

Subterranean environments contribute to three-quarters of classified ecosystem services

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69 **Abstract**

70 Beneath the Earth's surface lies a network of interconnected caves, voids, and
71 systems of fissures forming in rocks of sedimentary, igneous, or metamorphic origin.
72 Though largely inaccessible to humans, this hidden realm supports and regulates
73 services critical to ecological health and human well-being. Subterranean
74 ecosystems are integral to major biogeochemical cycles, sustain diverse surface
75 habitats, and serve as the primary source of irrigation and drinking water. They also
76 offer non-material benefits, including scientific discovery, education, and cultural
77 practices. Yet, these contributions often go unrecognized, partly due to the lack of a
78 unified synthesis of ecosystem services across terrestrial, freshwater, and marine
79 subterranean compartments. This gap limits effective communication of their value to
80 scientists, practitioners, and the public. Through a systematic expert-based review,
81 we show that subterranean ecosystems contribute to up to 75% of classified
82 ecosystem services. Notably, many of these contributions are described only
83 qualitatively, lacking numerical or economic quantification. Next, we provide
84 examples of the main services to offer a global overview of their multifaceted value
85 and vulnerability to environmental change. We believe this synthesis provides
86 researchers and practitioners with concrete examples and targeted metaphors to
87 more effectively communicate the importance of subterranean ecosystems to diverse
88 audiences.

89

90 **Keywords:** Groundwater; Hypogean; Nature value; Drinking water; Food production;
91 Biotechnology; Geothermal energy; Sustainability; Ecotourism; Cultural heritage

92 **Introduction**

93 Whether engaging in high-stakes discussions with policymakers or navigating casual
94 conversations at social gatherings, scientists studying subterranean biodiversity may
95 find themselves in the uncomfortable position of defending the very essence of their
96 work. Questions like, “*Why waste your time in a muddy cave to count tiny beetles?*”,
97 “*Are we really worried about some blind shrimp no one's ever seen?*” or “*What’s next*
98 *—national parks for glow-in-the-dark worms?*” are all too common. They reflect a
99 deep misunderstanding of the hidden world beneath our feet, the fragile ecosystems
100 it sustains, and the profound influence it has on the surface environments where
101 humans live.

102 Studying “unremarkable” species thriving beneath the Earth surface might
103 seem like an indulgent pursuit, far removed from the pressing concerns of modern
104 life. After all, how could the presence of a whitish shrimp in a remote cave pond
105 possibly contribute to global challenges such as economic growth, public health, or
106 technological development? Far from trivial, these discussions reflect a broader
107 struggle to spotlight the invisible services provided by nature. The challenge, then, is
108 not merely defending one’s research but broadening collective understanding of
109 biodiversity’s essential functions—its intrinsic value and its critical role in maintaining
110 a healthy, habitable planet. The public cannot grasp what is at risk if scientists fail to
111 communicate these values.

112 When the concept of ecosystem services gained momentum after 1997, it
113 offered biodiversity scientists a powerful framework to articulate the societal
114 relevance of their work. Ecosystem services encompass all the functions and
115 products of ecosystems that benefit humans and contribute to societal welfare.
116 Initially conceived as a metaphor, the concept quickly evolved into a robust research
117 agenda focused on cataloging, quantifying, and mapping humanity’s reliance on
118 nature¹⁻³. For example, ecosystem services are frequently categorized into:
119 provisioning services (e.g., food, water), regulation and maintenance services (e.g.,
120 climate regulation, pollination, air and water quality), and cultural services (e.g.,
121 recreational, traditional practices and spiritual well-being). Notwithstanding the

122 inherent risk of putting a price tag on nature¹⁰, many of these services are also often
123 measured economically. This reflects the need to highlight the value of services that
124 are, in part, subjective and difficult to perceive outside of academic contexts^{11,12}.

125 While the quantification of ecosystem services has occupied the research
126 community for decades, knowledge remains incomplete for subterranean
127 ecosystems. Despite their hidden nature, subterranean ecosystems (Box 1) provide
128 and regulate services that are as critical to human well-being and ecological health
129 as those in surface ecosystems (Figure 1). The benefits derived from subterranean
130 ecosystems are remarkably diverse, with direct and indirect links to essential
131 functions such as freshwater provisioning, food production, and the regulation of
132 diverse biogeochemical and physical processes^{13–16}. Subterranean ecosystems also
133 contribute to essential “non-material” values, including scientific research and
134 inspiration^{17–19}, ecotourism^{20,21}, aesthetic appreciation^{22,23}, and cultural practices^{24,25}.

135 The questions driving this review are straightforward yet important: What
136 services do subterranean ecosystems provide, and how many of these have been
137 quantified to some extent? Answering these questions is urgent because,
138 paraphrasing the common adage, “you can’t manage what you can’t see and
139 measure”. Currently, information on the benefits provided by subterranean
140 ecosystems is scattered across numerous sources, many of which remain
141 inaccessible to the public. While a handful of reviews have compiled subsets of
142 these services for specific subterranean ecosystems^{16,26–30} or species³¹, a
143 comprehensive scheme that unifies all services across terrestrial, freshwater, and
144 marine subterranean compartments is still lacking. Moreover, integrating quantitative
145 rigor into this mapping exercise could enhance the perceived importance of these
146 services and help establish connections to the eco-evolutionary processes that
147 sustain them. Such an understanding could shift the narrative—from viewing
148 subterranean ecosystems merely as sources of water, geothermal energy, and
149 minerals to recognizing their broader ecological value. This, in turn, would reinforce
150 the importance of even partial data in designing conservation strategies that prioritize
151 ecosystem functions over isolated species or habitats³².



154 **Figure 1.** A visual summary of the main services associated with subterranean ecosystems. Original
 155 illustration by Jagoba Malumbres-Olarte.

156 **Box 1. What do we mean by “subterranean ecosystem”?** Subterranean
157 ecosystems are globally distributed and vary widely in extent and type of matrix.
158 Following the function-based classification of Earth’s ecosystems^{33,34}, we considered
159 ecosystems belonging to these biomes in terrestrial, freshwater, and marine
160 domains: ‘Subterranean’ (S) [including the ‘Subterranean lithic’ (S1) and
161 ‘Anthropogenic subterranean voids’ (S2) biomes], ‘Subterranean-freshwater’ (SF)
162 [including the ‘Subterranean freshwater’ (SF1) and ‘Anthropogenic subterranean
163 freshwater’ (SF2) biomes], and ‘Subterranean tidal’ (SM1). These include various
164 types of caves (e.g., aerobic caves, lava tubes, volcanic pits, anchialine caves, sea
165 caves) and other voids (e.g., fissure systems, deep scree strata), groundwater
166 ecosystems and their ecotones (e.g., aquifers, underground streams, ponds, lakes,
167 subterranean estuaries, anchialine pools, sinkholes, cenotes, blueholes, springs,
168 hyporheic systems), as well as anthropogenic subterranean voids (e.g., mines,
169 underground bunkers and tunnels, water pipes, subterranean canals, wells).
170 Conversely, excluded ‘Endolithic systems’ (S1.2)³³ or, in other words, the deep
171 biosphere—microbial communities occurring kilometers beneath the Earth’s surface
172 —due to the limited ecological data available and the uncertainty regarding their
173 connectivity to shallower ecosystems and ecosystem service provision^{35,36}.

