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Chapter

Thriving at Low pH: Adaptation Mechanisms of Acidophiles

Xianke Chen

Abstract

Acid resistance of acidophiles is the result of long-term co-evolution and natural selection of acidophiles and their natural habitats, and formed a relatively optimal acid-resistance network in acidophiles. The acid tolerance network of acidophiles could be classified into active and passive mechanisms. The active mechanisms mainly include the proton efflux and consumption systems, generation of reversed transmembrane electrical potential, and adjustment of cell membrane composition; the passive mechanisms mainly include the DNA and protein repair systems, chemotaxis and cell motility, and quorum sensing system. The maintenance of pH homeostasis is a cell-wide physiological process that adopt differently adjustment strategies, deployment modules, and integration network depending on the cell's own potential and its habitat environments. However, acidophiles exhibit obvious strategies and modules similarities on acid resistance because of the long-term evolution. Therefore, a comprehensive understanding of acid tolerance network of acidophiles would be helpful for the intelligent manufacturing and industrial application of acidophiles.

Keywords: acidophiles, acid-resistance, pH homeostasis, adaptation, evolution

1. Introduction

Both natural and man-made acidic habitats are widely distributed in global land and ocean ecosystems, such as acidic sulfur-rich thermal springs, marine volcanic vents, and acid mine drainage (AMD) [1]. However, these unique habitats harbor the active acidophilic organisms that are well adapted to the acidic environments. Undoubtedly, acidophiles are distributed randomly throughout the tree of life and prevalent in the acidity or extreme acidity habitats, archaea and bacteria in particular, and they represent an extreme life-forms [2–4]. Generally, acidophilic archaea and bacteria mainly include members of phylum *Euryarchaeota*, *Crenarchaeota*, *Proteobacteria*, *Acidobacteria*, *Nitrospira*, *Firmicutes*, *Actinobacteria* and *Aquificae* such as *Ferroplasma*, *Acidiplasma*, *Sulfolobus*, *Acidianus*, *Acidiphilum*, *Acidithiobacillus*, *Acidihalobacter*, *Ferrovum*, *Acidiferrobacter*, *Acidobacterium*, *Leptospirillum*, *Sulfobacillus*, *Acidibacillus*, *Acidimicrobium*, and *Hydrogenobaculum* [5–7]. More importantly, acidophiles, as an important taxa of microorganisms, are closely related to the biogeochemistry cycles, eco-environment and human development, such as driving the elemental sulfur and iron cycles [8], the water and soil polluted by acidic effluents [9], biomining-bioleaching techniques and bioremediation technologies [9–11]. Thus, a comprehensive understanding of the acid-resistance networks and modules of acidophiles would be helpful for the

