres and industries in the animal production sector are of paramount importance to enable the application of novel and safe technologies in the consumer market. With recent technological advances in all areas of biotechnology, probiotics are a thriving option for controlling pathogens in animal production and provide zootechnical gains, enabling a more sustainable production, allied to the principles of promoting animal health and welfare.

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