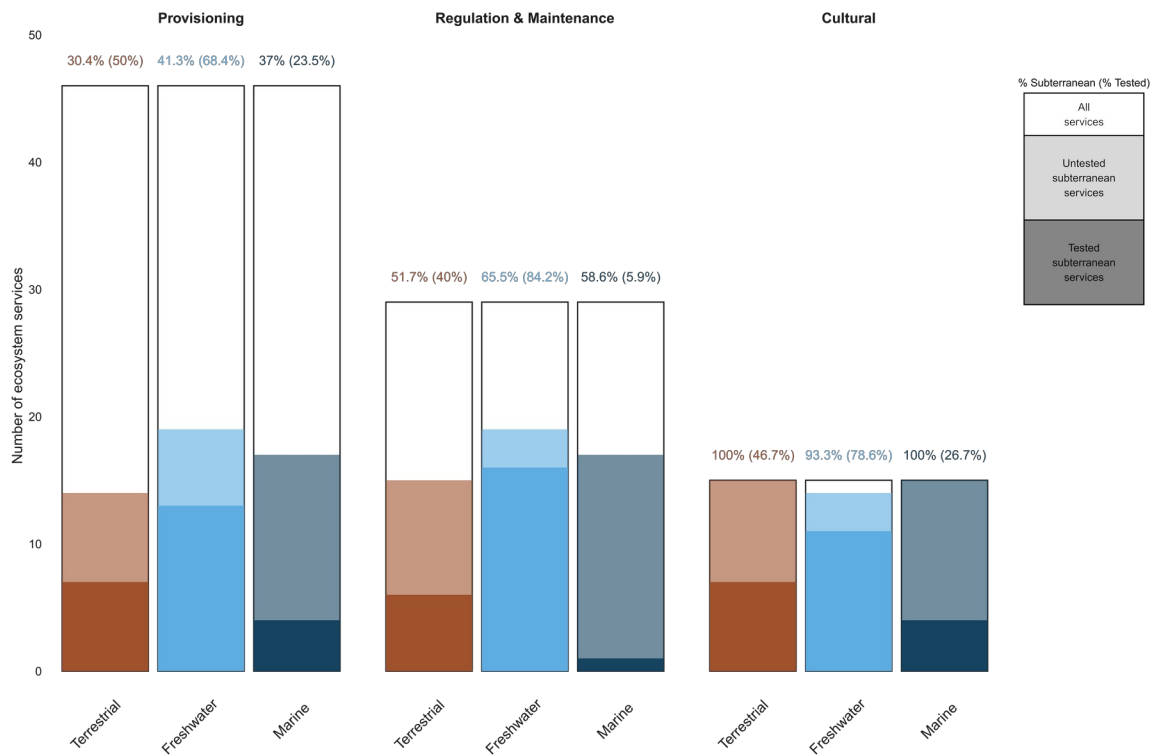
174 **Subterranean ecosystems services in numbers**

175 To map subterranean ecosystem services, we used the Common International
176 Classification of Ecosystem Services (CICES Version 5.1). CICES is a classification
177 scheme designed to measure, account for, and assess ecosystem services ⁹. The
178 services are categorized into three main “Sections” (Provisioning, Regulation &
179 Maintenance, and Cultural services) and two broad types within each section (biotic
180 and abiotic), with further breakdowns into levels of Division, Group, and Class.
181 Conveniently, CICES is interoperable with other ecosystem service classification
182 systems by providing equivalency across various schemes. CICES lists 90 primary
183 services—63 biotic and 27 abiotic. Using this backbone classification, we assessed
184 whether subterranean ecosystems contribute to the various ecosystem services
185 listed in CICES based on our expert knowledge and the literature. To strengthen our
186 evaluation, we conducted a literature review for each service to assess quantitative
187 estimates of the services provided by subterranean ecosystems.

188 According to our mapping exercise (see [Data availability statement](#)),
189 subterranean ecosystems contribute to up to 75% (68 out of 90) of the ecosystem
190 services classified by CICES. This contribution is higher than the estimations for
191 ecosystem services provided by grasslands (36%)³⁷, urban water bodies (43%)³⁸,
192 mangrove ecosystems (33% of the biotic services)³⁹, or vineyards (64%)⁴⁰. When
193 considering specific systems, terrestrial, freshwater, and saltwater subterranean
194 compartments match 48%, 57%, and 54% of the services classified by CICES,
195 respectively.

196 Of all the 68 matching services, between one third and a half have been
197 quantified (i.e., measured numerically) ([Figure 2](#)), primarily by local case studies.
198 Most of the identified services benefit society at large, although specific services
199 appear to be most important for specific economic sectors ([Figure 3](#)). Groundwaters,
200 particularly freshwater systems, dominate in the percentage of measured ecosystem
201 services. This is likely both due to their accessibility and measurability compared to
202 terrestrial and marine systems and the crucial importance of groundwater for drinking
203 and irrigation. Indeed, human settlements are often located where there is access to

204 aquifers, through springs, caves, wells and boreholes. These features allow for direct
205 sampling and regular monitoring. In comparison, terrestrial and marine subterranean
206 ecosystems are less accessible, often requiring specialized and costly technologies
207 for exploration⁴¹⁻⁴³.



210 **Figure 2.** The number of Provisioning, Regulation & Maintenance, and Cultural services provided by
 211 terrestrial, freshwater, and saltwater subterranean ecosystems (colored bars) compared to the total
 212 services mapped by the Common International Classification of Ecosystem Services (white bars).
 213 Darker shades indicate the fraction of subterranean services that have been quantitatively assessed
 214 in at least one study.

215 **Provisioning services**

216

217 Provisioning ecosystem services are the tangible goods and resources that
218 ecosystems provide to humans⁹. These services are the direct products we obtain
219 from nature, such as freshwater, food, raw materials, medicinal resources, and
220 energy. Subterranean ecosystems contribute to as many as 63% of the provisioning
221 ecosystem services classified by CICES (Figure 3).

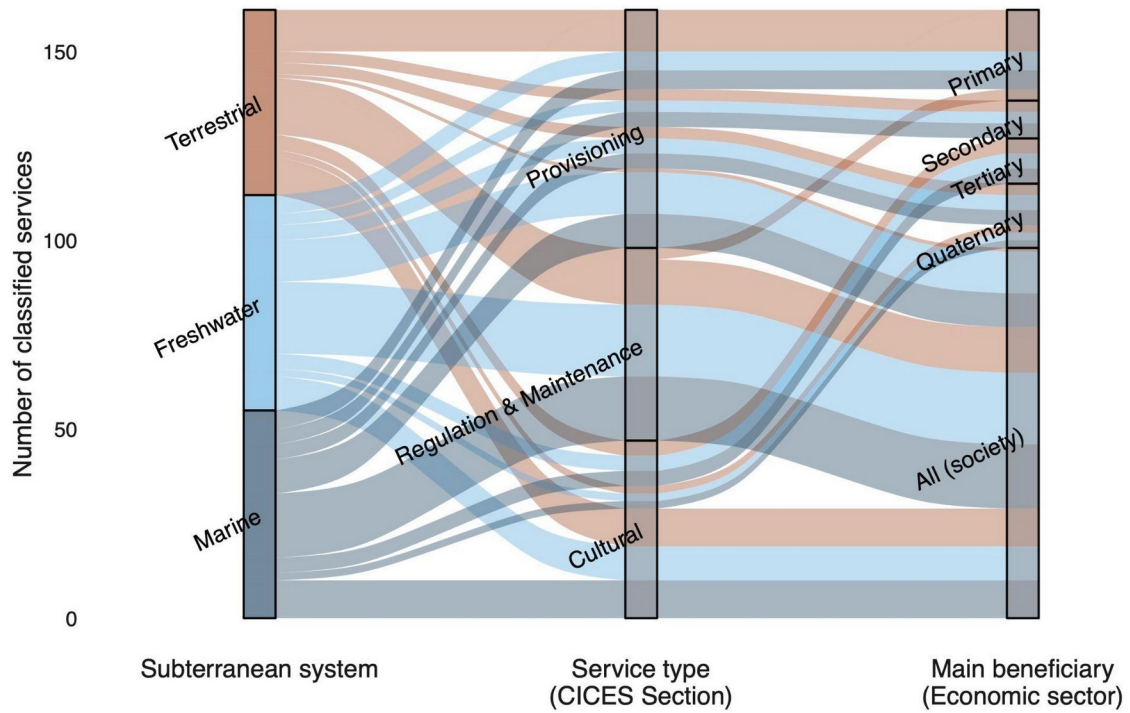
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223 *Water supply*

224

225 Groundwater, the largest unfrozen continental reserve of freshwater globally^{44,45}, is a
226 prime source of water for drinking, irrigation, and industrial use¹³ (Figure 4A, 4B). It is
227 estimated that groundwater constitutes approximately 95% of the planet's accessible
228 liquid freshwater resources, including drinking water. Over a quarter of the global
229 population relies on this resource, either partially or entirely⁴⁶. Current human
230 groundwater use is estimated to exceed the capacity of aquifers by about 3.5 times
231 and groundwater decline is accelerating at the global scale⁴⁷. About 43% of irrigation
232 water and 49% for domestic use is sourced from groundwater⁴⁸, and this figure is
233 likely to become even more pronounced due to continuous population growth and
234 increasing frequency of droughts and extreme events connected with climate change
235 intensity^{48,49}.

