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The definitive publisher version is available online at <https://doi.org/10.1016/j.scitotenv.2023.168210>

1 Biomining for sustainable recovery of rare earth elements from mining waste: a
2 comprehensive review

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16

17 **Abstract**

18 Rare earth elements (REEs) are essential for advanced manufacturing (e.g., renewable energy,
19 military equipment, electric vehicles); hence, the recovery of REEs from low-grade resources has
20 become increasingly important to address their growing demand. Depending on specific mining
21 sites, its geological conditions, and sociodemographic backgrounds, mining waste has been
22 identified as a source of REEs in various concentrations and abundance. Yttrium, cerium, and
23 neodymium are the most common REEs in mining waste streams (50 to 300 µg/L). Biomining has

24 emerged as a viable option for REEs recovery due to its reduced environmental impact, along with
25 reduced capital investment compared to traditional recovery methods. This paper aims to review
26 (i) the characteristics of mining waste as a low-grade REEs resource, (ii) the key operating
27 principles of biomining technologies for REEs recovery, (iii) the effects of operating conditions
28 and matrix on REEs recovery, and (iv) the sustainability of REEs recovery through biomining
29 technologies. Six types of biomining will be examined in this review: bioleaching, bioweathering,
30 biosorption, bioaccumulation, bioprecipitation and bioflotation. Based on a SWOT analyses and
31 techno-economic assessments (TEA), biomining technologies have been found to be effective and
32 efficient in recovering REEs from low-grade sources. Through TEA, coal ash has been shown to
33 return the highest profit amongst mining waste streams.

34 **Keywords**

35 Biomining, Rare earth elements, Bioleaching, Biosorption, Bioaccumulation.

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37

38 **1. Introduction**

39 Rare earth elements (REEs) are a group of 17 metallic elements, including scandium (Sc) and
40 yttrium (Y), in addition to 15 lanthanides. REEs have unique chemical and physical properties
41 useful for electrical, optical, and magnetic applications. Hence, REEs are essential for advanced
42 manufacturing (e.g., renewable energy industries and electronic equipment manufacture) in
43 forming products with unique properties (e.g., catalytic, metallurgical, electrical, magnetic, and
44 luminescence). Given their essential role in modern industry, REEs have exceptionally high
45 commercial value, with recent valuation estimates of \$2 billion USD in 2020 ([Department of](#)
46 [Industry, 2021](#)). In 2017, the global production of REEs was 130,000 tons, of which China

47 accounted for 80%, with an expected increase in worldwide demand for REEs of up to 210,000
48 tons by 2025 (Mwewa et al., 2022). Most REEs are dispersed in the Earth's crust at low
49 concentrations, so they are unsuitable for extraction using conventional mineral processing
50 techniques (Stormcrow, 2020). Further, the security of REE supply chains is under significant
51 threat due to uneven geographical distribution, uncertainty in global geopolitics, challenges in the
52 purification of REEs at industrial scale (Mwewa et al., 2022; Xie et al., 2014).

53 Given the uncertainty of future availability of REEs, there is increasing interest in REEs extraction
54 from low-grade resources to meet the projected demand. Due to economic and technical
55 constraints, this strategy is preferable to finding a replacement element for REEs or new REE
56 deposits. Mining wastes such as gypsum, red mud, and acid mine drainage are typically low-grade
57 resources for REEs; fortunately, the concentrations of REEs in mining wastewater are
58 approximately 10,000 times higher than in natural waters such as lakes and rivers (Cao et al.,
59 2021). In Australia, there are over 52,000 abandoned mines (Unger et al., 2012), providing a
60 scalable opportunity for commercial production of REEs, while simultaneously allowing for
61 environmental remediation. Similarly, red mud, a by-product of the aluminum extraction process,
62 contains up to 500 mg/kg of cerium (Ce). However, only 2% of the 150 million tons of red mud
63 produced per year is reused (Čížková et al., 2019). Therefore, the current mining residue/waste
64 recycling rate is still very modest compared to its vast potential.

65 Existing methods for REEs recovery such as hydro-, thermal- and electro-metallurgical
66 technologies, are associated with substantial secondary pollutants (e.g., thorium (Th), uranium
67 (U)), as well as being chemically and energy-intensive (Čížková et al., 2019). Biomining provides
68 a potential solution that mitigates these issues as biomining exploits a microorganisms'
69 biogeochemical processes to recover REEs. Significant progress in biomining of heavy metals has
70 been reported with relevance to a wide range of microorganisms such as: bacteria, microalgae,

71 macroalgae, fungi and higher plants. However, there is still no systematic review regarding the
72 progress in biomining research, and understanding of biomining technologies for REEs recovery
73 (Abashina & Vainshtein, 2023; Liapun & Motola, 2023). Apart from systematic improvements in
74 biomining technologies, the influence of operating conditions on REEs recovery efficiency is also
75 needed. In addition, it is essential to perform an in-detail analysis of treatment technologies for
76 their strength, weakness, opportunity, and threat (SWOT); and a techno-economic analysis to
77 establish a baseline for universal usage.

78 This paper aims to review (i) the characteristics of mining waste as a low-grade REEs resources,
79 (ii) the fundamental working principle of biomining technologies for REEs recovery, (iii) the
80 effects of operating conditions and matrix on REEs recovery, and (iv) sustainable approaches for
81 REEs recovery from low-grade resources.

82 **2. Low-grade REEs resources from mining wastes**

83 Mining waste is a matrix of solids, minerals and REEs, and can be classified into two categories:
84 (i) the processing side streams, such as red mud slurry; and (ii) the extraction side streams, such
85 as acid mine drainage (AMD). Due to the presence of REEs, mining waste has been attracting
86 attention in recent years for its potential as a source of low-grade REEs (Table 1). Importantly, the
87 abundance and concentration of REEs is dependent on the characteristics of the mining waste,
88 such as; the specific mining site where the mining waste was sourced, geological conditions of the
89 site, and sampling locations (such as internal mine drains, site-level wastewater, open pits, and
90 drainage of waste rock tails or piles).

91 In addition, the composition and abundance of the ore deposit and the relevant processing
92 technologies play a critical role in forming the characteristics of mining waste. For example, the
93 concentration of total REEs ($\sum\text{REE}$) in AMD of closed uranium mines, was significantly higher

94 than other mining wastewater. This high REEs concentration stems from accumulation over long
95 time spans (Felipe et al., 2021). The variation of REEs in mining waste is also subject to
96 geochemical and sociodemographic conditions. The highest concentration of REEs in coal mine
97 waste streams was mostly Y; while Ce was the most dominant in mineral ores (e.g., Au, Zn, Pb)
98 (Table 1). A comprehensive assessment of the literature indicates that light and medium weight
99 REEs are predominantly present in mining waste (Myagkaya et al., 2016; Prudêncio et al., 2015;
100 Shahhosseini et al., 2017; Vass et al., 2019)

101 Other chemistry factors in mining waste such as pH and ligands, also impact the presence of REEs
102 (Gammons et al., 2003; Olías et al., 2018). Ligand complexes in mining waste can be classified
103 into four predominant classes: REEs-sulfate complexes, free metal species, REEs-carbonate
104 complexes, and inorganic complexes. Studies have reported that stable REE-SO₄⁺ and REE-SO₄⁻²
105 complexes are the dominant species in acidic conditions with pH < 5 (Migaszewski et al., 2019;
106 Xia et al., 2023), followed by REEs complexes with free metal species (Royer-Lavallée et al.,
107 2020). The reason for the substantial presence of these ligand complexes in mining waste is low
108 pH (< 3), along with the atomic number of associated REEs, as REEs presence decreases with
109 increasing atomic number (Zhao et al., 2007).

110 In addition, the sulfate and acid levels in mining waste affects REEs concentration (Mwewa et al.,
111 2022). A good example is the difference in the distribution of REEs in the above and below ground
112 drainage of mining waste streams (Vass et al., 2019). Lower pH can be observed in the above-
113 ground drainage of mining waste streams, resulting in higher REEs concentrations (Agboola et al.,
114 2020). This is caused by higher concentrations of sulfate, whereby formation of their stable
115 complexes inhibit the precipitation of REEs (Royer-Lavallée et al., 2020). In contrast, the below
116 ground drainage of mining waste streams is alkaline due to limited pyrite oxidation in aqueous
117 conditions and the accumulation of bicarbonate buffer. When pH increases (pH > 5), carbonate

118 complexes are formed which leads to a depletion of REEs, especially light REEs, due to their re-
119 adsorption into metal oxides and hydroxide colloids, and subsequent precipitation ([Mwewa et al.,](#)
120 [2022](#)).

Table 1. REEs occurrence in mining waste from various sources

Mine type	Country	Waste	pH	Σ REE											Ref.
				Y	La	Ce	Pr	Nd	Eu	Gd	Tb	Dy	Sc		
Coal mine	China, Iran, North America, United States, Indonesia, China, India	AMD	2 - 6	1 - 714	0.2 - 72	0.15 - 91	0.23 - 284	0.04 - 38	0.15 - 135	0.01 - 18.2	0.06 - 79.2	0.01 - 15.8	0.05 - 57.4	3.2 - 46	[1], [2], [3], [4], [5], [6], [7]
	Gold deposit		Russia	AMD	1.9	1239	-	190	470	61	260	17	55	8	47
Closed uranium mine	Brazil	AMW	3.4	120208	5600	49865	38953	4368	16294	158	1509	270	796	49	[9]
Wisniowka mining area*	Poland	AMD-Pools	1.4 - 2.2	17916.5	-	1907	5272	731	3413	335	1752	267	1416	-	[10]

Inactive Zn–Pb mine	Cuba	AMD**	2.5 - 2.6	370 - 860	-	36.7	121.3	18.7	104	15.3	49.7	8.4	43		[11]
Red mud disposal facility	Slovakia	Red mud	-	1320	230	-	690	-	-	-	290	-	-	110	[12]
Mining complex	Portugal	Pit lake, AMD	2 – 4	351 - 888	221.8	47 - 86	13 - 167	11 – 24.1	80 – 125.6	3 – 10.9	20 - 60	3.8 – 9.5	16.6 - 44	64.6	[13], [14]