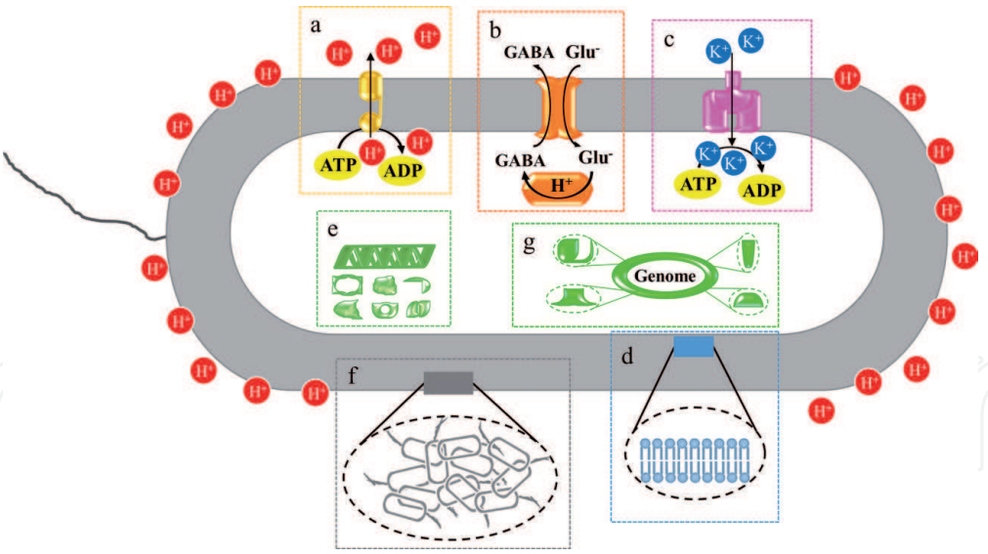


Figure 1.
The active and passive acid-resistance mechanisms in acidophiles. (a) Proton pump: F_1F_o–ATPase complex pump protons out of the cells though ATP hydrolysis. (b) Proton consumption modules: GadB-GadC system can consume excess intracellular protons. (c) Reversed transmembrane electrical potential (Δψ) modules: Generating a reversed Δψ is by positive ions transport (e.g. K^+ transport). (d) Membranes system: The highly impermeable cell membranes structure. (e) Macromolecules protection modules: A larger proportion of DNA and protein repair systems such as Dps, GrpE, MolR, and DnaK proteins. (f) Escaping system: QS system, biofilm, chemotaxis and cell motility modules. (g) Other modules: Some possible mechanisms of imperfect classification, including iron "rivet", degradation proteins of organic acids, surface proteins of high pI values, and outer membrane porin.

understanding of the evolutionary processes, ecological behaviors and industry applications of acidophiles.

Acidophiles thrive at an extremely low pH and maintain a relatively neutral cytoplasm pH [12], namely maintenance several orders of magnitude difference in proton concentrations in cell; thus, one of the main challenges to these microorganisms living in acidic habitats is the extremely acidic stress environments. Acidophiles have evolved a large number of mechanisms to withstand the deleterious effects of fluctuations in proton concentration (**Figure 1**), due to the fact that acidophiles face the challenge of maintaining a near neutral intracellular pH. Currently, the mechanisms of growth and acid tolerance of typical extreme acidophiles in extremely low pH environments have been widely studied [13–15]. Herein, we, specifically focusing on acid-tolerant mechanisms, strategies, functions, and modules instead of species types, reviewed and summarized the current knowledge of the acid-resistance networks adopted by acidophiles for coping with acid or extreme acid environments. In addition, owing to space constraints and complexity of acidophiles types, we limit our discussion of the acid-tolerant adaptation mechanisms to typical acidophiles (archaea and bacteria) that populate acidic habitats.

2. Acid-resistant mechanisms of acidophiles

2.1 Active support of acidophiles pH homeostasis

Microorganisms tend to maintain a high proton motive force (PMF) and a near-neutral pH in cytoplasm. The transmembrane electrical potential (Δψ) and transmembrane pH gradient (ΔpH) could vary as a function of the external pH. The immediately available energy source for acidophilic cell is this pre-existing transmembrane proton gradient, due to the external environments are frequently in the pH range of 1.0–3.0, while the typical pH of cytoplasms are close to 6.5

(that is, the differential proton concentrations of 4–6 orders of magnitude). The ΔpH across the membrane is a major part of the PMF, and the ΔpH is linked to cellular bioenergetics. Acidophiles, such as *Acidithiobacillus ferrooxidans* and *Acidithiobacillus caldus*, are capable of using the ΔpH to generate a large quantity of ATP [16, 17]. However, this processes would lead to the rapid acidification of the cytoplasm of alive cells. Because a high level of protons concentration would destroy essential molecules in cell, such as DNA and protein, acidophiles have evolved the capability to pump protons out of their cells at a relatively high rate. The F_1F_o–ATPase consists of a hydrophilic part (F_1) composed of α, β, γ, δ, and ε subunits and a hydrophobic membrane channel (F_o) composed of a, b, and c subunits; among them, the F_1 catalyzes ATP hydrolysis or synthesis and the F_o translocates protons. This mechanism pumps out protons from cells by hydrolyzing ATP (**Figure 1**), thereby efficiently protecting cells from the acidic environments. In several microorganisms, transcriptional level of the *atp* operon upregulated by exposure to the acidic environments, including *A. caldus, Acidithiobacillus thiooxidans*, and *Lactobacillus acidophilus* [18–20], suggesting its critical role in acid resistance of cell. Several proton efflux proteins have also been identified in the sequenced genomes of *A. ferrooxidans*, *A. thiooxidans*, *A. caldus*, *Ferroplasma acidarmanus*, and *Leptospirillum* group II [21, 22]. The H^+-ATPase activity and NAD^+/NADH ratio were upregulated in *A. thiooxidans* under the acid stress [19]. The cells actively pump out protons by a respiratory chain from cell. For example, under the acid stress, the *A. caldus* increases its expression of respiratory chain complexes that can pump protons out of the cells [20]. Meanwhile, NAD^+ involved in glycolysis as the coenzyme of dehydrogenase, generating large amount of ATP and contributing to pump protons out of the cells though ATP hydrolysis.