236 Still, there are large uncertainties in global estimations of the total volume of
237 groundwater^{44,45}, where it is distributed⁴⁵, its depth⁵⁰, recharge rates⁵¹, and patterns of
238 human extractions⁵². Besides quantity, water quality is very relevant, which primarily
239 depends on geochemical processes and anthropogenic impacts but also, at least
240 partially, on the presence of subterranean organisms (see section "Regulation &
241 Maintenance Services").



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Figure 3. Importance of ecosystem services provided by terrestrial, freshwater, and marine subterranean ecosystems to socio-economic sectors (primary: resource extraction; secondary: manufacturing; tertiary: services; quaternary: knowledge-based activities). “All society” represents services with transversal benefits, not limited to a single sector.

248 *Energy production*

249 Subterranean ecosystems are increasingly used for heating, cooling, and direct
250 energy production. Geothermal heat pump systems, which use heat from shallow
251 underground sources, are the fastest-growing segment of geothermal technology
252 and one of the fastest-growing renewable energy options in the world. Other direct
253 uses, such as heating buildings, bathing, swimming, industrial processes, farming
254 (especially greenhouses), and fish farming, are generally based on deep
255 hydrothermal resources⁵³. Deep geothermal energy plants produce hot water,
256 directly used for heating purposes (e.g., via district heating networks) or turn the heat
257 into electrical power. The global geothermal energy production of 95 TWh yr⁻¹
258 represents about 10% of the sustainable electricity generated annually. Among
259 renewables, geothermal power has the highest potential in the future accounting for
260 about 67%. Solar power, wind power, power from biomass, and hydropower account
261 for 21%, 8%, 3.5%, and 0.1%, respectively^{53–55}.

262 When considering subterranean ecosystems, it is the use of shallow
263 geothermal energy that requires the most attention. In geology, the boundary
264 between 'shallow' and 'deep' is typically set at a depth of 400–500 meters, which
265 corresponds, with only a few exceptions, to the deepest known occurrence of
266 subterranean fauna⁵⁶. Most geothermal heat pump systems operate with relatively
267 shallow closed-loop borehole heat exchangers, often complemented by open,
268 groundwater-based systems. The shallow subsurface is warmer in winter and cooler
269 in summer compared to the outside air. By using geothermal heat pump systems,
270 this temperature difference can provide heating in winter and cooling in summer.
271 However, it is important to note that extracting heat or cold from the subsurface can
272 alter thermal conditions in ways that may be harmful from an ecological perspective.
273 It can also induce temperature fluctuations resembling surface seasonality, though
274 with much smaller temperature differences. Among these effects, warming is the
275 main factor that puts pressure on subterranean communities⁵⁷. Warming also
276 accelerates the metabolism of both microbes and fauna, leading to faster
277 consumption of dissolved oxygen and potentially resulting in hypoxic or anoxic
278 conditions. These oxygen-depleted conditions can cause the disappearance of fauna

279 and are followed by a decline in water quality⁵⁸. Thus, energy production through
280 geothermal use can be in conflict with the health of subterranean ecosystems—
281 alongside other global driver of subsurface warming such as climate change⁵⁹ and
282 urbanisation^{60,61}.

283

284 *Food production*

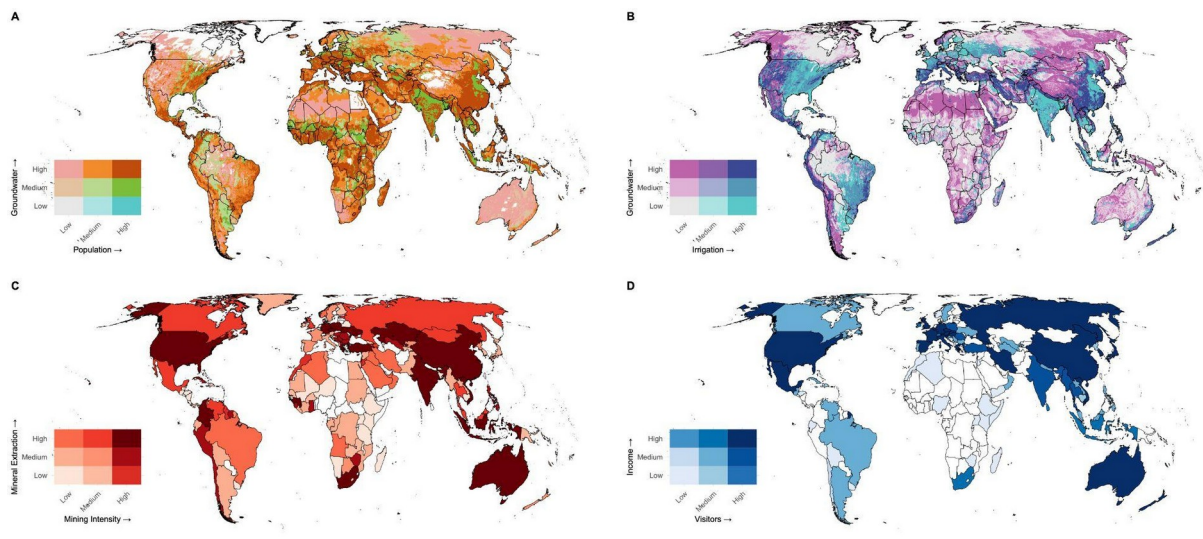
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286 Groundwater is critical for global food security, supplying over 40% of the water used
287 for irrigation and supporting approximately 13% of total food production⁶² (Figure
288 4B). Groundwater enables both large- and small-scale farmers to enhance
289 agricultural output, particularly in regions where rainfall is insufficient to meet crop
290 water demands⁶³. Even though the negative effect of irrigation can be mitigated^{64,65},
291 groundwater resources are increasingly being overexploited, especially in major
292 agricultural regions such as California’s Central Valley, the High Plains Aquifer in the
293 U.S. Midwest, the Middle East, the Indus and Ganges Basins, and the North China
294 Plain⁶⁶. Currently, India is the world’s largest consumer of groundwater, supplying
295 approximately 60% of its irrigation needs⁶⁷. Among internationally traded crops, rice
296 is the most groundwater-intensive, accounting for 29% of global usage, followed by
297 wheat (12%), cotton (11%), maize (4%), and soybeans (3%). Citrus and sugar crops
298 also account for approximately 5% of groundwater use for irrigation each⁶⁸.

299 Beyond these agricultural trends, subterranean environments have been
300 central to food production and foraging practices for millennia. Shepherds have
301 historically used caves and caverns as shelters to protect livestock from harsh
302 weather conditions^{69,70}. Additionally, caves were integral to traditional food
303 preservation and production, particularly in cheese and wine-making, as well as
304 mushroom cultivation, where their stable temperatures and humidity make them
305 natural analogs to cellars^{71,72}. A case-in-point is *Penicillium roqueforti*, a fungus
306 discovered in the limestone caves above Roquefort, France, where the mold
307 accidentally transformed cheese into a flavorful delicacy, now renowned as
308 Roquefort cheese.