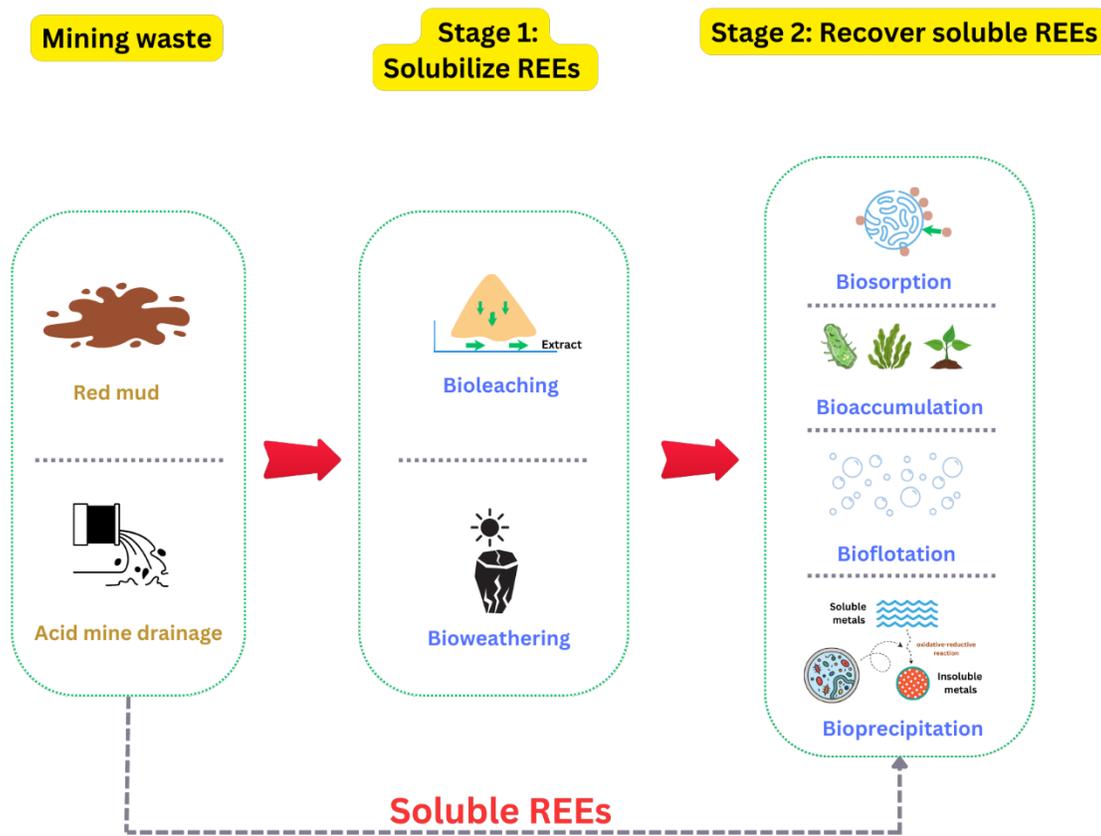
*Quartzite quarries, acid water bodies and tailings piles

**Mine-waste dumps and in the open pit produces acid mine effluents

References: [1]: Zhao et al. (2007), [2] Shahhosseini et al. (2017), [3] Vass et al. (2019), [4] (Stewart et al., 2017), [5]] Meriestica et al. (2021), [6] Li and Wu (2017), [7] Sahoo et al. (2012), [8] Myagkaya et al. (2016), [9] Felipe et al. (2021), [10] Migaszewski et al. (2019), [11] Romero et al. (2010), [12] Salman et al. (2021), [13] Gomes et al. (2022), [14] Ferreira da Silva et al. (2009)

127 **3. Key principles of biomining technologies for REEs recovery**

128 Biomining technologies for REEs recovery include; bioleaching, bioweathering, biosorption,
129 bioaccumulation, bioprecipitation, and bioflotation. Each of these technologies are applicable for
130 specific mining waste, and at specific stages of the recovery processes (Fig. 1). Bioleaching and
131 bioweathering are the first stages in which REEs in solids (e.g., red mud) are solubilized by the
132 lixiviant - acidic excretion - of microbes. The soluble REEs in lixiviant can be recovered in subsequent
133 stages via biosorption, bioaccumulation, bioprecipitation, and bioflotation, with additional help
134 from a range of organisms (e.g., bacteria, microalgae, macroalgae and plants). Regarding REEs
135 present in soluble form in mining wastewater, biosorption, bioaccumulation, bioprecipitation, and
136 bioflotation technologies can be used to recover REEs without an initial extraction stage.



137

138 **Fig. 1.** Process diagram of REEs recovery using various biomining technologies.

139 3.1 Bioleaching

140 Bioleaching is characterized by the mobilization of REEs from the solid to liquid phase. A solid
141 matrix (such as ore deposits) containing REEs is solubilized by microbial activity, which releases
142 REEs. (Fig. 2), followed by mobilization of REEs via three biochemical processes: redoxolysis,
143 acidolysis, and complexolysis. Redoxolysis is a two-step reaction consisting of either contact or
144 non-contact mechanisms. Contact redoxolysis involves an oxidative reaction of Fe^{2+} to Fe^{3+} under
145 aerobic conditions, which stems from the transfer of electrons from minerals to microorganisms.
146 Non-contact redoxolysis involves an oxidative dissolution of REEs, resulting in $\text{REE}^{+}_{(\text{aq})}$.
147 Acidolysis involves acid dissolution of REEs from minerals by sulfur-oxidizing or phosphate-
148 oxidizing bacteria. Where sulfur-oxidizing bacteria oxidize sulfide to produce sulfuric acid,
149 phosphate-oxidizing bacteria release phosphate. Complexolysis involves the solubilization of
150 REEs via microbial organic acids and siderophores. Microbial organic acids are released to
151 dissolve the REEs from solid minerals, while extracellular siderophores function as iron-carriers
152 to transport iron back into the cell from the environment, thereby forming stable complexes with
153 REEs, which allows for further release of REEs.

154 From an industrial viewpoint, bioleaching of REEs from ore deposits and e-waste needs to be
155 validated under pilot-plant conditions (Barnett et al., 2020; Brown et al., 2023). Bioleaching is an
156 effective industrial technique for extracting copper and gold ores, but it has not been widely
157 developed for REEs extraction. Different bioreactors, such as rotating drums, stirred tanks and
158 fluidized bed reactors. have been applied in bioleaching of metals (Adetunji et al., 2023; Roberto
159 & Schippers, 2022). In contrast, bioleaching of REEs is limited to laboratory-scale applications,
160 highlighting the need for further development work such as environmental impact assessments,
161 before the technology can be applied to an industrial scale (Tezyapar Kara et al., 2023). As the
162 process upscaling of bioleaching would be based on the identification of effective microorganisms

163 as well as optimum conditions of operation, an overview of microorganisms applied for
164 bioleaching is presented next.

165 There is a wide range of microorganisms that are suitable for bioleaching applications, including
166 (i) Fe-S oxidizers, (ii) heterotrophic bacteria, and (iii) cyanogenic bacteria (Brown et al., 2023)
167 (Table 2). Each microorganism group mentioned, has a unique biochemical function to solubilize
168 metallic substances, including iron/sulfur oxidation, organic acid extrusion, and cyanide based
169 lixiviant production. The literature shows that heterotrophic cultures are preferred for producing
170 acid for REEs solubilization, likely as they are more resilient to mining waste (Tayar et al., 2022).
171 This is demonstrated by reduced leaching efficacy of Fe-S oxidizing bacteria due to interference
172 from components in ore deposits compared to the leaching efficacy of heterotrophic
173 bacteria. *Acidithiobacillus ferrooxidans*, a typical Fe-S oxidizer, is only effective in clay-rich
174 bauxite sources (Barnett et al., 2020), whereas a culture of heterotrophs produces a range of
175 metabolites that can be more effective for REEs leaching than a sole organic acid (Antonick et al.,
176 2019). For example, *Aspergillus niger* and *Yarrowia lipolytica* produce citric acid, which leaches
177 90% of REEs. Oxalic acid produced by *A. niger* is also beneficial for REEs recovery by forming
178 soluble Ce in concentrations greater than 1.37 mg/L (Bahaloo-Horeh & Mousavi, 2022).

179 Several carbon sources have been used as a nutrient source for heterotrophic microbes to enhance
180 the production of organic acid. With glucose as a carbon source, *A. niger* was found to reach its
181 highest leaching efficiency of 91%, whereas when sucrose was used, *A. niger* and *Y lipolytica*
182 reached a leaching efficiency of 66%, and 34% respectively (Shen et al., 2023). The organic acids
183 excreted by *A. niger* is comprised of oxalic, citric, and succinic acid and a trace amount of malic
184 acid. *Y. lipolytica* excretes a lixiviant with a more straightforward matrix, comprising of citric,
185 malic, and succinic acid. Therefore, the composition of other lixiviants needs to be further

186 investigated, given the bioleaching efficiency of heterotrophic microbe derived lixivants are very
187 promising (Park & Liang, 2019).

188 The operation of bioleaching is executed in two ways: (i) contact/direct reaction in which microbes
189 and ore deposits directly interact, and (ii) noncontact/indirect reaction in which the lixiviant of
190 microbes is extracted and applied for bioleaching. Application of *in-situ* direct contact bioleaching
191 is limited due to difficulty in site access, compromising system setups, and proper operation and
192 maintenance requirements. Alternatively, indirect bioleaching can be applied offsite and under
193 more controlled environments. Interestingly, indirect bioleaching of REEs showed a higher REE
194 leaching efficiency (98% Nd, 60% Ce, and 58% La) compared to direct bioleaching (28% Nd,
195 17% Ce, and 18% La) (Tayar et al., 2022).