Among the active mechanisms, the proton consumption systems are necessary to remove excess intracellular protons. Once protons enter the cytoplasm, some mechanisms and patterns are required to mitigate effects caused by a high concentration of proton in cells. Under the acidic conditions, there is increased expression of amino acid decarboxylases enzymes (such as Glutamate decarboxylase-β (GadB)) that could consume the cytoplasmic protons by the catalytic reactions [23]. GadB, coupling with a glutamate/gamma-aminobutyrate antiporter (GadC), catalyzed glutamate to γ-aminobutyric acid (GABA) and exchanged with glutamate substrate to achieve continued decarboxylation reactions (**Figure 1**) [24]. It consumed a proton during the decarboxylation reactions and thus supported the intracellular pH homeostasis. And, it would contribute to a reversed Δψ in most bacteria. Similarly, the *gadB* gene was found in *Ferroplasma* spp., and the gene transcription was upregulated under acid shock conditions in *A. caldus* [20, 22]. Therefore, in order to maintain pH homeostasis of cell, acidophiles need to be able to consume excess protons from the cytoplasm.

A second major strategy for the active mechanisms used by acidophiles to reduce the influx of protons is the generation of an inside positive Δψ that generated by a Donnan potential of positively charged ions. A positive inside transmembrane potential was contributed to a reversed Δψ that could prevent protons leakage into the cells. The acidophiles might use the same strategies to generate a reversed membrane potential to resist the inward flow of protons, Na^+/K^+ transporters in particular (**Figure 1**) [25]. Previous data showed that some genomes of acidophiles (*A. thiooxidans*, *F. acidarmanus*, *Sulfolobus solfataricus*, etc.) contain a high number of cation transporters genes and these transporters were probably involved in the generation of Donnan potential to inhibit the protons influx [21, 22, 25, 26]. The genome of *Picrophilus torridus* also encodes large number of proton-driven secondary transporters which represents adaptation to the more extremely acidic environment [27]. Furthermore, we found that the maintenance of Δψ in *A. thiooxidans*

was directly related to the uptake of cations, especially the influx of potassium ions [25]. Further evidence of chemiosmotic gradient created by a Donnan potential to support acid resistance is the Donnan potential created by a passive mechanism, that is, a small residual inside positive Δψ and ΔpH are maintained in inactive cells of *A. caldus*, *A. ferrooxidans*, *Acidiphilium acidophilum*, and *Thermoplasma acidophilum* [28–30]. The residual Δψ and ΔpH studies have been criticized because of measurement methods [31]. However, subsequent data showed that the energy-dependent cation pumps played an important role in generating an inside positive Δψ. In addition, acidophilic bacteria are highly tolerant to cations and are more sensitive to anions. In summary, the inside positive Δψ is a ubiquitous and significant strategy in maintaining the cellular pH homeostasis.

Although improving the efflux and consumption of protons and increasing the expression of secondary transporters are a common strategy, the most effective strategy is also to reduce the proton permeability of cell membrane [32, 33]. Acidophiles can synthesize a highly impermeable membrane to respond to proton attack (**Figure 1**). These physiological adaptations membranes are composed of the high levels of iso/anteiso-BCFAs (branched chain fatty acids), both saturated and mono-unsaturated fatty acids, β-hydroxy, ω-cyclohexyl and cyclopropane fatty acids (CFAs) [34]. It was found that cell membrane resisted the acid stress by increasing the proportion of unsaturated fatty acid and CFAs in some bacteria, such as *A. ferrooxidans* and *Escherichia coli* [35–37]. Although the cytoplasmic membrane is the main barrier to protons influx, the destruction of the membrane caused by protons may cause this barrier to break down. The key component of membranes preventing acid damage seems to be CFAs, which contributes to the formation of cell membrane compactness. Supporting this mechanism is that *E. coli* with a mutation in the *cfa* gene became quite sensitive to low pH and can overcome this sensitivity by providing the exogenous *cfa* gene [36]. Meanwhile, the transcription of *cfa* gene was upregulated under the acid stress in *A. caldus* [20], and it suggests that changing the fatty acid content of the cell membrane is an adaptive response to acid stress. In brief, the CFAs is important for maintaining membrane integrity and compactness under the acid conditions.