309 Subterranean ecosystems and their ecotones also contribute to the service of
310 food production by enabling aquaculture or as habitat for commercially or culturally

311 important species. For example, anchialine pools have been used to keep fish for
312 fresh consumption or even to cultivate fish bait used in traditional mackerel
313 fisheries⁷³, as in the case of the red shrimp *Halocaridina rubra* (‘ōpae‘ula) in
314 Hawai‘i⁷⁴. The nests and eggs of cave swiftlets (*Collocalia linchi*) and Cory’s
315 shearwaters (*Calonectris diomedea*) are harvested for their nutritional ⁷⁵ or traditional
316 medical value⁷⁶. Oilbirds (*Steatornis caripensis*) are exploited in South America for
317 their flesh and fat (oil), used for cooking and lighting⁷⁷. Bats are hunted as a meat
318 source in Asia and Africa⁷⁸. Depending on species and locations, bats are either
319 considered a delicacy or an affordable source of protein during times of food
320 scarcity^{79,80}. However, such practices may threaten endangered species and their
321 habitats⁸¹.



323

324

325 **Figure 4. Global mapping of major subterranean ecosystem services based on proxy variables.**

326 A) Groundwater depth and human population density, illustrating potential hotspots where there will

327 be pressure in terms of groundwater extraction. Pink areas indicate regions where groundwater is

328 deeply underground and difficult to access, with low population densities. Dark orange areas

329 represent regions where groundwater is also difficult to access but have high population densities. B)

330 Groundwater depth and irrigation intensity, illustrating potential hotspots where there will be pressure

331 in terms of groundwater extraction. Dark blue areas indicate regions that are highly irrigated and face

332 greater difficulty accessing groundwater. In both A and B, groundwater availability is measured as the

333 depth from the land surface to the point where groundwater begins (source: ref. ⁸²). A shallow depth

334 means groundwater is close to the surface, whereas a greater depth indicates it is further

335 underground. Dark orange and dark blue areas highlight regions where accessing groundwater is

336 particularly challenging, especially in the absence of shallow water resources. C) Global mining

337 pressure, illustrating potential hotspots where mining activities may reduce subterranean habitat

338 availability. Mining intensity is calculated based on the percentage of each country's area occupied by

339 mines (source: ref. ⁸³) and the total extracted tonnage of target minerals (source: World Mineral

340 Statistics contributed by permission of the British Geological Survey). D) Annual number of show cave

341 visitors per country and associated income, estimated based on cave entrance fees (in dollars)

342 (source: ref. ²⁰). Note that political borders in the maps are based on open sources, and do not reflect

343 the views of the coauthors or the institutions in which the work.

344 *Raw materials*

345

346 Rock, mineral, and materials extracted from subterranean ecosystems account for a
347 major part of the global economy (Figure 4C). The effects of mining, including rock or
348 mineral extraction itself and all the infrastructure involved, potentially influences 50
349 million km² of the planet's surface⁸⁴. In 2025, the global production of minerals is
350 expected to reach 15 billion tons⁸⁵, with a value exceeding 7 trillion USD in 2024 and
351 constituting an important part of the national GDP in many countries⁸⁶.

352 Many of the mining areas coincide with protected, key biodiversity and
353 wilderness areas. Hence, mining activities impact subterranean ecosystems, either
354 directly (e.g., loss of habitat) or indirectly (aquifer contamination)^{87,88}. For example,
355 iron ore production in Brazil accounts for approximately 1.6% of the country's GDP,
356 generating around 31 billion US\$ in 2022. With thousands of caves associated with
357 iron ore landscapes, mining activities severely threaten these unique subterranean
358 ecosystems, which are recognized for their significant diversity of cave-restricted
359 species^{89,90}.

360 A special case of mining involves bat and bird guano, which can be locally
361 abundant—millions of bats gathering in cave colonies can produce guano piles as
362 high as 10 meters⁹¹. Guano is widely used as a fertilizer due to its high nitrogen and
363 phosphorus content⁹², or as a source of chitin and chitosan for cosmetics,
364 pharmaceuticals, and textiles^{93,94}. Bat guano fertilizer typically costs US\$ 2.50–24.00
365 per 1 kg⁹².

366

367 *Biomolecular resources and emerging technologies*

368

369 Subterranean ecosystems are a promising source of molecules and compounds with
370 biotechnological applications, though bioprospective activities are still in their early
371 stages. Subterranean microbial biofilms often influence mineral precipitation and
372 dissolution⁹⁵, particularly through polymeric substances that are produced and
373 secreted by microbes (mediating microbial adhesion on surfaces) and may serve as
374 nucleation sites for mineral precipitation, promoting the growth of cave formations
375 (speleothems)^{96–98}. Secondary metabolites produced^{96–98} by microbes within those

376 biofilms may have biotechnological and pharmaceutical applications as well,
377 including use as enzymes, biosurfactants, or as antitumoral, immunosuppressive,
378 and immunostimulatory agents^{98–105}. Some subterranean microorganisms with
379 extracellular hydrolytic activity and antimicrobial compound production may be
380 relevant against multidrug-resistant pathogens^{99,106,107}. For example, extracts of
381 bacterial isolates from lava tubes of Lanzarote (Canary Islands) showed
382 antimicrobial activity against the pathogenic strains *Staphylococcus aureus*,
383 *Escherichia coli*, and *Pseudomonas aeruginosa*, and exhibited antiproliferative
384 activity against human breast cancer cells¹⁰⁴.

385 Beyond microbes, larger subterranean organisms have also been explored for
386 their biomolecular potential. For example, many sessile invertebrates in marine
387 caves (e.g., sponges, anthozoans, bryozoans, and tunicates) contain or secrete
388 compounds with significant application potential^{108–112}. This biotechnological potential
389 may also arise from more subtle interactions between microscopic and macroscopic
390 organisms. For instance, animal excrement in caves, which often harbors pathogenic
391 viruses, may stimulate microorganisms to produce antiviral substances¹¹³.

392 Finally, the unique biological adaptations of several subterranean species
393 hold promise for biomimicry, particularly in developing sensors, biomaterials,
394 adhesives, and biologically inspired robotic movement¹⁹. In recent years, medical
395 applications inspired by subterranean adaptations have also gained attention,
396 ranging from potential treatments for diabetes¹¹⁴ and autism¹¹⁵ to innovations in
397 blindness research¹¹⁶. Despite these possibilities, this potential remains largely
398 untapped, with most studies still far from yielding concrete applications.

399

400 **Regulation & Maintenance services**

401

402 Regulation & Maintenance services provide the abiotic and biotic processes and
403 environmental conditions that benefit living organisms, including humans⁹. Hence,
404 these services offer stability, safety, and resilience to both ecosystems and human
405 societies, and subterranean ecosystems contribute to as many as 82% of these
406 (Figure 3).

407

408 *Regulation of physico-chemical conditions*

409

410 Subterranean ecosystems are central to global water and (bio)geochemical cycles,
411 including carbon, nitrogen, and other key elements (e.g., phosphorus, sulphur, and
412 iron)^{13,36,117}. Given their role in maintaining freshwater, seawater, and atmospheric
413 balance, subterranean ecosystems are increasingly recognized as vital to global
414 sustainability efforts. In particular, subterranean environments may be integral to
415 Earth System governance frameworks such as the planetary boundaries, where
416 groundwater has already been proposed as a key component¹³. The planetary
417 boundaries define a set of critical biogeophysical processes that collectively regulate
418 the stability and resilience of the Earth System^{118,119}.