196 Compared to traditional extraction and purification methods, bioleaching's performance still lags
197 behind thermochemical processes. Recent efforts to improve the extraction efficiency of
198 bioleaching have included genetic engineering of acid-producing microbes such as *Gluconobacter*
199 *oxydans* (Schmitz et al., 2021). Genome knockout experiments were conducted on wild-type *G.*
200 *oxydans* to identify genes responsible for its acidification capability. Researchers found that 304
201 genes were involved in the biosynthesis of acidic bio-lixiviant (Schmitz et al., 2021). Mutant
202 strains were identified that produced either more acidic biolixiviant or a faster rate of acidification
203 than the wild-type. Disruption of genes involved in the phosphate-specific transport system led to
204 the development of mutant strains that produced a more acidic biolixiviant, whereas genes related
205 to carbohydrate metabolism and respiration controlled the rate of acidification. It was reported that
206 disrupting a single gene within the phosphate signalling control of biolixiviant production,
207 increased bioleaching by 18%; however, disrupting the supply of the pyrroloquinoline quinone
208 (PQQ) cofactor to the membrane-bound glucose dehydrogenase, significantly impaired
209 bioleaching by up to 94%. This investigation offers great insight into improving the performance

210 of bacteria for bioleaching purposes, as the production rate of lixiviant must be increased to
211 overcome a critical limitation of bioleaching technology: the long production time (Petersen,
212 2016). Subsequently, more genetic engineering interventions are still required to develop a new
213 mutant that can simultaneously produce a more acidic biolixiviant at a faster rate than the wild-
214 type.

215 Another strategy to improve the recovery of REEs is co-culturing with autotrophic bacteria such
216 as *A. ferrooxidans*, or the fungi *Penicillium* sp. CF1 (Corbett et al., 2018). The consortium of
217 heterotrophic *Enterobacter aerogenes* and autotrophic *A. ferrooxidans* can improve REEs leaching
218 to a final concentration of up to 40 mg/L (Fathollahzadeh et al., 2018b). The underlying mechanism
219 is the synergistic effect of mixing organic acid and sulfuric acid produced by the heterotrophic and
220 autotrophic bacteria. Through imaging techniques such as electrostatic force microscopy (EFM)
221 and atomic force microscopy (AFM), the mixed cultures were shown to have produced more
222 extracellular polymeric substances than the monocultures (Florian et al., 2010).

223 There are several known acid-tolerant microalgae (e.g, *Stichococcus bacillaris*, *Chlamydomonas*
224 *acidophila*, *Chlamydomonas pitschmannii*, *Viridiella fridericana*) that can survive at a pH below
225 3, and can also be co-cultured with heterotrophic bacteria to improve the REEs leaching yield
226 (Abiusi et al., 2022). It should be noted that microalgae cannot produce acidic lixiviant, however
227 they can support the growth of heterotrophic bacteria via the production of extracellular polymeric
228 substances (EPS) and oxygen, which act as a nutrient source for the heterotrophic bacteria (Aditya
229 et al., 2022). This synergistic relationship between microalgae and heterotrophic bacteria is an
230 emerging research field in biomining and is therefore worth further investigation.

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Table 2. Bioleaching of REEs by different microbes.

Microbes	REEs resources	Lixiviants	Leaching efficiency	Ref.
<i>Acidithiobacillus thiooxidans</i>	Phosphogypsum Gold mine tailing	Sulfuric acid	39 - 98%	[1], [2], [3]
<i>Aspergillus</i> sp.	Bauxite, Electronic waste, Coal fly ash, Rare earth ore, Fluorescent powder	Organic acid	31 – 91%	[4], [5], [6], [7], [8]
<i>Acidithiobacillus ferrooxidans</i>	Bauxite, Phosphate rock	Sulfuric acid	26.2 - 62.8%	[4], [9], [10]
<i>Gluconobacter oxydans</i>	Phosphogypsum, Rare earth ore	Phosphoric acid, Sulfuric acid, Organic acid	16 - 100%	[11], [12]

<i>Yarrowia lipolytica</i>	Rare earth ore	Organic acid	34 – 91%	[6]
<i>Candida bombicola</i> <i>Phanerochaete chrysosporium</i> <i>Cryptococcus curvatus</i>	Fly ash	n.d.	28 – 63%	[13]
<i>Enterobacter aerogenes</i>	Monazite	Organic acid	0.4 - 40 mg REEs/L	[14], [15], [9]
<i>Penicillium</i> sp. <i>Pantoea agglomerans</i> <i>Pseudomonas putida</i>	Monazite	Organic acid	12.3 – 23.7 mg REEs/L	[15]
<i>Burkholderia thailandensis</i>	Monazite	Rhamnolipids	-	[16]

237 References: [1] Tayar et al. (2022), [2] Hong et al. (2023), [3] Hosseini et al. (2022), [4] Barnett
238 et al. (2020), [5] Bahaloo-Horeh and Mousavi (2022), [6] Shen et al. (2023), [7] Ma et al. (2023),
239 [8] Castro et al. (2023b), [9] Fathollahzadeh et al. (2018b), [10] Tian et al. (2022b), [11] Antonick
240 et al. (2019), [12] Gao et al. (2023), [13] Park and Liang (2019), [14] Fathollahzadeh et al. (2018a),
241 [15] Corbett et al. (2018), [16] Castro et al. (2023a)

242

243 3.2 Bioweathering

244 Bioweathering is the erosion, decay, and decomposition of minerals mediated by living microbes,
245 through biomechanical and/or biochemical invasion of the minerals. The mechanism of
246 bioweathering is similar to bioleaching in which microbes excrete lixiviant such as organic acid to

247 accelerate the solubilization of the elements in the ores/rocks (Fig. 2). Bioweathering occurs under
248 natural conditions, whereby microbes and minerals come into direct contact without artificial
249 intervention, while bioleaching requires the mineral to be ground and actively cultured in a
250 bioreactor. There are some reports of microbial weathering at the laboratory scale to find the effects
251 of different parameters (He et al., 2023; Kang et al., 2021; Sachan, 2019); however, bioweathering
252 in a laboratory setting is meaningless because, as mentioned, it occurs in natural environments.
253 Interestingly, the implementation of bioweathering in a wide-spread area can be done at a level
254 that is commercially viable (Parnell et al., 2023).

255 Bioweathering studies have focused on elucidating microbial communities' influence on
256 bioweathering leaching efficacy, with the popular bacteria strains being: *Nocardioides*, *A.*
257 *thiooxidans*, *Pseudomonas*, *Sphingomonas*, *Bacillus*, and *Paenibacillus* (Chikkanna et al., 2021;
258 Potysz et al., 2020; Sun et al., 2020). Although research in bioweathering is popular for other
259 elements (e.g., Fe, P, Si), research into REEs recovery is still limited (Chikkanna et al., 2021).

260 A typical bacterium strain for bioweathering for REEs recovery is *A. niger*, whereby evidence of
261 *A. niger* colonization was observed on the surface of monazite ores in the form of etched patterns.
262 This bioweathering is possible due to the excretion of organic acids such as oxalic acid (46 mM)
263 and citric acid (5 mM) (Kang et al., 2021). This study showed that after 4 weeks of incubation, the
264 concentration of REEs in the biomass increased from 0.4 mg/L to 1.1 mg/L.

265 To accelerate the bioweathering process, comparison experiments using biostimulation,
266 bioaugmentation, root exudates, and water were conducted. It was found that bioaugmentation
267 using *A. thiooxidans* and root exudate was the most effective for metals leaching (Swęd et al.,
268 2021). In addition, the level of bioweathering occurring in minerals depends on the type of mineral.
269 For example, goethite crust with quartz was more prone to bioweathering than the calamine-type
270 rock, with the underlying reason being the presence of goethite and smithsonite in the minerals

271 which can be dissolved to a greater extent than the other elements. *A. thiooxidans* and *A.*
272 *ferrooxidans* can also be bioaugmented to accelerate bioweathering of pyrite and biotite-like
273 minerals, with the result of bioaugmentation being a 30% mobilization of metals (Liu et al., 2021).
274 As the bioweathering process is not conducted in an artificial bioreactor, bacteria are the most
275 viable organism for this technology, potentially in conjunction with plants, while microalgae are
276 unlikely to be feasible in this context due to contamination concerns.

277 3.3 Biosorption

278 Biosorption involves a liquid phase containing a culture of suspended organisms that are active
279 (alive) or inactive (dead) in which the biomass acts as the biosorbent material. The surface of the
280 microorganisms plays a crucial role in this process by offering negative (such as carboxyl,
281 hydroxyl, and phosphate) and positive (such as amine) functional groups. While ion-exchange is
282 responsible for binding negatively charged groups to metal cations, electrostatic interactions or
283 hydrogen binding forces are responsible for the adsorption of anions. Additionally, amine groups
284 can also chelate cations. In this sense, the adsorption of REEs on the cell wall falls into four sub-
285 categories: electrostatic interaction, ion exchange, surface complexation, and surface precipitation
286 (Fig. 2).

287 This process is an economical, simple, and environmentally friendly process for pre-concentration
288 and separation of REEs; although there are extensive studies on the potential of biosorption of
289 REEs from various resources, the application of the process is limited to laboratory scale studies.
290 This raises the question of how feasible this technology is commercially (Brown et al., 2023;
291 Liapun & Motola, 2023; Sachan, 2019).

292 3.3.1 Active biomass for adsorption

293 Active biomass for REEs adsorption involves microalgae, macroalgae, plants, and bacteria.
294 Typically, green microalgae are used, such as: *Chlorella vulgaris*, *Calothrix brevissima*, *Chlorella*
295 *kessleri*, and *Spirulina*. However, those microalgae strains have a wide variation of adsorption
296 capacity. *C. vulgaris* can absorb Nd to a maximum of 126.1 mg Nd³⁺/g, which is roughly 2 times
297 higher than activated carbon (Kucuker et al., 2017). A comparison study was conducted to assess
298 the REEs adsorption capacity of two microalgae strains (*C. brevissima*, *C. kessleri*) and one moss
299 (*Physcomitrella patens*), with the highest REEs adsorption being found in *P. patens* at 0.74 mmol
300 Nd³⁺/g and 0.48 mmol Eu³⁺/g (Heilmann et al., 2021). *Spirulina* is also a popular strain applicable
301 for REEs adsorption. The commercial powder form can take up a maximum of 38.2 mg Ce⁺³/g,
302 while the endemic strain shows an uptake maximum of 18.1 mg Ce⁺³/g (Sadovsky et al., 2016).
303 Other potential cyanobacteria strains for REEs adsorption are *Anabaena* sp. and *Anabaena*
304 *cylindrica* (Fischer et al., 2019), particularly in the biosorption of Eu, Sm and Nd.