To maintain the pH homeostasis of cells, acidophilic archaea cells have a highly impermeable cell membrane to restrict proton influx into the cytoplasm. One of the key characteristics of acidophilic archaea is the monolayer membrane typically composed of large amount of GDGTs, which are extremely impermeable to protons [38–40]. Although acidophilic bacteria have a variety of acid-resistant adaptation strategies, compared with acidophilic archaea, it has not been found that these bacteria would exhibit excellent growth ability below pH 1. The special tetraether lipid is closely related to acid-tolerance capability, because the ether linkages are less sensitive to acid hydrolysis than ester linkages [41]. And, the results of studies on acidophilic archaea indicated that tetraether lipids may be more resistant to acid than previously thought [42]. Therefore, the contribution of tetraether lipids to adaptation of archaea to extremely low pH is enormous. To a certain extent, it also supports the reason why dominance of archaea under extremely acidic environments. Similarly, the extreme acid tolerance of archaea can be attributed to cyclopentane rings and the vast methyl-branches [43]. In addition, it was found that the less phosphorus in the lipoprotein layer of acidophilus cell can contribute to higher hydrophobicity, which was beneficial for resisting extreme acid shock [13]. Irrespective of the basic composition of cell membranes, bacteria and archaea have extensively reshaped their membrane components to overcome the extremely low acid environments. In summary, the impermeable of acidophilic cell membrane is an important strategy for the pH homeostasis of acidophiles formed by restricting the influx of protons into the cells.

3. Passive strategies for acidophiles living

When the cells are attacked or stressed by higher concentrations of protons, the passive mechanisms of pH homeostasis would support the active mechanism. If protons penetrate the acidophilic cell membrane, a range of intracellular repair systems would help to repair the damage of macromolecules [13]. The DNA and protein repair systems play a central role in coping with acid stress of cells (**Figure 1**). Because DNA carries genetic information of cell life and protein plays an important role in the physiological activities of cells, DNA or protein damage caused by protons would bring irreversible harm to cells. When the cells are exposed to a high concentration of proton environments or protons influx into the cells, a great number of DNA repair proteins and chaperones (such as Dps, GrpE, MolR, and DnaK protein) would repair the damaged DNA and protein [19, 44, 45]. Previously reported study showed that a great number of DNA and protein repaired genes presence in wide range of extreme acidophiles genomes might be related to the acid resistance, for example, a large number of the DNA repaired proteins genes in *P. torridus* genome [27, 46]. Indeed, the transcription and expression of these repair systems were upregulated under the extreme acid stress, for example, the transcription of molecular chaperones repair system-molR and DnaK were enhanced in *A. thiooxidans* [19]. In addition, the GrpE and DnaK proteins expression were significantly improved in *Acetobacter pasteurianus* for coping with acetic acid stress [47]. Similarly, the molecular chaperones involved in protein refolding were largely expressed in *L. ferriphilum* under the AMD biofilm communities [48]. And, the chaperones were also highly expressed in *F. acidarmanus* during aerobic culture [49].

Quorum sensing (QS) system is a ubiquitous phenomenon that establishes the cell to cell communication in a population through the production, secretion and detection of signal molecules. In addition, The QS system is also widely involved in various physiological processes in cell such as biofilm formation, exopolysaccharides, motility, and bacterial virulence [50–52]. Moreover, the QS system can contribute to bacteria tolerating extreme environmental conditions by regulated biofilm formation. For example, bacteria showed the strong resistance to extremely low pH, due to these bacteria grown in a biofilm environment [53]. In case of acidophiles, QS system has been reported in *A. ferrooxidans* by producing the stable acylated homoserine lactones (AHLs) signal molecules under acidic conditions and overexpression strains promoted cell growth by regulated genes expression [54, 55].

Flagella is an important cell structure for the motility and chemotaxis in most bacteria, and is also involved in the biofilm formation [56]. Flagella-mediated chemotaxis is essential for cells to respond to environmental stimuli (pH, temperature, osmotic pressure, etc.) and find nutrients for growth. The chemotaxis and motility of cells is a complex physiological behavior regulated by the diverse transcription factors, such as RpoF (σ^{28} or FliA) of the σ factors and ferric uptake regulator (Fur) of the global regulator, and has strictly spatiotemporal characteristics [20, 56]. For example, the mutant strain of *A. caldus fur* gene significantly upregulated some genes (*cheY*, *cheV*, *flhF*, *flhA*, *fliP*, *fliG*, etc.) related to cell chemotaxis and motility under the acid shock conditions [20]. Similarly, *F. acidarmanus* was capable of motility and biofilm formation [57]. This indicates that although the chemotaxis and cell motility ability of acidophiles cannot directly involve in acid resistance and maintain cell pH homeostasis, they have the ability to avoid extremely unfavorable acid environments to improve cells survival. Altogether, we suggest that the QS system and chemotaxis and cell motility are essential part of escaping the extremely acidic environments in passive mechanisms (**Figure 1**).