419 Hotspots for these biogeochemical processes are typically located along
420 environmental gradients, redox interfaces, ecotones, and other transition zones in
421 both terrestrial (e.g., subsurface-surface atmosphere, sediment/rock-atmosphere
422 interfaces) and aquatic settings (e.g., land-sea, sediment-water, and water-
423 atmosphere interfaces)¹²⁰. These environmental gradients span micro (<mm) to
424 regional scales (>km), and their role in regulating chemical fluxes and ecosystem
425 functioning is often disproportionately large relative to their size¹²¹. Some of these
426 processes may also be mediated within the so-called “deep biosphere” (Box 1)—
427 following the recognition that bacteria and archaea can occur kilometers deep in the
428 Earth's crust³⁵. Yet, major gaps remain in our understanding of their extent, function,
429 and role in global biogeochemical cycling³⁶.

430 Biogeochemical processes associated with subterranean ecosystems
431 primarily regulate the chemical conditions of freshwater and marine habitats. Natural
432 and anthropogenic inputs of nutrients and organic matter from the surface into the
433 groundwater increase dissolved organic carbon (DOC) and nitrate concentrations—
434 important indicators of water quality—that are then attenuated through microbial
435 activity¹⁶. For instance, redox-driven microbial processes under aerobic or anaerobic
436 conditions (e.g., denitrification and iron reduction) can substantially consume nitrate
437 and reduce or transform DOC as groundwater migrates through subterranean
438 freshwater environments¹⁵ or discharges into the sea¹²². Marine caves and cavities in

439 tropical regions are also areas of heterotrophic DOC consumption¹²³, which depletes
440 dissolved oxygen¹²⁴.

441 Fresh groundwater discharge only accounts for a minor portion (~0.6%) of the
442 total freshwater input to the world's oceans¹²⁵, but it can be critical locally for coastal
443 ecosystem functioning due to its high solute and nutrient loads¹²⁶. At the land-sea
444 interface, the region of a coastal aquifer where seawater and groundwater mix—the
445 subterranean estuary—is a biogeochemical reaction zone that modulates nutrient
446 and carbon fluxes from rocky, sandy, and muddy coastlines to marine ecosystems
447 and fisheries^{122,127}. For example, microbial activity reduces nitrate and methane
448 concentrations in groundwater discharged from sandy coasts^{128,129}, and methane and
449 DOC in groundwater discharging from karstic coastlines^{130,131}. Moreover, sinkholes
450 along karst coastlines are hotspots for carbon burial¹³², highlighting their potential for
451 inclusion in blue carbon stocks. Given that approximately 40% of the world's
452 population lives within 100 km of the coast, understanding these dynamics is of
453 growing global importance¹³³.

454 Beyond biogeochemical cycles, subterranean ecosystems regulate key
455 physical conditions in the environment. For example, hydrogeological conditions in
456 aquifers control land subsidence, a phenomenon mainly driven by excessive
457 groundwater extraction and aquifer compaction, a process that occurs when an
458 aquifer's volume and storage capacity decreases due to the removal of water, often
459 resulting in land subsidence. Globally, land subsidence leads to the loss of aquifer
460 storage (~17 km³/year) and affects mainly cropland and urban areas (73%)¹³⁴.
461 Consequences include damage to infrastructure, increased flood hazards, and
462 substantial economic and human impacts^{135,136}.

463 Groundwater also supports ecosystem services provided by groundwater-
464 dependent ecosystems¹³⁷, such as water storage, purification, and flood control. In
465 turn, groundwater-fed vegetation controls erosion rates¹³⁸, buffers and attenuates
466 mass movement, and regulates the overall hydrological cycle and water flow, and
467 contributes to flood control and coastal protection. For example, tidal marsh
468 vegetation stabilizes sediment and prevents shoreline erosion¹³⁹, while riparian trees
469 like willows (*Salix* spp.) reduce erosion along riverbanks during heavy flow¹⁴⁰. The
470 value of groundwater-fed vegetation in flood control has been estimated at about €16

471 billion in the EU alone¹⁴¹. Moreover, groundwater provides essential baseflow to
472 rivers, particularly during dry seasons, sustaining river flow and influencing nutrient
473 cycling and contaminant transport. Globally, baseflow is estimated to account for
474 59% ± 7% of river flow¹⁴².

475

476 *Regulation of biological conditions*

477

478 Subterranean ecosystems largely support surface vegetation^{137,143} and marine
479 habitats^{122,144}. Approximately 37% of the world's vegetation depends on groundwater
480 to some extent^{145,146}. The quality and availability of groundwater influence the
481 distribution, diversity, functioning, and resilience of these plant communities¹⁴³. This
482 dependency is particularly pronounced in drought-prone regions, where threshold
483 levels of groundwater availability serve as indicators of potential drought refugia¹⁴⁷.
484 Groundwater discharged into the marine environment delivers nutrients and affects
485 water quality in estuaries, coral reefs, lagoons, mangroves, and saltmarshes^{122,148}.

486 Subterranean ecosystems also act as temporary, daily, or seasonal habitats
487 for many surface animals and plants, all of which are integral to interconnected
488 subterranean-surface food webs¹⁷. Surface vertebrates shelter or nest in cave
489 entrances^{149–151}, while bats mate near entrances, but breed and hibernate in deeper
490 sections¹⁵². Different vertebrates and invertebrates move in and out of terrestrial
491 caves, often guided by circadian rhythms or seasonal cues^{151,153–155}. Aquatic insects,
492 crustaceans, and fish seek refuge in the hyporheic zone of rivers during droughts¹⁵⁶.
493 Groundwater inputs also heavily influence freshwater fish behavior, migration,
494 spawning, and distribution¹⁵⁶. Similarly, marine caves host diverse sessile
495 invertebrates (e.g., sponges, corals, bryozoans and brachiopods), fishes, and
496 crustaceans, including many economically and ecologically valuable species such as
497 the precious red coral *Corallium rubrum*¹⁵⁷. As climate become more unpredictable,
498 these subterranean refugia are expected to grow in importance because of their
499 environmental stability⁵⁷.

500 Arguably, cave-dwelling bats represent the best-studied example of biological
501 regulation by subterranean ecosystems. Bats provide critical pollination and seed
502 dispersal services for economically important plants, including figs, durian, mango,

503 and agave^{31,158}. For instance, the pollination services of *Eonycteris spelaea* to durian
504 farmers in Sulawesi, Indonesia, were valued at US\$117 per hectare during each
505 fruiting season¹⁵⁹. Another notable example is the mutualistic relationship between
506 bats and agave. The pollination of agave relies on bats, particularly the cave-
507 dwelling *Leptonycteris nivalis*, which, in turn, depend on agave during their seasonal
508 migrations¹⁶⁰. Agave holds cultural and economic significance in Mexico as a source
509 of food, spirits (tequila and mezcal), and fiber.

510 Insectivorous bats are also key biological controllers due to their hunting
511 efficiency. For example, the cave-dwelling species *Pteronotus gymnonotus* and *P.*
512 *personatus* consume 5–28% of their body weight in insects each night¹⁶¹. At least 81
513 species of insectivorous bats, including several obligate or facultative cave-dwellers,
514 prey on over 760 species of insect pests that affect economically important crops
515 such as corn, coffee, cotton, rice, apples, macadamia nuts, cocoa, and grapes¹⁶².
516 Some of these species form massive colonies. For example, Mexican free-tailed bats
517 (*Tadarida brasiliensis*) can form colonies of millions of individuals. During the
518 summer, when bat populations peak in Bracken Cave, Texas, they can remove
519 approximately 100 tons of insects per night, with the annual value of this pest
520 suppression estimated at US\$3.42 million³¹. The economic importance of
521 insectivorous bats in Northern America has been estimated to be as high as
522 exceeding US\$3.7 billion per year¹⁶³.