305 Macroalgae such as *Ulva* sp., also work well for REEs recovery from wastewater. Kinetic
306 modelling showed that *Ulva* sp. can adsorb Ce the fastest, at a rate of up to 92%. In this case, REEs
307 were primarily localized in the outer fraction, and bonded to the sulfated polysaccharide of *Ulva*
308 sp. (Viana et al., 2023). To enhance REEs sorption, polysulfone was immobilized onto *Turbinaria*
309 *conoides* macroalgae, and through mono and binary aqueous solution tests, the polysulfone-
310 immobilized macroalgae demonstrated a competitive sorption capacity of 98.9% Pr³⁺ and 99.5%
311 Tm³⁺ (Rangabhashiyam et al., 2021).

312 Magnetic bacteria are the prevailing microbes for REEs recovery, with *Magnetospirillum*
313 *magneticum* capable of adsorbing 37.2 mg La³⁺/g. Further, *M. magneticum* also has the potential
314 for REEs recovery in saline wastewater, with varying salinity and temperature conditions having
315 no significant effect on La³⁺ adsorption. Additionally, the sorption kinetics is fast (8 min) and can
316 be recycled for 5 cycles (Mohammadi et al., 2022).

317 Other bacteria that have been used for REEs recovery include *Bacillus licheniformis*, *A. niger*,
318 *Acutodesmus acuminatus*, and *E. coli*. *A. niger* is notable for its recovery of up to 3500 mg La/L
319 (Rezk & Morse, 2023), with a biosorption performance of 99.9% uptake, even in the presence of
320 competing ions and interference from other metals. This strain was also highly effective in
321 biosorption of other REEs such as Ce, Nd, and Dy (Kazak et al., 2021). In another study,
322 polyethyleneimine-coated polysulfone-*E. coli* can uptake 121.2 mg Ru/g, which is significantly
323 higher than conventional ion exchange resins such as M 500 (17.9 mg/g), Amberjet 4200 (31.2
324 mg/g), and TP 214 (61.9 mg/g) (Kim et al., 2016). *A. acuminatus* has the highest biosorption
325 capacity of Eu (174.2 mg Eu/g) (Furuhashi et al., 2019), however, it should be noted that
326 biosorption capacity is highly dependent on the matrix effect, such as temperature, pH, and the
327 presence of competing ions. The real matrices consist of highly acidic mixtures of metals, along
328 with various inorganic and organic components. In most cases, the leachate solution comprises
329 much higher concentrations of base metals than those of REEs. In such cases, the biosorption of
330 the target metals is influenced by the competitive interactions among different REEs and metal
331 species for binding sites, except in rare cases such as *A. niger* as mentioned above.

332 Molecular and genetic engineering has been explored to improve REEs recovery by biosorption
333 with promising results. A common molecular engineering technique is to transform cells to express
334 specific proteins which enhance REEs extraction, such as lanthanide-binding tags (LBT). Typical
335 LBTs include Lanmodulin, silica-binding protein, and OmpA protein, with *E. coli* being the ideal
336 host for recombinant plasmid production. An engineered strain of *Yarrowia lipolytica* that had
337 competent cells that expressed the REE-binding protein Lanmodulin bound to the cell surface,
338 showed a superior biosorption capacity (Xie et al., 2022b). Further, *Y. lipolytica* was shown to
339 have excellent multicomponent biosorption capacity of up to 49.8 mg Yb/g, 50.3 mg Tm/g, 49.9
340 mg Er/g, and 48.7 mg Tb/g. Lanmodulin also allowed for high selectivity absorption of REEs,

341 particularly in acidic conditions. This is done via chelation with phosphate/carboxylate groups and
342 excessive binding sites introduced in the protein. Further, a transformed *E. coli* strain that
343 expressed an LBT and silica-binding protein, showed a Tb adsorption capacity maximum of 42
344 mg Tb/g dried biomass, along with other REEs of which, up to 90% was recovered (Xie et al.,
345 2022a). Another binding tag is OmpA protein. This protein increased biosorption efficiency 2 to
346 10-fold, while the affinity for heavy REEs was also improved. LBT-producing bacteria therefore
347 exhibit superior REEs biosorption via increased biosorption sites. The binding tags also possess a
348 2-fold higher REEs biosorption stability constant compared to common carboxyl functional groups
349 (Chang et al., 2020). This indicates a potential application for low-grade REEs sources (Park et
350 al., 2017). In addition to LBT, a genetically-engineered *E. coli* and native *Arthrobacter nicotianae*
351 were tested for REEs biosorption capacity, resulting in a total of 80 %, and over 90% recovery of
352 total REEs, and middle to heavy REEs respectively (Park et al., 2020).

353 3.3.2 Inactive biomass for biosorption

354 Besides active biomass, inactive biomass is another biosorbent with potential for REEs recovery.
355 The inactive biomass can be either the dried biomass of microalgae (*Galdieria sulphuraria*) or the
356 extraction of macroalgae with or without modification (*Ulva* sp.). For example, a bead was
357 produced from extracting inactive biomass (e.g., sericin, alginate, and poly(ethylene glycol)
358 diglycidyl ether) to recover REEs, with a biosorption capacity that ranges from 0.28 mmol Eu³⁺/g
359 to 0.63 mmol Eu³⁺/g (da Costa et al., 2023). Freeze-dried biomass of *G. sulphuraria* microalgae
360 was used to effectively recover REEs (Palmieri et al., 2022), while dead *Ulva* sp. biomass
361 recovered 90.7% La, 95.1% Ne, and 93.8% Dy (Arul Manikandan & Lens, 2022). Interestingly,
362 desorption using HCl and EDTA can recycle the sorbent six times.

363 Although biosorption studies on multi-element synthetic solutions provide a more comprehensive
364 assessment of the performance of biosorbents, studies using real wastewater matrices are scarce.

365 Most biosorption research has been conducted using binary or ternary metal solutions, hence
 366 underestimating the effect of anions on the competitive biosorption of these metals. Another point
 367 for improvement is the limited usage of other microbes other than bacteria. Since bacteria have
 368 been used for REEs biosorption extensively, microalgae and macroalgae receive little attention.
 369 This is despite microalgae and macroalgae demonstrating a comparative biosorption capacity
 370 compared to bacteria, up to 180 mg REEs/g biomass (Table 3); hence there is great potential in
 371 microalgae and macroalgae REEs biosorption, necessitating further investment in research to
 372 popularize microalgae and macroalgae usage in biomining.

373 **Table 3.** The performance of different microalgae for REEs recovery.

Specie name	Groups of organisms	Resource	Sorbate	q_{\max}	Mechanism	Ref.
<i>C. vulgaris</i>	Microalgae	Industrial waste	Nd	188.68 mg/g	Langmuir isotherm Pseudo-second order	[1]
<i>C. brevisissima</i> , <i>C. kessleri</i>	Microalgae	Spiked solution	Nd, Eu	Nd: 0.74 mmol/g Eu: 0.48 mmol/g	Langmuir isotherm Freundlich isotherm	[2]
<i>Arthrospir a</i> sp.	Cyanobact eria	Spiked solution	Ce	18.1 – 38.2 mg/g	Langmuir isotherm	[3]

					Freundlich isotherm	
<i>Ulva</i> sp.	Macroalgae	Industry wastewater	Y, Eu, La, Ce	382 mg Y/g 198.2 mg La/g 184.9 mg Eu/g 191.5 mg Ce/g	Pseudo second order	[4]
<i>Ulva</i> sp.	Macroalgae	Spiked solution	La, Nd, Dy	171 mg La/g 187 mg Nd/g 189 mg Dy/g	Langmuir isotherm Pseudo-second order	[5]
<i>Magnetospirillum magneticum</i>	Bacteria	Spiked solution	La	6.0 mg/g	Langmuir isotherm	[6]

<i>Bacillus licheniformis</i>	Bacteria	Spiked solution	Ce	38.93 mg/g	Freundlich model Pseudo-second order	[7]
<i>Acutodesmus acuminatus</i>	Bacteria	Industrial waste	Eu	174.2 mg/g	Langmuir isotherm model	[8]

374 References: [1]: Kucuker et al. (2017); [2]: Heilmann et al. (2021); [3]: Sadovsky et al. (2016);
375 [4]: Viana et al. (2023); [5]: Arul Manikandan and Lens (2022); [6]: Mohammadi et al. (2022);
376 [7]: Cheng et al. (2022); [8]: Furuhashi et al. (2019).

377 3.4 Bioaccumulation

378 Bioaccumulation is the intracellular uptake of REEs through various metabolic pathways of the
379 host microbes (Fig. 2). A fundamental mechanism of uptake is the intracellular transport of REEs
380 by carrier biomolecular substances such as proteins, in addition to endocytosis (Kohl et al., 2023).
381 After intracellular accumulation, REEs are bound to several substances including proteins, lipids,
382 chlorophyll, and peptide ligands (Řezanka et al., 2016; Shen et al., 2002), along with accumulating
383 in cellular vacuoles and organelles that are localized in the chloroplast and cytoplasm of cells. To
384 alleviate the stress induced by REEs, cells start replacing other divalent cations (e.g., Ca²⁺ and
385 Mg²⁺) with REEs (Wu et al., 2016). REEs accumulation then enhances the enzymatic activity of
386 cells via increasing activity of superoxide dismutase, peroxidase, and catalase. The most popular
387 candidates for REEs bioaccumulation studies are bacteria, microalgae, macroalgae, and plants;
388 however, bioaccumulation of REEs has also been reported in other hosts (e.g., eel, oyster, mussel,

389 fish). Given that studies reporting bioaccumulation of REEs in hosts other than bacteria,
390 microalgae and macroalgae focus on toxicity rather than REEs recovery, these studies are
391 considered to be outside the scope of this review and have therefore been excluded.