It could be seen from the classification description above that there are a variety of mechanisms and strategies by which acidophiles can tolerate or resist the acidic or extremely acidic environments. However, some possible mechanisms have been imperfectly understood or classified, for example, the distinctive structural and functional characteristics of extremely acidophilic microorganisms (**Figure 1**) [13, 15]. First, iron may act as a "rivet" at low pH, which plays an important role in maintaining proteins activity, for example, the high proportion of iron proteins in *F. acidiphilum*. And, it has been found that the removal of iron from proteins can result in the loss of proteins activity [58, 59]. Secondly, the strategy of cell surface charges. The surface proteins of acidophiles have a high pI values (a positive surface charges), which can act as a transient proton repellent on the cell surface. For example, the isoelectric point (pI) of the OmpA-like protein in the outer membrane of the *A. ferrooxidans* is 9.4, whereas that of *E. coli* OmpA is 6.2 [60]. It may be the functional requirements that the possession of positive surface charges could reduce the permeability of *A. ferrooxidans* cells to protons. Then, adjustment of pore size of membrane channels is also used to minimize inward proton leakage under acid stress. For example, under the acid shock, the expression of outer membrane porin (Omp40) of *A. ferrooxidans* was upregulated [61], which could control the size and ion selectivity of the entrance to the pore. Ultimately, since organic acids could diffuse into the cells in the form of protonation at low pH environments and then the proton dissociation quickly acidify the cytoplasm, the degradation of organic acids might be a potential mechanism for maintaining pH homeostasis, especially heterotrophic acidophiles. Although the genes that degrade organic acids in some acidophile (such as *F. acidarmanus, P. torridus*) have been identified, it is unclear whether the degradation of organic acids would contribute pH homeostasis [27, 62]. In summary, these possible mechanisms remain to be confirmed but these genes of existence and identification could be a mechanism associated with low pH tolerance.

4. Evolution of low pH fitness of acidophiles

In the past few decades, studies have confirmed that acidophilic microorganisms are widely present in the three domains of bacteria, archaea and eukarya, indicating that acidophiles have gradually developed in the evolution of life on earth, rather than from a single adaptation events. Although the extremely acidic environments are toxic to most organisms, there are still large number of indigenous microorganisms that can thrive in these habitats. The generally accepted view is that acidophiles can be divided into moderate acidophiles that have pH optima of between 3 and 5, extreme acidophiles that have pH optima for growth at pH < 3, and hyperacidophiles that have pH optima for growth below pH 1 [1]. Generally, with the acidity becomes more extreme, biodiversity also gradually decreases. Accordingly, as would be anticipated, the most extremely acidic environments hold the less biodiversity, for example, hyperacidophiles includes the relatively few species (e.g. *F. acidarmanus* and *Picrophilus oshimae*) [1]. Acidophiles can survive in the acidic or extremely environments and are the source of acidity environment [1, 63, 64]; thus, they have the ability to resist the acidic environments that evolved during evolution.

Acidic hydrothermal ecosystems, such as Tengchong hot springs, Crater Lake, and Yellowstone National Park, are dominated by archaea [40, 65], and suggesting that the acidophilic archaea evolved in the extremely acidic hydrothermal environments after the emergence of oxygenic photosynthesis [66]. Based on the niche similarity and physiological adaptation among archaea, it showed that the long-term acidity stress is the main selection pressure to control the evolution of archaea and leads to the co-evolution of acid-resistant modules [66]. Although the

species diversity decreases significantly as the pH decreases, the high abundance of acidophilic taxa, such as *Gammaproteobacteria* and *Nitrospira*, was detected in acid habitats. Indeed, for the dominant lineages such as *Acidithiobacillus* spp. and *Leptospirillum* spp., this pH-specific niche partitioning was obvious [67]. Consistent with this, *Ferrovum* is more acid-sensitive than *A. ferrooxidans* and *L. ferrooxidans*, and prefers to grow under the near-moderate pH [68]. Interestingly, the majority of acidophiles growing at extremely acidic (i.e. pH < 1) are heterotrophic acidophiles that are capable of utilizing organic matter for growth such as *T. acidophilum* and *P. torridus*. In addition, although the *Acidiplasma* spp. and *Ferroplasma* spp. can oxidize ferrous iron in biomining, organic carbon can also be used for growth, and their relative abundance would increase with the mortality of other bioleaching microorganisms [69, 70]. Therefore, they can be regarded as scavengers of the dead microorganisms and help the material and energy cycle in acidic habitats. To sum up, coexisting species may occupy different niches that could be affected by the pH changes, resulting in the changes in their distribution patterns.