523

524 *Mitigation of pollutants*

525

526 The Chemical Abstracts Service lists >200 million organic and inorganic synthesized
527 compounds, with 20,000–30,000 new entries added daily¹⁶⁴. Many of these
528 chemicals, especially those produced in large volumes, are released into the
529 environment and eventually make their way underground, either passively (e.g.,
530 through percolating water) or intentionally (historically, shallow aquifers and caves
531 were often used as waste disposal sites)^{165,166}.

532 Against this backdrop, a critical service is self-purification—the removal or
533 immobilization of pollutants by natural processes²⁷. Subterranean microorganisms
534 are key actors in this process, transforming harmful substances into more stable or

535 less toxic forms. For example, bacteria such as *Alcaligenes*, *Acinetobacter*, and
536 *Pseudomonas* can immobilize heavy metals or dissolve phosphate minerals, aiding
537 in the removal of contaminants¹⁶⁷. As for organic pollutants, microbes can degrade or
538 mineralize compounds like petroleum hydrocarbons and halogenated solvents,
539 particularly in point-source contamination scenarios¹⁶⁸. However, these processes
540 are often slow, as microbial activity in subsurface environments is limited, and
541 groundwater contamination can persist for years^{169,170}. For example, nitrates persist
542 in groundwater for decades unless hypoxic or anoxic conditions and an appropriate
543 electron donor (e.g., organic matter, pyrite) are present¹⁷¹.

544 Self-purification processes may be stimulated via amendment of electron
545 acceptors (e.g., dissolved oxygen), electron donors (e.g., molasses), and bacterial
546 strains (termed bioaugmentation)¹⁷². Managed aquifer recharge systems can
547 effectively remove contaminants¹⁷³, including pharmaceuticals and antibiotics,
548 through degradation processes that depend on the aquifer's redox state and
549 temperature¹⁷⁴. However, biotransformation processes can sometimes produce
550 byproducts that are recalcitrant to further degradation or more toxic than their parent
551 compounds, highlighting the complexity of chemical regulation in groundwater
552 systems¹⁷⁵.

553 Beyond microorganisms, larger subterranean fauna may also contribute to
554 water purification through bioturbation of sediments and filtration^{176,177}. Based on
555 consumption rates and rough density estimates of the isopod *Phreatoicus typicus* in
556 New Zealand, it has been estimated that a population of 100 individuals can process
557 approximately 7–28 tonnes of sediment per hectare annually and assimilate 120–
558 650 grams of organic carbon per hectare annually¹⁷⁶. Synergistic effects with
559 microorganisms appear to be particularly important in this context. Amphipods,
560 isopods, and other invertebrates bioturbate and aerate sediments, creating favorable
561 conditions for microbial communities to degrade contaminants^{176–178}. For example,
562 the isopod *Coecidotaea tridentata* enhances both planktonic and sedimentary
563 bacterial abundance and activity through the excretion of nitrogen, which promotes
564 microbial growth, the disturbance of sediments, and the direct consumption of
565 bacteria¹⁷⁹.

566

567

568 *Potential for climate change mitigation*

569

570 Subterranean ecosystems—particularly karst environments and caves—play a
571 surprisingly important yet understated role in locally regulating atmospheric
572 composition. Microbially-mediated formation of speleothems, such as moonmilks,
573 sequesters and stores CO₂^{180,181}. Furthermore, aerobic caves act as net sinks for
574 atmospheric methane (CH₄), actively consuming this greenhouse gas through
575 microbial oxidation mediated by methane-feeding (methanotrophic) bacteria^{182–184} or
576 through other processes¹⁸⁵. Within flooded caves of a karst subterranean estuary, it
577 is estimated that ~1.4 tons of methane was consumed during 6 months across a
578 ~100 km² catchment region in the Yucatán Peninsula¹³¹. It is unlikely that this
579 magnitude of methane removal would affect global greenhouse gas budgets, but it
580 quantifies the contribution of a critical energy source for an anchialine food web¹³⁰.

581 Beyond gas fluxes, subterranean ecosystems exert influence on microclimatic
582 conditions. Their ability to buffer temperature and maintain high humidity levels
583 creates stable environments that interact with aboveground climates, especially in
584 regions with extensive karst topography^{186,187}. In terrestrial systems, this kind of
585 regulation is often aided by bryophyte cushions (mosses and liverworts) developing
586 in the entrance-zone of caves, which function as living sponges, intercepting rainfall,
587 fog, and dew and retaining water volumes several times their dry mass. By slowly
588 releasing this stored moisture into the substrate and underlying fissures, they buffer
589 hydrological extremes at the subterranean-surface interface, sustain high local
590 humidity for microbial and faunal communities, and contribute measurably to the
591 water-storage service of groundwater-dependent ecosystems¹⁸⁸. In aquatic and
592 marine settings, flooded caves and other subterranean environments have an
593 important role in heat transfer through groundwater transport. Aquifers in rocky
594 coastlines, such as karstic and volcanic platforms, are distinct from others, because
595 the fissures and conduits enhance hydraulic transport and exchange of material with
596 the sea through diffuse processes or submarine springs^{144,189,190}. Tidal driven
597 oscillation of fresh groundwater discharge has been shown to transport heat to the
598 sea from a volcanic platform¹⁹¹. On the contrary, tropical carbonate platforms may

599 cool the nearby sea through fresh groundwater discharge while facilitating the
600 marine-derived saline water to import heat from the coast to inland¹⁹².

601 Beyond caves, groundwater-dependent ecosystems such as groundwater-fed
602 wetlands, fens, riparian forests, and woodlands facilitate atmospheric CO₂ uptake
603 through photosynthesis, root respiration, bicarbonate formation in soil, and the
604 subsequent storage of carbon in groundwater or its precipitation as calcium
605 carbonate¹⁹³. Vegetation supported by groundwater, such as the redwood forests of
606 Northern California, grows more robustly and for longer periods compared to
607 vegetation without groundwater access, sequestering significantly more carbon¹⁹⁴.
608 Notably, areas with groundwater-dependent ecosystems store approximately 790
609 million tons of CO₂—nearly double California’s annual emissions¹⁹⁴. However, these
610 benefits can be counterbalanced by the dewatering of groundwater-dependent
611 ecosystems. For example, estimates suggest that wetlands could emit ~408 gigatons
612 of CO₂ between 2021 and 2100 if degraded or drained¹⁹⁵.

613

614 **Cultural services**

615

616 Cultural ecosystem services are the non-material benefits people derive from
617 ecosystems, contributing to cultural identity, spirituality, scientific endeavors, and
618 quality of life⁹. Subterranean ecosystems contribute to all ([Figure 3](#)).

619

620 *Tourism and recreation*

621

622 Terrestrial and marine caves are among the most frequently visited geo- and
623 ecotourism attractions worldwide. A recent synthesis identified 1,223 show caves
624 across 95 countries, involving an estimated 79 million visitors in 2019²⁰. This
625 generates around 800 million euros in entrance fees, with an even greater economic
626 impact when considering related tourist activities—souvenir shops, restaurants, bars,
627 and local transport ([Figure 4D](#)). Inevitably, this level of tourism comes not without
628 impacts, including structural damage to caves, alterations to local climatic conditions,

629 the introduction of external organic matter and non-native fungi, bacteria, and
630 animals, and the growth of photosynthetic organisms due to artificial lighting²¹.

631 Furthermore, geothermal phenomena linked to subterranean ecosystems—
632 such as boiling lakes, mud ponds, and geysers—serve as striking natural attractions,
633 drawing visitors to destinations that blend wonder with recreation. Some of these
634 features also fuel the wellness sector. Thermal springs, long used by humans—and
635 other apes¹⁹⁶—for health and wellness, are increasingly being transformed into
636 modern hot spring resorts and water parks. Similarly, speleotherapy, particularly
637 speleoclimatotherapy and radon therapy, offers drug-free therapeutic benefits. For
638 example, the unique microclimate of salt caves and mines—characterized by fine
639 aerosols of NaCl, K⁺, and Mg²⁺, high humidity, low radiation, light air ions,
640 hypoallergenic air, and stable temperature—effectively alleviates different respiratory
641 syndromes¹⁹⁷.