392 Microalgae have been studied extensively for REEs bioaccumulation with a wide range of strains
393 and REEs of interest. Three microalgae strains (e.g., *Desmodesmus quadricauda*, *Chlamydomonas*
394 *reinhardtii*, *Parachlorella kessleri*) were assessed for their REEs accumulation efficiency
395 (Čížková et al., 2019). It was found that *D. quadricauda* demonstrated the highest REEs
396 accumulation capability, up to 27.3 mg/kg/d, which is higher than *C. reinhardtii* and *P. kessleri*
397 by approximately 10% and 50% respectively. Another promising microalga strain for REEs
398 recovery is *Nannochloropsis oculata*, which exhibits an excellent stress tolerance to REEs. It can
399 accumulate 83.4% of Ce at an initial concentration of 6.0 mg/L (Wu et al., 2022). The red alga
400 *Galdieria sulphuraria* can also accumulate REEs at significant levels (26 µg Ce/g, 15 µg Nd/g, 11
401 µg La/g, and 11 µg Y/g) (Náhlík et al., 2022).

402 Bioaccumulation of REEs result in changes in biochemical functions in microalgae cells due to
403 REEs-induced stress, likely due to protein misfolding in the endoplasmic reticulum. In cases where
404 REEs mixtures are present in the microalgae culture media, transcriptomic analysis suggests REEs
405 compete with each other for bio-uptake, resulting in the inhibited expression of genes involved in
406 carbon fixation and ribosome biogenesis, which are critical pathways in REEs related stress
407 resistance (Morel et al., 2021). A transcriptomic analysis of *N. oculata* (XJ006) exposed to cerium
408 (Ce), showed that Ce exposure inhibited the expression of genes in the carbon fixation and
409 photosynthesis pathways in conjunction with the expression of ribosome biogenesis genes.
410 Further, glycerol kinase and acetyl-CoA biosynthesis-related genes were upregulated, thereby
411 enhancing resistance of REEs related stress in response to Ce exposure via lipid accumulation (Wu
412 et al., 2022).

413 Macroalgae (e.g., *Ulva lactuca*, *Ulva intestinalis*, *Fucus spiralis*, *Fucus vesiculosus*, *Osmundea*
414 *pinnatifida* and *Gracilaria* sp.) can also accumulate REEs, with *U. lactuca* the only macroalgae
415 able to accumulate all REEs tested such as: Y, Ce, Pr, Nd, Eu, Gd, Tb and Dy (Pinto et al., 2020).
416 In addition, this macroalgae strain is able to remove more than 60% to 90% of all studied REEs.
417 The removal kinetic also shows that reduction happens rigorously in the first 24h. Though
418 macroalgae are capable of accumulating REEs, green (*Codium tomentosum*, *Ulva rigida*), red
419 (*Gracilaria gracilis*, *Osmundea pinnatifida*, *Porphyra* sp.), and brown species (*Saccorhiza*
420 *polyschides*, *Undaria pinnatifida*) show a different level of REEs accumulation as well as the ratio
421 of light:heavy REEs accumulated in the cells (Milinovic et al., 2021). The REEs accumulation in
422 green and red macroalgae ranges from 0.7 to 1.7 µg/g which is much higher than in other species
423 (0.1 – 0.2 µg/g). The ratio of light:heavy REEs in brown macroalgae was higher than in green
424 macroalgae, indicating brown macroalgae preferentially accumulate heavy REEs.

425 Higher plants also have the potential for REEs recovery from mining wastewater (e.g., *Salix*
426 *myrsinifolia*, *Salix schwerinii*, *P. americana*, and *P. marigold*). *Salix* species (*Salix*
427 *myrsinifolia* and *Salix schwerinii*) can uptake a range of REEs such as La, Y, Nd, Dy and Tb
428 effectively, with La accumulation of up to 8,400 µg/g dry weight in root tissue alone (Mohsin et
429 al., 2022). They also display phytostabilization potential through translocation and
430 bioconcentration factors. Other plants such as *P. americana*, can accumulate REEs in leaves at
431 concentrations of up to 1,040 µg/g (Liu et al., 2021). Variation of REEs accumulation in plants
432 can be attributable to a range of factors, including available P, pH, and TOC (Zhang et al., 2023).

433 Biosorption (active biomass) and bioaccumulation technologies complement each other to recover
434 the chemicals of interest in an aqueous solution. Like biosorption, bioaccumulation is best suited
435 for bacteria (and plants) as they thrive well in the harsh conditions of mining waste. As mentioned
436 above, some microalgae strains can adapt well to similarly harsh conditions (Abiusi et al., 2022;

437 Náhlík et al., 2022) and can therefore be applied in various forms of microalgae-based
438 technologies. These technologies include; flat plate and tubular photobioreactors, high-rate algae
439 ponds, or even membrane photobioreactors, following the bioleaching stage (Vo et al., 2019). This
440 hybrid system is promising as microalgae produce pigment which has high commercial value and
441 grow faster than some bacteria. Currently, most microalgae biotechnology focuses on recovering
442 nitrogen and organic carbon from mining wastewater rather than REEs (Geng et al., 2022; Wang
443 et al., 2023). Like other techniques for REE biomining, bioaccumulation has not been fully
444 developed to offer a cost-effective, feasible alternative for recycling REEs commercially (Opare
445 et al., 2021).

446 3.5 Bioprecipitation

447 In conventional REE extraction technologies, REEs are precipitated by adding chemicals, whereas
448 in bioprecipitation, microorganisms play a critical role in the oxidative-reductive reaction for
449 precipitation to occur. Carbonate, phosphate, sulphide, etc. are produced by microbial metabolisms
450 that precipitate REEs. Moreover, bacterial oxidation precipitates biogenic minerals (e.g., silica,
451 iron oxides, manganese oxide) that absorb REEs, which then co-precipitates with them (Fig. 2).
452 Phosphate precipitation is a common process of bioprecipitation. When enough organic phosphate
453 is supplied in the medium, phosphatase located externally in the microbial polymeric matrix,
454 precipitates REEs by catalyzing REEs' binding to this phosphate.

455 Some typical strains of bacteria that facilitate the precipitation of metals are *Desulfosporosinus*
456 *acididurans*, *Desulfosporosinus acidiphilus*, *Thermodesulfobium narugense*, *Thermodesulfobium*
457 *acidiphilum*, *Acinetobacter* sp. H12 (Frolov et al., 2017; Sánchez-Andrea et al., 2015; Wu et al.,
458 2021). The sulfate-reducing bacteria *A. thiooxidans* has also been shown to precipitate 90% of
459 soluble metals via the formation of metal sulfates (Fang et al., 2011). Bioprecipitation also works
460 in conjunction with biosorption in microbial consortia in recovering metals. It was found that the

461 wild type strains of *Paraclostridium bifermentans* and *Klebsiella pneumoniae*) can remove
462 between 83.8% - 91.1% of soluble metals after 30h (Saikia et al., 2022). However, the metal
463 precipitates formed are microbial strains specific. The sulfate salt and zerovalent metals are the
464 primary precipitates driven by *P. bifermentans*, whereas chloride and phosphate salts are the main
465 products of *K. pneumoniae*. Further, the composition and concentration of the leaching solution
466 strongly effects the chemical form of the precipitates. The symbiotic interaction of sulfate-
467 reducing, metal-reducing, sulfur-oxidizing, and denitrifying bacteria participates in the whole
468 process of bioprecipitation (Cilliers et al., 2022). In addition, metals can also be precipitated
469 through a calcium precipitation process catalyzed by *Acinetobacter* sp. H12 (Wu et al., 2021).
470 Some of the precipitation was facilitated by bacteria to form biocrystal seeds. In addition, some
471 microorganism strains can simultaneously precipitate REEs and fix nitrogen which is beneficial to
472 the environment (Sakpirom et al., 2019).

473 Further, bioprecipitation derived biogenic sulfides are more effective than chemically derived
474 sulfides in precipitating metals, with up to 44-60% of metals vs 4-6% of metals being precipitated
475 via biogenic sulfides or chemically derived sulfides respectively (Saikia et al., 2022). However,
476 there is little published research related to bioprecipitation of REEs and other heavy metals to date.
477 The underlying reason might be attributable to the trace concentrations of REEs in the ore, which
478 is technically challenging to harvest using the right precipitate. As a result, leaching is the primary
479 solution for recovering high-purity REEs. In addition, bioprecipitation is unique to bacteria and
480 does not work with microalgae, macroalgae, and plants.

481 A comprehensive investigation reveals that processes of bioprecipitation have been developed at
482 a pilot scale for resources of metals during hydrometallurgical processing (Sethurajan &
483 Gaydardzhiev, 2021), which shows the maturity of this technique for metal extraction. In contrast,
484 REE bioprecipitation has been implemented mostly in controlled conditions, making the upscaling

485 process of bioprecipitation unsuitable as the operating parameters are widely variable (Kachieng'a
486 & Unuofin, 2021).

487 3.6 Bioflotation

488 Bioflotation is the process in which microbial metabolism and the bioproducts (such as surfactants
489 or froth) is used to harvest minerals and metals of interest (Fig. 2). This is achieved by altering the
490 surface state of REEs which significantly contributes to a high yield flotation.

491 The first form of bioflotation is using microorganisms that act as inhibitors. For instance,
492 *Rhodococcus opacus* attaches to the surface of malachite, changes the hydrophobicity of this
493 mineral which contributes to the recovery of 93% of minerals after bioflotation (Kim et al., 2017).
494 Similarly, *A. ferrooxidans* bacteria degrades pyrite in galena and sphalerite minerals (Mehrabani
495 et al., 2011).

496 Microbial metabolism is the second form of bioflotation for REEs recovery. A typical example of
497 this bioflotation form is Fe(II) oxidation from pyrite to Fe(III) by *Thiobacillus ferrooxidans*.
498 Again, the surface characteristics of minerals were altered by *T. ferrooxidans*, allowing for the
499 recovery of REEs through flotation (Hosseini et al., 2005). Another study used a group of bacteria
500 (*Halobacillus* sp. and *Marinobacter* sp.) to oxidize surface pyrite and chalcopyrite to form
501 hematite. The hematite surface, together with both types of bacteria, promoted pyrite deposition
502 and chalcopyrite buoyancy (González-Poggini et al., 2021). In addition, microbial oxidation also
503 changes the hydrophobicity of the mineral surface. *Citrobacter* sp. was found to oxidate sulfur in
504 the galena (PbS) and sphalerite (ZnS) ores, leading to a significant recovery of 80–90% of metals
505 (Sanwani et al., 2021).

