



## Probiotic characters of *Bifidobacterium* and *Lactobacillus* are a result of the ongoing gene acquisition and genome minimization evolutionary trends



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### ABSTRACT

*Bifidobacterium* and *Lactobacillus* are the main probiotic genera. Collectively, these two genera harbor over 200 species among which are many strains have been introduced as probiotics. These health-promoting microbes confer health benefits upon the host and so used in food productions and as supplements. Considering the economic importance of probiotics, the biochemistry, genomics, phylogeny and physiology of such genera have been exhaustively studied. According to the genomic data, the probiotic capabilities are strain specific which may be a result of the niche-specialization of the genomes of these bacteria to certain ecological niches like gastrointestinal tract of a diverse range of animals. These microbes have a wide distribution but the culture-based studies and either genomics data suggest selective affinity of some *Lactobacillus* and either *Bifidobacterium* species to certain ecological niches. An ongoing genome degradation, which is thought to be a result of passage through an evolutionary bottleneck, is the major trend in the evolution of lactobacilli. Further, evolutionary events resulted into two categories of lactobacilli: habitat generalists and habitat specialists. In place, the main trend in the evolution of bifidobacteria tend to be the gene acquisition. However, probiotic features are the results of a co-evolutionary relationship between these bacteria and their hosts and the aforementioned evolutionary trends have driven the evolution of these probiotic genera.

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## 1. Introduction

The microbiome of the gastrointestinal tract has a critical role in immunity, metabolism and many other functional features of the host impacting the health and life of the host, inevitably [1–4]. The human gut microbiome has a very close association with various aspects of our nutrition, metabolism, and health. It may be interesting that the microbial community of the gastrointestinal tract can interfere with metabolic diseases and disorders like obesity [4]. The gut microbiome comprises a huge microbial diversity [5] and each of the species may represent different strains that themselves may encode significantly different sets of genes and either a different number of copies of each gene [6–8]. Such an intraspecies variation suggest that any given species in our microbiome has potentially distinct functional capabilities [9]. Recent studies on individual isolates/strains of bacterial species have shed light on such an intraspecies variability [6,10] which can be expressed as intraspecies phenotypic variability in drug resistance [11–14], motility [15,16] growth rate [17], physiology [18,19], and virulence features [12,20,21] in a wide range of pathogens. Interestingly, the strain-specific features may, in turn, have some ecological advantages for the whole species resulting in species able to occupy a considerable range of niches [22]. Such an intraspecies variability has been reportedly detected in significant bacterial pathogens. Sharon et al. [23] studied the genomic differences of antibiotic resistance, molecular transport system, and biofilm formation capabilities among three strains of *Staphylococcus epidermis* and similarly, Morowitz et al. [24] have also identified such a strain specificity in *Citrobacter* species.

The strain-specific characters are also highly important in health-promoting bacteria: probiotic genera. Probiotic genera have a fermentative metabolism and most of them are defined as lactic acid bacteria (LAB). This descriptive group of Gram-positive bacteria includes a considerable number of genera of firmicutes which their metabolism is based on fermentation of carbohydrates into lactic acid [25]. LAB includes many species in Lactobacillaceae (*Alloiococcus*, *Lactobacillus*, *Paralactobacillus*, *Pediococcus*, *Sharpea*) and Leuconostocaceae (*Fructobacillus*, *Leuconostoc*, *Oenococcus*, *Weissella*); the two main families in Lactobacillales. However, genera of Streptococcaceae (*Lactococcus*, *Lactovum*, *Streptococcus*) and some *Bacillus* species (*B. coagulans*) have been also introduced as LAB. In place, *Bifidobacterium*, which is a well-known probiotic genus, belongs to Actinobacteria and is different from LAB in as its species produce lactic and acetic acids as byproducts of their saccharolytic metabolism [26]. Many strains of various species of the abovementioned metabolic groups of Gram-positive bacteria have probiotic properties, but *Lactobacillus* and *Bifidobacterium* are regarded as the most diverse probiotic genera [27–30]. Having functional probiotic properties is shown to be the result of a co-evolutionary relationship between these microbes and their hosts. Such association between bacteria and their multicellular eukaryotic hosts comprises a complex mutualistic relationship which formed through coevolution of both parts. Probiotic microbes as members of the gastrointestinal tract microbiome may have coevolved with their vertebrate hosts.

*Bifidobacterium* and *Lactobacillus* harbor many species that are also used for the fermentation of dairy and other food products at the industrial scale [27–30]. Further, like the other LAB genera,

various members of these genera are naturally associated with mucosal surfaces in gastro intestinal tract (GIT), the oral cavity and the vagina [31–33]. Besides, these beneficial microbes are widely reported as indigenous to food-related habitats: cereal grains, fruits, meat, milk, plants, vegetables and vinegar [34–36]. Even, many strains of *Bifidobacterium* and *Lactobacillus* can be found in the market as probiotic cosmetics, drug supplements or medical devices which their consumption results in health benefits [30,37–39].

The process of bacterial adaption to environmental variables has been deciphered in details [40,41]. The cellular adaptation to ecological niches is linked to diverse changes in the genomic scale, indicating that bacterial genomes reflect the environmental properties of their habitats [42]. But, there are some highly adaptable species of bacteria which can be found in varied environments with no common characteristics [43]. Further, the extent of genomic variation within a species is believed to contribute to the ecological and phenotypic potentials that the bacterial species require not only for survival, but also for exploitation of different ecological niches and in general responding properly to the environmental fluctuations [44,45]. It is interesting that the recent genomic data highlighted such an association between the functional complexity of microbial genomes and the ecological niches of these microscopic organisms [46,47].

Thank to recent genomic analyses, it is shown that a given microenvironment, habitat, or ecological niche can harbor bacterial species with a defined range of genome sizes. It shows that the evolutionary phenomena are in a close relation with the characteristic environmental factors of the microenvironment, habitat, or ecological niches. It is therefore postulated that the bacterial species with larger genomes are physiologically and ecologically more adaptable as their genomes encode for a larger metabolic and stress tolerance capacities [48,49]. Consequently, a larger genome size is expectable in habitat generalist bacterial species (saprobes and facultative pathogenic species). For example, recent studies highlighted a considerable intraspecies variation of *Escherichia coli* genomes, leading to the physiological and ecological adaptability of this well-known model species. On the other hand, bacterial species with smaller genomes mostly live in very specific and static environments. Hence, habitat specialist bacterial species (symbionts, obligatory parasites/pathogens, and other niche specialist species) do not need to respond many environmental stresses and they have very condensed genomes [50–53].

It is well documented that a large number of pseudogenes, accumulation of insertion sequence (IS) elements and lowered G + C content are all characteristics of reductive genome evolution, and may reflect passage through an evolutionary bottleneck [54,55]. Actually, such evolutionary events play a major role in the host-specificity and eco-physiological adaptation of pathogenic and either non-pathogenic microbial species [56–60]. It is shown that many opportunistic bacterial pathogens have undergone through an extensive genome decay process, which can be attributed to a lack of selection pressure during evolutionary conversion from free-living to a host-associated lifestyle [61]. Such an association between genome minimization and ecological distribution (host-specificity and ecophysiology) has been previously highlighted in significant human pathogens including *Mycobacterium leprae* [54,62], *Buchnera* spp. APS [63,64], and *Shigella* spp. [61].

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