642 Terrestrial and aquatic caves are popular recreational sites for activities such
643 as caving, snorkeling, scuba diving, and boat tours^{198,199}. These activities range from
644 spontaneous experiences lasting a few hours, undertaken solo or in groups, to more
645 structured expeditions and cave trips that require advanced speleological knowledge
646 and skills. Often this kind of tourism brings visitors to caves that would be closed to
647 humans otherwise, which may cause local impact to the ecosystems but also
648 enhance scientific knowledge by citizens, amateur scientists, and speleologists.

649 Finally, subterranean-related ecotourism offers opportunities for wildlife
650 enthusiasts to observe animals in their natural habitats. For instance, bat-watching is
651 increasingly popular worldwide²⁰⁰. The nightly emergence of millions Mexican free-
652 tailed bats from caves in the Southwestern US is estimated to attract over 240,000
653 visitors each year, conservatively valued at \$6.5 million annually²⁰¹. Such activities
654 support local economies and provide unique educational experiences for the public,
655 raising awareness about the ecological significance of subterranean ecosystems.

656

657 *Aesthetic and artistic value*

658

659 Subterranean landscapes inspire and support a range of artistic expressions^{22,23}. For
660 instance, artistic practices have explored groundwater as a theme through creative

661 expressions of its sensory qualities—tastes, smells, sounds, textures, and
662 movements—as well as its landscapes, cultural significance, and community
663 connections²³. Contemporary abstract art frequently draws from the textures and
664 patterns of speleothems, as seen in the cave-inspired works of artist Ana Teresa
665 Barboza. Literature has frequently embraced subterranean themes, such as Jules
666 Verne’s *Journey to the Center of the Earth* and Haruki Murakami’s *Hard-Boiled*
667 *Wonderland* and the *End of the World*. Music, too, draws inspiration from
668 subterranean acoustics, with composers like John Luther Adams creating pieces that
669 echo the resonant and mysterious qualities of caves. Architecture has similarly
670 demonstrated how caves and sinkholes can be reimagined into cultural and artistic
671 venues, with spaces like *Los Jameos del Agua* in Lanzarote, shaped by César
672 Manrique and Jesús Soto. These are just a few examples among many^{22,23}.

673 It has been argued that subterranean-related art may improve scientific
674 communication and support the conservation of subterranean ecosystems^{22,23,202}. For
675 example, projects such as the virtual reconstructions of cave art by the Chauvet
676 Cave team not only preserve these fragile environments but also educate the public
677 about their ecological and historical significance. Likewise, the Cenoteando initiative
678 (<https://cenoteando.mx/>) in Mexico, has developed several educational materials that
679 combine scientific accuracy with artistic expression to promote environmental
680 awareness and proper stewardship of cenotes, promoting a sustainable interaction
681 with these fragile environments. Similarly, artworks and photography that highlight
682 the fragility of subterranean ecosystems, such as those by environmental artists like
683 Agnes Denes and Martin Broen, can galvanize support and financial backing for
684 conservation campaigns. Lastly, there is a practical significance to exploring
685 aesthetics of subterranean features. For example, groundwater aesthetics—taste,
686 odor, color, and clarity—is essential in shaping cultural perceptions and public trust
687 in water supplies²⁰³.

688

689 *Scientific research*

690 Terrestrial caves have long been regarded as model systems for scientific research
691 across various fields^{18,204,205}. The convergent adaptations of subterranean organisms
692 make subterranean ecosystems a rich subject for evolutionary research, with a

693 lineage of studies tracing back to Charles Darwin²⁰⁶. Several cave-adapted species,
694 such as cavefish and crustaceans, serve as established model organisms for
695 evolutionary studies and beyond⁴². Furthermore, due to their climatic stability, low
696 biological diversity, simple habitat structure, and often isolated nature, caves allow
697 researchers to minimize many confounding factors that typically complicate
698 ecological studies in surface environments¹⁷. Similarly, marine caves in the littoral
699 zone have been described as “deep-sea mesocosms”, providing direct human
700 access to deep-sea-like conditions²⁰⁷.

701 Importantly, this expanding research agenda builds upon the observations
702 made by individuals who regularly explore subterranean environments, often driven
703 by personal passion and a deep appreciation for nature. Speleological and cave
704 diving clubs are typically composed of highly experienced, non-scientific explorers
705 who possess the technical expertise necessary to access and map these
706 underground spaces. Scientific research is also increasingly supported by dedicated
707 subterranean research facilities, such as the Moulis Experimental Ecology Station in
708 France and the Boulby Underground Laboratory in the UK, which provide controlled
709 environments for ecological and evolutionary experiments⁴². Other underground
710 laboratories, including Gran Sasso (Italy) and SNOLAB (Canada), further highlight
711 the broader scientific value of caves, extending beyond biology to fields such as
712 astroparticle physics.

713 Caves play a crucial role in archaeology and paleontology by safeguarding
714 fossils, sediments, prehistoric artifacts, and even recently extinct species—such as
715 certain birds known only from cave deposits in Macaronesia^{208,209}—as well as
716 numerous human remains discovered in caves around the world^{210,211}. Stalagmites
717 are archives for paleoclimate research, offering high-resolution records of past
718 climatic fluctuations through isotopic and geochemical analyses²¹², while sediment
719 deposits within cave systems record paleoenvironmental history, such as changes in
720 sea level^{213–215}. All these archives provide clues into past ecosystems useful for
721 reconstructing paleoenvironments and their biodiversity—yielding important
722 implications for establishing baseline references for conservation and restoration
723 efforts²¹⁶. For example, the analysis of speleothems has provided evidence of past

724 environmental changes and the anthropogenic impacts that contributed to the well-
725 documented ecocide on Easter Island²¹⁷. Similarly, speleothems from lava tubes in
726 the Galapagos Islands have revealed biomarkers of surface vegetation changes and
727 human-induced pollution, emphasizing the need for robust conservation policies to
728 mitigate the impact of anthropogenic activities²¹⁸.

729 The inspirational value of caves may even extend beyond Earth^{219–221}. The
730 detection of volcanic caves on Mars and their protective properties against surface
731 radiation, extreme temperatures, and atmospheric variability, have led researchers to
732 explore caves on Earth from planetary science and astrobiological perspectives. A
733 rich research agenda is shaping up, showing that these subterranean environments
734 could serve as analogs for space exploration and planetary research^{220,222}, and offer
735 insights into the possibility of extraterrestrial life^{223,224}. Specifically, microbial
736 metabolism and mineral interactions in caves and lava tubes on Earth generate a
737 variety of biosignatures^{222,225–227}, which provide reference models for potentially
738 detecting extraterrestrial microbial life²²⁸. Moreover, deep caves offer polygons for
739 training for astronauts (programme by European Space Agency), allowing them to
740 practice behavior and tasks in harsh environments that resemble conditions in
741 space.

742
743 *Education*

744
745 Subterranean ecosystems offer vast educational potential, especially for fostering
746 scientific literacy and environmental awareness. Every cave provides visitors with an
747 unforgettable experience, combining natural beauty with rich site-specific educational
748 opportunities. Cave interpretation centers, guided tours, and interactive activities can
749 help students and visitors appreciate the uniqueness of cave ecosystems and the
750 importance of their conservation. Similarly, groundwater-fed springs enhance the
751 natural beauty of their surroundings and serve as ideal settings for educational
752 school trips. These sites allow students and teachers to observe firsthand the
753 interactions between groundwater systems, biodiversity, and human activities²²⁹.
754 Activities such as water quality testing, species identification, and habitat mapping

755 can transform these visits into living labs, offering hands-on learning experiences
756 that reinforce classroom lessons.