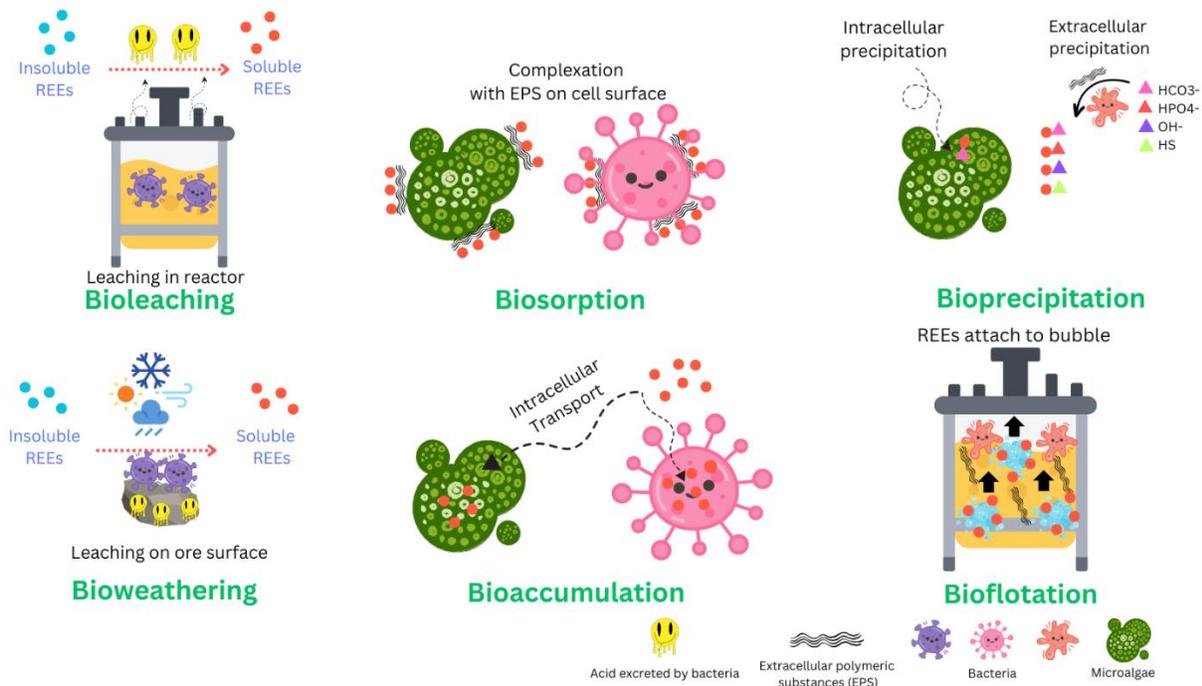
506 The last form of bioflotation involves using microorganism by-products that act as a biopolymer
507 in the form of extracellular polymeric substances (EPS). EPS facilitates the fixation of REEs

508 surrounding the cells and in some cases, where excreted EPS is foamable, REEs can be recovered
509 by collecting the foam.

510 *Alicyclobacillus* sp. have been found to secrete surfactants that have contributed to the recovery of
511 80-90% of metals (Sanwani et al., 2021). Similarly, *Staphylococcus carnosus*, through the
512 secretion of some exopolymers, were found to change the surface charge of coal, allowing for the
513 recovery of up to 90% of metals in 12 h (Ramos-Escobedo et al., 2016), while crude biosurfactant
514 extracted from *Rhodococcus opacus* has been found to support the buoyancy of hematite, allowing
515 for approximately 95% recovery of hematite through bioflotation at pH 5. The addition of *R.*
516 *opacus* also made hematite more hydrophobic in an acidic environment (Puelles et al., 2021).

517 Bioflotation technology efficiently recovers minerals and metals such as iron, copper, lead, zinc,
518 etc. However, this technology is still under consideration for REEs recovery applications as the
519 concentrations of REEs is comparatively low, while the purification of REEs in the supernatant
520 will add to the recovery cost making this method less effective than other methods. Furthermore,
521 there are some limitations in the upscaling process that are mostly related to the direct usage of
522 microorganisms in flotation. The application of biosurfactants can prevent the limitations related
523 to operational issues; however, environmental and economic investigations are still needed to
524 evaluate the feasibility of pilot and commercial developments (Asgari et al., 2022).

525



526

527

Fig. 2. Mechanisms of REEs recovery by biomining processes from leachate.

528

4. Effects of operating conditions and matrix on REEs recovery

529

4.1 pH

530

One of the most critical physicochemical factors impacting REEs recovery is pH. It significantly

531

affects speciation of REEs in solution, with most studies indicating a pH range of 1 to 7 as the

532

optimum range for the speciation of REEs. Conversely, at higher pH, insoluble hydroxides will

533

form which decreases REEs recovery through different biosystems (Abd El-Magied et al., 2017;

534

Rasoulnia et al., 2021). This explains why microbes (e.g., *A. ferrooxidans*, *A. thiooxidans*) were

535

applied to leach REEs, as their lixiviant can reduce the pH of a solution down to 1.8 – 2 (Hosseini

536

et al., 2022; Tian et al., 2022a). pH also has a reverse relationship with redox potential; whereby

537

decreasing pH will increase redox potential and support the leaching of REEs (Castro et al., 2020).

538

Due to this importance of pH in biomining technologies, the operating conditions of the relevant

539

technologies should be optimized for the desired microorganism. For example, sustainable

540 production of sulfuric acid excreted by *A. ferrooxidans* in order to maintain a low pH level has
541 been found to require optimal operating conditions (640 – 680 mV Eh, pH 1.3 – 1.5, 4 – 6 d HRT
542 and 6% pulp ratio) in order to maintain consistent acid production (Sarswat et al., 2022).

543 In addition, based on the type of biomining technologies, pH also needs proper adjustment to avoid
544 negatively impacting REEs recovery. For example, when REEs sorption is a downstream process
545 after the bioleaching process, the pH will need to be adjusted after the bioleaching process
546 depending on the REEs of interest and the applied sorbents (Castro et al., 2020). Increased pH
547 compromises the sorption capacity due to the low affinity to the cell surface, while a neutral pH
548 increases the sorption of light REEs. In comparison, a low pH increases the sorption of heavy
549 REEs. For example, Y and lanthanide are preferentially adsorbed at pH 4.5 to 6.5, whereas the
550 optimal pH for Sc is from 3 to 5 (Lozano et al., 2020). In addition, there is a preferential range of
551 pH in which each type of microbes can absorb REEs at a maximum level. At pH 3 – 5, the
552 availability of oxygen-rich functional groups on the cell surface is substantial, such as carboxyl in
553 gram-negative bacteria or phosphate in gram-positive bacteria (Kazy et al., 2006). The range of
554 pH should therefore be determined according to the type of REEs, the microorganism, and the
555 process conditions.

556 4.2 Temperature

557 Temperature is also a complicated factor considering that it also impacts various aspects such as
558 chemical reactions, solubility of REEs, and the growth rate of microorganism. Based on the
559 optimal growth temperature, microorganisms can be classified into three main groups:
560 psychrophilic, mesophilic, and thermophilic (Cao et al., 2021; Dev et al., 2020). Each biomining
561 technology also requires a specific range of temperature. A typical energy-efficient temperature
562 range for REEs recovery is between 17°C and 32°C (Gupta et al., 2019).

563 Solubility of most REEs complexes decreases with an increase in temperature, except for
564 complexes of REE-chlorides and nitrates (Cao et al., 2021; Das et al., 2017; Das et al., 2019;
565 Meshram et al., 2016; Muravyov et al., 2015). In addition, the solubility of oxygen and carbon
566 dioxide, which are essential for bioactivity, also decreases with increasing temperature. In contrast,
567 chemical reactions increase with a temperature rise; thus, it positively affects REEs extraction
568 (Rasoulnia et al., 2021). As a result, gas solubility and chemical reactions work against each other
569 in relation to temperature. In terms of biochemical function, at optimal temperature, an extra
570 benefit is an increased production of extracellular polymeric substances, escalating the microbes'
571 attachment to the metal surface (Bellenberg et al., 2015; Kachieng'a & Unuofin, 2021).
572 Considering the multi-dimensional effects of temperature on REEs recovery, the optimal range of
573 temperature should be determined based on the desired circumstances.

574 Sorption is an endothermic process in which temperature is directly proportional to the adsorption
575 capacity (Gupta et al., 2019; Iftekhar et al., 2017). Sorption is suppressed at temperatures ranging
576 from 20-35°C, while higher temperatures increase sorption capacity via elevated surface activity
577 and energy kinetics of REEs (Vijayaraghavan & Yun, 2008). However, high temperatures beyond
578 the tolerance level of microbes will inhibit microbe growth and result in cellular damage. In this
579 sense, it is challenging to screen microorganism strains that are tolerant to high temperatures for a
580 more selective and faster REEs recovery (Engelbrekton et al., 2018; Sethurajan et al., 2018). For
581 example, *G. sulphuraria* and *Thermus scotoductus* SA-01 have been successfully used for REEs
582 recovery at 42°C (Ciniglia et al., 2014; Minoda et al., 2015) and 65°C (Maleke et al., 2019b).
583 Meanwhile, increasing the temperature to 75°C enhances REEs sorption in the culture of
584 *Cupriavidus necator* (Adekanmbi et al., 2020). The same results were reported for bioleaching of
585 Y, Sc, and La, where an increase in temperature from 28 to 45°C increased the leaching of REEs
586 (Muravyov et al., 2015). In the case of bioaccumulation or biosorption using active cells, an

587 optimal temperature to keep the cells alive is necessary (Dhankhar & Hooda, 2011; Panda et al.,
588 2021).