The reasons for the dominance of these particular microorganisms in acidic ecosystems are presumed to their adaptive capabilities. Adaptations to acid stress dictate the ecology and evolution of the acidophiles. Acidic ecosystems are a unique ecological niche for acid-adapted microorganisms. These relatively low-complexity ecosystems offer a special opportunity for the evolutionary processes and ecological behaviors analyses of acidophilic microorganisms. In the last decade, the use of high-throughput sequencing technology and post-genomic methods have significantly promoted our understanding of microbial diversity and evolution in acidic environments [68]. At present, metagenomics studies have revealed various acidophilic microorganisms from environments such as the AMD and acidic geothermal areas, and found that these microorganisms play an important role in acid generation and adaptability to the environments [71, 72]. For example, because the comparative metagenomics and metatranscriptomics directly recover and reveal microbial genome information from the environments, it has the potential to provide insights into acid-resistance mechanisms of the uncultivated bacteria, such as *clpX*, *clpP*, and *sqhC* genes for resistance against acid stress. In addition, metatranscriptomics and metaproteomics analyses further uncovered the major metabolic and adaptive capabilities in situ [71], indicating the mechanisms of response and adaptation to the extremely acid environments.

The continuous exploration of acidic habitats and acidophilic microorganisms is the basis for comprehending the evolution of acidophilic microbial acid-tolerant modules, strategies, and networks. First, methods based on transcriptomics and proteomics are the key to understanding the global acid-tolerant network of individuals under acid stress [19, 73]. Secondly, comparative genomics plays a vital role in exploring the acid adaptation mechanism of acidophiles and studying the evolution of acidophiles genomes [74]. Ultimately, the emerging metagenomics technologies play an important role in evaluating and predicting microbial communities and their adaptability to acidic environments [75]. Moreover, metagenomics approaches could also provide a large amount of knowledge and functional module analysis on the acid tolerance of acidophiles to fully develop their potential in the evolution of acid tolerance [76]. With the publication of large number of metagenomics data, the evolution of the acid-tolerant components of these extremophiles would be better illustrated in the future.

5. Conclusions

Understanding the maintenance of pH homeostasis in acidophiles is of great significance to comprehend the mechanisms of cells growth and survival, as well as

to the eco-remediation and application of biotechnology; thus, it is essential to fully understand the acid-tolerant networks and strategies of acidophilic microorganisms. The aims of this chapter presents the acid-resistant modules and strategies of acidophiles in more detail, including the proton efflux and consumption, reversed membrane potential, impermeable cell membrane, DNA and protein repair systems, and QS system (**Figure 1**). However, at present, several of the pH homeostatic mechanisms still lack clear and rigorous experimental evidence to support their functions from my point of view. In addition, we also discussed the evolution of acidophiles and its acid-resistant modules. In brief, the true purpose of acidophilic microorganisms evolving these mechanisms is to tolerate the extremely acidic environments or reduce its harmful effects for cell survival.

Acidophiles are known for their remarkable acid resistance. Over the last decades, the combination of molecular and biochemical analysis of acidophiles with genome, transcriptome, and proteome have provided new insights into the acid-resistant mechanisms and evolution of the individual acidophiles at present. Using these genome sequences in a functional context through the application of high throughput transcriptomic and proteomic tools to scrutinize acid stress might elucidate further potential pH homeostasis mechanisms. However, the disadvantages of genomics, transcriptomics, and proteomics are that the data are descriptive and analogous and more work is required to verify the hypotheses such as the mutational analyses and genetic markers. One of the main obstacles to the current research on acid tolerance of acidophiles is the lack of genetic tools for in-depth analysis. Therefore, the development of genetic tools and biochemical methods in acidophile would facilitate elucidating the molecular mechanisms of acidophile adapting to extremely acidic environments, such as vector development remain largely unexplored. In addition, as most acidophiles are difficult to isolate and culture, our ability to understand acid resistance of acidophile is limited. The emerging omics technologies would be a crucial step to explore the spatiotemporal transformation patterns of acidophilic microbial communities, microbial ecophysiology and evolution in the future.

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Conflict of interest

We declare no conflicts of interest.

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