589 4.3 Presence of metals

590 Metals can compromise REEs recovery for two reasons: (i) causing toxicity to the microbial
591 community and (ii) competing with REEs in the sorption process. The toxicity effects of metals
592 can be classified into two levels: substitution of intracellular essential ions in enzymatic or nutrient
593 transport systems; and an impediment in microbial metabolism due to intracellular accumulation
594 and enzymatic inhibition (Jia et al., 2019; Monballiu et al., 2015). For instance, substituting vital
595 calcium ions with REEs adversely impacted bacterial growth (Homer & Mortimer, 1978; Yang et
596 al., 2016). This is why a higher concentration of REEs leads to a decrease in microbial growth.
597 The metal toxicity issue can also be expanded to other metal ions in the solution (Vijayaraghavan
598 & Yun, 2008). For example, concentrations of Eu^{3+} higher than 16.7 mg/L adversely affected the
599 growth of *Clostridium sp.* 2611 (Maleke et al., 2019a). Moreover, concentrations of Ce^{3+} and Gd^{3+}
600 higher than 6.4 mg/L had a toxic effect on *Vibrio fischeri* (Kurvet et al., 2017).

601 The presence of competing ions (e.g., Cs^+ and Cu^{2+}) decreased Nd^{3+} recovery due to competition
602 for available active sites on biosorbent surfaces (Hisada & Kawase, 2018). The biosorption
603 capacity was found to be influenced by the electronegativity of the cations; Cu (1.90), Nd (1.14),
604 Na (0.93), and Cs (0.79), with higher electronegativity enhancing the sorption of ionic atoms on
605 the charged surface of a biosorbent. Cu can easily replace Na in $-\text{COONa}$ rather than H in $-\text{COOH}$,
606 leading to a more significant impact on biosorption efficiency (Hisada & Kawase, 2018).

607 4.4 Aeration

608 Chemolithotrophic microorganisms used in REEs recovery obtain their energy for growth and
609 proliferation by oxidation of inorganic molecules. In this regard, oxygen utilized as the terminal

610 electron acceptor must be sufficiently supplied (Barros et al., 2019; Dev et al., 2020). It has been
611 reported that high-rate aeration could provide enough oxygen in bioleaching by *A. ferrooxidans*
612 (Gu et al., 2017). However, the way to introduce air into bioreactors which are influenced by their
613 type and configuration, should also be considered. For example, baffles are used on the wall of
614 bioreactors to create high turbulence, however significant shear stress becomes a factor for
615 microbial attachment and biofilm formation (Dev et al., 2020).

616 Traditionally, atmospheric air at low and medium temperatures is purged into the system to supply
617 dissolved oxygen for microbes; however, the high loading of suspended solid and sulfide
618 necessitates an increase in dissolved oxygen supply in order for bacteria to thrive. Oxygen-
619 enriched air is an alternative given that, at a specific solid load of 20% (w/w), the dissolved oxygen
620 level in the culture is maintained at 4 – 13 ppm (Guezennec et al., 2017). Beyond 17 ppm, the
621 microbial activity significantly decreased and compromised leaching efficiency. Therefore,
622 efficient bioleaching operation is also linked to the aeration regime and bioreactor configuration.

623 4.5 Other factors

624 Another factor that is crucial for efficient REEs recovery is pulp density. Pulp density (as %) is
625 defined as the mass of a mineral per volume unit. Pulp density is an important factor since it not
626 only limits the input flux of oxygen and carbon dioxide, but it reduces microbial growth when
627 heavy metal concentrations are high (Brandl et al., 2016; Wang et al., 2014). Pulp densities higher
628 than 5% in red mud have been shown to elevate the pH of the solution during REEs recovery due
629 to the following reasons: i) the higher pulp density intensified microbial toxicity resistance, and ii)
630 enhanced acid-neutralizing capacity of red mud. This affects the efficiency of REEs bioleaching,
631 with a red mud pulp density of 20 g/L allowing for the most efficient bioleaching (Qu & Lian,
632 2013). Further, an increase in pulp density from 1% to 5% significantly reduces La recovery from
633 63% to 33% (H.M & Baral, 2019).

634 The other essential factor in using live cells is balancing culture media and essential nutrients
635 (Dhankhar & Hooda, 2011). Although the cost of organic nutrients can be high, cheaper
636 alternatives such as sugar cane bagasse, vinasse, whey, and molasses can be used to reduce costs
637 when recovering REES from mining wastewater (Panda et al., 2021). For example, bagasse which
638 is rich in sucrose, was used as a carbon source in the REEs bioleaching process using *A. niger* and
639 *P. simplicissimum* (Shah et al., 2020). The additional nutrients not only improved the growth of
640 microbes, but also accelerated the REEs extraction process. Similarly, glucose, glycerol, and
641 $\text{NH}_4\text{Mo}^{+2}$ can effectively increase siderophore production, which is central to bioextraction and
642 release of REEs from mineral sources (Sethurajan et al., 2018).

643 Bioleaching efficiency is also mining-site specific. For instance, the maximum leaching
644 efficiencies of light and heavy REEs were 54% and 6% respectively in the 'DT' site (Ontario,
645 Canada); whereas they reached 58% and 14% in the 'RAT' site (Ontario, Canada) (Reynier et al.,
646 2021). The leading cause of this discrepancy was the composition of the tailing between two ores.
647 The tailing of the 'RAT' mine has quartz as the main component, which is much simpler than in
648 the 'DT' mine tailing (e.g., quartz, pyrite, gypsum, silicate). This suggests that the complicated
649 matrix of mining tailings can compromise bioleaching efficacy.

Table 4. Key technical principles of biomining treatment technologies

Technologies	REEs Resources	Participated microorganisms	pH	Temperature (°C)	Pulp density (w/v)	REEs Extraction efficiency	Country	References
Bioleaching	Inactive uranium mine, monazite, phosphogypsum, bauxite	Sulfur- and iron-oxidizing bacteria, fungi	2	30 – 50 °C	10%	14 – 89%	Canada	[1], [2], [3]
Biosorption	Wastewater, ore leachate	Bacteria, cyanobacteria, microalgae, macroalgae, moss	2 – 5.6	20 – 60 °C	-	99% 182 mg/kg	China, China, Japan	[4], [5], [6], [7], [8], [9], [10]

Bioaccumulation	Red mud, mining waste	Microalgae, macroalgae, plant	10% v/v HNO ₃	26 °C	-	83.4% 11 - 26 mg/kg	China, Italy	[11], [12], [13]
Bioprecipitation	Mining wastewater	Incomplete oxidizers, complete oxidizers, sulfate-reducing bacteria	pH 5.5	-	-	-	USA	[14], [15], [16], [17]
Bioflotation	Pyrite, sphalerite – galena mineral	Bacteria	pH 8.0	-	25 - 50%	70 – 80%	Indonesia, India	[18], [19]
Bioweathering	Monazite, basalt, rhyolite,	Bacteria, biotic respiration	Oxalic acid	-	2%	0.4 – 1 mg/L	United Kingdom, Canada	[20], [21]

	granite and schist		(~46 mM) Citric acid (~5 mM)			5.2 – 46.8 nmol/g biomass.		
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References: [1] Reynier et al. (2021); [2] (Shen et al., 2023), [3] (Park & Liang, 2019), [4] Giese and Jordão (2019), [5] Liang and Shen (2022), [6] Kim et al. (2011), [7] (Heilmann et al., 2021), [8] (Fischer et al., 2019), [9] (Viana et al., 2023), [10] (Mohammadi et al., 2022), [11] Wu et al. (2022), [12] Náhlík et al. (2022), [13] (Čížková et al., 2019), [14] Murray et al. (2015), [15] (Saikia et al., 2022), [16] (Cilliers et al., 2022), [17] (Sánchez-Andrea et al., 2015), [18] Sanwani et al. (2016), [19] Vasanthakumar et al. (2012)

614

615 **5. Sustainability of biomining technologies for REEs recovery**

616 Biomining is undoubtedly beneficial for industry, the economy, and the environment, particularly
617 from a sustainability standpoint. Sustainable biomining should be comprised of four main criteria:
618 (i) promoting environmental resilience, (ii) cost-effectiveness and high revenue, (iii) viability of
619 technologies, and (iv) availability of low-grade REEs sources. The below SWOT and Techno-
620 economic assessment are discussed based on these criteria.

621 5.1 SWOT analysis

622 SWOT analyses were conducted to assess biomining technologies' sustainability and suitability
623 for recovery of REEs (Table 5). Three criteria are used in this review: technical, environmental,
624 and economic aspects. About 25 peer-reviewed articles out of 45 searched articles were selected
625 for SWOT analysis.

626 The result of SWOT analysis indicates that biomining is a sustainable approach for REEs recovery
627 from low-grade resources with low environmental impact. Biomining comes with the added
628 benefit of reducing the CO₂ footprint of pyro- and hydrometallurgy technologies and recycling
629 wastes from other sources (e.g., agricultural waste, food waste, industrial waste) by utilising them
630 as a nutrient source for microbes. Biomining technologies also do not produce hazardous by-
631 products unlike traditional REEs recovery methods. Regarding the economic aspect, biomining is
632 a low-cost technology requiring low ongoing operational costs, energy, and workforce
633 requirements. Biomining technologies are expected to be partly or close to fully automated in the
634 future; however, this depends on the market requirement of REEs purity, which would affect the
635 overall cost of post-processing. For example, one kg of Sc metal costs \$3,000 USD/kg (99.99%
636 purity) or \$6,000 USD/kg (99.999% purity) (ISE, 2019).

637 Regarding technical feasibility, biomining has been demonstrated to be highly efficient and
638 selective for REEs recovery. However, it does have a long operational time from months to years
639 and is not versatile in harsh environmental conditions which are significant limitations that must
640 be addressed (Petersen, 2016). A potential solution would be the development of a high throughput
641 screen, which would allow for the rapid identification of an optimal strain of microorganism for a
642 specific REEs resource recovery application. Currently in the US, there is no prototype at a
643 technology readiness level higher than 4 (scale 1- 9) for biomining of REEs, although biomining
644 has been commercially widespread for precious metals (e.g., Au, Ag, Cu) recovery (Brown et al.,
645 2023). Countries such as Finland, Chile, and Uganda progressively use biomining technologies
646 (Marcos, 2018), with one example being a two stage biohydrometallurgy process. The first stage
647 involves the use of acidophilic iron, and sulfur-oxidizing microbes to extract base metals, and the
648 second stage involves the solubilization of rare earth and precious metals (Magoda & Mekuto,
649 2022). Biomining technologies are also scalable, which allows for varying amounts of REEs to be
650 extracted. This makes biomining technologies more flexible to adapt to local geographical
651 conditions. Many biomining technologies, such as bioflotation, bioprecipitation,
652 bioelectrochemical, have not been well studied despite their immense potential.

Table 5. SWOT analysis of biomining technologies for REEs recovery.

Considered aspects	Considered Criteria	Strengths	Weaknesses	Opportunities	Threats
Technical aspects	Overall treatment performance	<p>High extraction efficiency (>80%).</p> <p>High selectivity for a range of REEs.</p> <p>Genetic engineering enhances recovery efficiency (56-87%).</p> <p>Biosorption coupled with other techniques increases extraction efficiency.</p>	<p>Slow reaction times</p> <p>High temperature required.</p> <p>Effects of functional groups on biosorption is not fully investigated.</p> <p>Low chemical resistance and mechanical strength</p>	<p>Optimal reaction time identified via optimal microbial growth.</p> <p>High throughput screening is necessary.</p> <p>Immobilized cells is preferable for industrial applications.</p>	<p>High cell densities required for leachate.</p> <p>Maintain optimal microbial growth conditions and continuous organic carbon supplements.</p> <p>Complicated microbial-mineral interactions (e.g., redoxolysis, acidolysis, complexolysis).</p> <p>Wide variation of applied bacteria strains, cell wall</p>

	Bioflotation is applicable to seawater.	Low resilience to harsh operating conditions.		composition, and reaction conditions.
Operating conditions	Temperature: 30 – 35°C. Optimal pH is metal-specific.	Overly high temperature compromises oxidation of elemental sulphur. Maximum recovery depends on whether processes are endothermic or exothermic.	Increasing temperature will increase biosorption rate (3 to 4-fold at 70 °C).	Wide fluctuation of temperature and pH inhibits microorganisms. Biosorption requires specific pH and temperature.
Extraction and recovery efficiency	Biobleaching and biosorption are	Extraction and recovery efficiencies vary	Reducing CAPEX and OPEX costs rather than pyro-	Bioelectrical technology has low resilience to mining wastewater.

		matured technologies.	among technologies and target elements. Bioelectrochemical and bioflotation still immature.	and hydrometallurgy technologies.	Challenge in applying bioelectrical technology for real wastewater.
	Toxicity	Considered environmentally friendly. Bioreagents are less toxic.	n.a.	n.a.	n.a.
Environmental aspects	Impact on aquifer / existing environment	Reduce hazardous waste and impacts to the environment.	Targeted at metal recovery, rather than environmental remediation.	Address national priorities, such as job creation and resource recovery.	Requires a large land footprint.
Economic aspects	Status of development	Focus on high-value metals (Nd, Sc).	n.a.	Economic viability at a commercial	Bioflotation: still at laboratory scale.

		Reuse phytic acid for bioprecipitation.		scale (e.g., bioleaching, biosorption).	Unclear techno-economic assessment.
	Treatment cost	Appropriate microorganisms' usage reduces OPEX cost (60%). Do not rely on expensive and aggressive reagents.	n.a.	Lower expenditure on carbon emission and energy.	Costs of some organic carbon feed are still high (44% overall cost).
	Resilient to difficult conditions (Tunnels, wetlands, riparian	Resilient to harsh red mud waste (<i>Galdieria sulphuraria</i>).	Cyanobacteria are vulnerable to high alkalinity.	n.a.	n.a.

	zones, populated zones).				
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*Data for SWOT analysis were retrieved from the previous section.

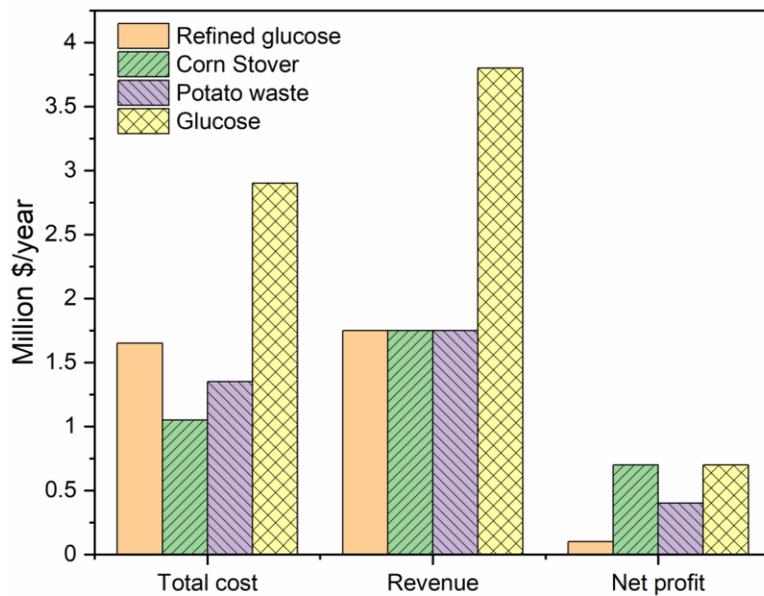
652 5.2 Techno-economic assessment

653 REEs recovery process should incorporate standards to make the process environmentally and
654 economically friendly and sustainable. To make biomining sustainable, it is required that the loop
655 of REEs recovery should be closed, meaning the waste of biomining should be circulated back
656 into the recovery process. This is challenging as the characteristics of REE secondary sources (e.g.,
657 concentration and abundance) vary widely.

658 The cost breakdown of the whole biomining process typically consists of processing/primary
659 leaching (77.1%), biosorption (19.4%), precipitation, and roasting (3.5%) (Jin et al., 2017). The
660 profitability of REEs extraction depends on a few factors: REEs concentration in the ores, the
661 composition of the feedstocks, the cost of pre-treatment, and mining waste management.
662 Processing of minerals always occupied the highest fraction of overall cost, especially for the low-
663 grade ores; however, this can be offset by the high value of minerals in the ores (Spooren et al.,
664 2020). For the feedstock, an extensive study has been conducted to investigate which feedstock
665 returns the highest profit. Results indicated that coal ash, which contains substantial REEs
666 fractions, returned the highest profit, while high-grade ores do not return as much profit as the
667 other feedstocks due to high material cost. The high cost of the primary leaching stage can be
668 attributed to the carbon source (e.g., glucose) used for feeding bacteria, as this can contribute up
669 to 44% of the total cost (Thompson et al., 2018). Wastewater from corn stover returns the highest
670 revenue amongst other carbon sources (Fig. 3). The major discrepancy between corn stover and
671 other carbon sources is that the collection cost is low, and the energy cost is low as burning lignin
672 residues offset electricity costs. The characteristic of REE sources also impacts the techno-
673 economic feasibility of technologies. REEs from fly ash has low solubility, so its techno-economy
674 feasibility when using some specific sorbents such as PEGDA beads and Si sol-gels for REEs
675 recovery is unlikely to be appreciated (Alipanah et al., 2020).

676 At this stage, there are few TEA analyses related to REEs biomining in the literature. The above
 677 discussion has indicated the importance of, and the need for comprehensive TEA analysis being
 678 conducted before commercial deployment of biomining. Based on the TEA analysis, several
 679 solutions have been proposed to make biomining a more realistic option for REEs recovery,
 680 including proper pulp ratio, optimization of mineral processing, and alternative for high cost
 681 lixivants.

682



683

684 **Fig. 3.** Total cost, revenue, and net profit for bioleaching process by *Glucobacter oxydans* of
 685 industrial waste using different feedstock (i.e., refined glucose, corn stover, potato waste, and
 686 glucose). Data was retrieved from various sources (Jin et al., 2019; Thompson et al., 2018). The
 687 scenario is built upon 285 tons of REEs being produced per year using 19,000 tons of raw material.

688 **6. Conclusion**

689 Biomining for REEs recovery is a viable and sustainable alternative. There are some critical points
 690 that must be addressed:

- 691 • The abundance and concentration of REEs in mining waste vary widely depending on the
692 specific mining sites, and geochemical and sociodemographic conditions. Hence, the
693 application of biomining for REEs recovery would require proper calibration to maximize
694 its performance and revenue.
- 695 • Bioleaching using bacteria is a mature technology with high extraction efficiency (>80%);
696 however, it is a time-consuming process (months to years) and is currently applied to other
697 metals at full scale.
- 698 • Biosorption and bioaccumulation comprise a range of hosts (e.g., bacteria, microalgae,
699 macroalgae, plant). There is a lack of pilot and full-scale applications.
- 700 • The recovery stage using bioprecipitation and/or bioflotation seems to be far off from full-
701 scale application.
- 702 • sSWOT and techno-economic assessment results indicate biomining is a sustainable
703 approach for recovery of REEs from low-grade resources with low environmental impact.
704 The carbon source for bacteria occupies 44% of the total cost. Amongst mining waste, coal
705 ash is shown to have the highest profit.

706

707 Given the success in REEs recovery from published biomining studies, conducting more in-
708 depth research and technology transfer is necessary to further optimize biomining
709 technologies. It is recommended that efforts in screening efficient strains and metabolic
710 engineering need to be improved for greater REEs recovery efficiency. While bacteria have
711 been applied widely in biomining, further investigation in microalgae/macroalgae driven REEs
712 recovery is needed as they can also add further value through pigment production. Apart from

713 technological improvement, relevant social, environmental, and economic assessments must
714 also be performed in order to provide a comprehensive understanding of sustainable biomining.

715 **Author contributions**

716 Phong H. N. Vo: Conceptualization; Formal analysis; Investigation; Methodology; Roles/Writing
717 - original draft. Soroosh Danaee: Roles/Writing - original draft. Ho Truong Nam Hai:
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719 Nguyen: Writing - review & editing. Unnikrishnan Kuzhiumparambil: Resources;
720 Conceptualization. Mikael Kim: Writing – review & editing. Long D. Nghiem: Conceptualization;
721 Supervision; Writing - review & editing. Peter J. Ralph: Conceptualization; Supervision; Writing
722 - review & editing.

723 **Declaration of Competing Interest**

724 The authors declare that they have no known competing financial interests or personal
725 relationships that could have appeared to influence the work reported in this paper.

726 **Acknowledgments**

727 Phong H. N. Vo is funded by the University of Technology Sydney (UTS) Chancellor's Research
728 Fellowship.

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