757 This interplay between natural and cultural elements creates opportunities for
758 educational projects that explore connections across disciplines such as biology,
759 earth sciences, history, and even art. For example, studying speleothems can teach
760 students about geological processes, offering a concrete visual representation of
761 time accumulation, while analyzing the unique adaptations of cave-dwelling
762 organisms can illustrate fundamental evolutionary principles. Importantly, these
763 educational activities can be reinforced through citizen science initiatives. A recent
764 citizen science project collected biological samples from over 300 municipal
765 groundwater sites across Switzerland. This initiative bridged educational objectives
766 with research goals, leading to the discovery of new species²³⁰ and enabling the
767 mapping of macroecological patterns at unprecedented resolutions^{231–233}.

768

769 *Cultural heritage and identity*

770 Subterranean ecosystems often shape traditions, customs, and identities, influencing
771 both positive and negative cultural narratives. Historically, caves were often
772 perceived as liminal spaces—thresholds between the world of the living and the
773 underworld. In European folklore, they often symbolize fear of the unknown and are
774 believed to be entrances to Hell or lairs for dragons, trolls, and other sinister beings.
775 This is illustrated in 17th-century engravings published in the monograph on the
776 Duchy of Carniola by J. V. Valvasor, a Slovenian scientist, which depicts the beliefs
777 of local inhabitants at the time²³⁴. Yet, caves have also held positive associations, for
778 example by serving as places of refuge²⁵. Quintessential examples are underground
779 cities in the Mediterranean region, such as Matera (Italy), Bulla Regia (Tunisia), and
780 Cappadocia (Turkey), with tunnels, living quarters, and even chapels carved into the
781 rock. Similarly, Coober Pedy, South Australia, is renowned for its man-made
782 “dugouts”, subterranean residences bored into the hillsides of the desert. Beyond
783 human-accessible cavities, features such as springs, anchialine pools, and oases
784 played vital roles in community life, fostering social interaction and cohesion.

785 Specific organisms, such as bats, are often protagonists of these cultural
786 narratives²³⁵. In some traditions, bats are feared as harbingers of darkness and
787 death, a view perpetuated by Gothic literature and popular media. However, bats are
788 also revered as symbols of luck, fertility, or protection. For example, in Chinese
789 culture, bats are associated with happiness and prosperity, as the word for bat (*fu*)
790 sounds like the word for good fortune. In the Americas, indigenous communities
791 such as the Maya often incorporate bats into their mythology, viewing them as
792 powerful guardians of the underworld.

793 Slovenia offers a prime example of how, even today, subterranean
794 landscapes and their fauna can be deeply intertwined with national identity. The
795 country is home to the renowned Postojna Cave, a UNESCO-listed site that has
796 become a source of national pride²³⁶. This is the cave where the first scientific
797 descriptions of exclusive cave-dwelling animals originated, beginning with the beetle
798 *Leptodirus hochenwartii*, which marks the start of speleobiological research in
799 1832²³⁷. Slovenia is also the land where the discovery and scientific description of
800 the olm (*Proteus anguinus*)—a blind, pale groundwater salamander—took place.
801 *Proteus* has achieved iconic status, celebrated across various facets of Slovenian
802 culture, from beer labels and public street art to the textile industry and contemporary
803 art projects.

804

805 *Spiritual and religious significance*

806

807 Caves, anchialine pools, subterranean rivers, springs, and cenotes were often
808 regarded as sacred or spiritually significant^{24,238}. For example, the caves of Crete
809 were religious sites for the ancient Minoans, while Zeus was believed to have been
810 born in a cave. In Greek mythology, the river Styx delineated Hades, the underworld
811 (the prefix “stygo-” is still used today for “stygo-bionts”, a technical term referring to
812 groundwater-dwelling organisms). Similarly, the cenotes of the Yucatán Peninsula
813 were viewed by the Maya as both gateways to Xibalba, the underworld, and
814 essential sources of life-giving water^{239,240}. Likewise, many anchialine pools in Hawai‘i

815 are revered as wahi pana (celebrated places), or strictly reserved for various uses,
816 including royal baths, rituals, ceremonies, and other daily activities²⁴¹.

817 Countless rock-cut churches and monasteries worldwide further highlight the
818 spiritual dimensions of subterranean sites²⁵. Likewise, groundwater provides spiritual
819 and religious services through sacred water sites, often linked to natural features
820 such as trees, stones, caves, and hills. These places offer a sensory connection to
821 spiritual practices, with holy wells and springs frequently serving as focal points for
822 rituals and supernatural engagement. While not all water sources are considered
823 sacred, many cultures believe in offering gifts to water spirits to sustain their
824 blessings. Springs emerging from caves hold particular significance, often seen as
825 miraculously pure and ritually powerful, with evidence of reverence spanning from
826 prehistoric times to contemporary cultures worldwide²³⁸. In Australia, many Aboriginal
827 nations consider groundwater sites fundamental to their Dreamtime creation stories,
828 in which the Rainbow Serpent is believed to have shaped landforms, springs, and
829 river upwelling zones. Many sacred sites associated with fertility, teachings of lore,
830 and cultural customs are linked to groundwater, holding immeasurable value for
831 these communities²⁴².

832

833 **Subterranean ecosystem disservices**

834

835 Alongside their many positive contributions, ecosystems can also have effects that
836 are perceived as harmful, unpleasant, or unwanted—termed “ecosystem
837 disservices”²⁴³. While research on subterranean ecosystem disservices is virtually
838 non-existent and beyond the scope of this assessment, it is important to briefly
839 mention the potential human health and infrastructural risks associated with these
840 environments. For instance, subterranean ecosystems can serve as reservoirs of
841 pathogens and facilitate disease transmission. They harbor harmful microbes, fungi,
842 and viruses, which may exist freely or be associated with specific organisms. Cave-
843 roosting bats, in particular, are significant vectors of pathogens, including
844 *Histoplasma* fungi found in bat guano, which can cause histoplasmosis in humans²⁴⁴.
845 Additionally, subterranean environments can accumulate potentially toxic gases such
846 as carbon dioxide, methane, hydrogen sulfide, and radon. These gases pose risks of

847 asphyxiation or poisoning, while radon may increase lung cancer risk for frequent
848 visitors.

849 At the same time, the public’s fascination with the underworld has often led to
850 unfortunate accidents, particularly when individuals engage in caving or cave diving
851 without adequate training or equipment—as in the famous Thailand cave rescue²⁴⁵ or
852 the harrowing account of Sheck Exley in the Túnel de la Atlántida²⁴⁶. Subterranean
853 ecosystems can also evoke some of the most common human phobias, as ranked
854 by ref. ²⁴⁷. These environments are often dark (nyctophobia), enclosed
855 (claustrophobia), contain deep pits or abysses (acrophobia/vertigo), and host fear-
856 inducing organisms such as spiders (arachnophobia) and bats (chiroptophobia),
857 potentially causing psychological distress in visitors. Beyond direct health risks,
858 subterranean environments also pose threats to human infrastructure. Natural
859 underground erosion, combined with human activities such as mining and
860 groundwater extraction, can lead to cave collapses and sinkholes, damaging
861 buildings and roads.

862 This discussion of disservices is far from exhaustive. Yet, it serves as a
863 placeholder for further research in this area. Indeed, studying ecosystem disservices
864 has been proposed as a way to better balance the benefits and drawbacks of nature,
865 ultimately leading to a more objective evaluation of its net impact on human well-
866 being²⁴⁸.

867 **Box 2. The economic dimension of subterranean ecosystem services**

868
869 Valuation of services provided by subterranean ecosystems is still in its early stages.
870 A recent review of over 1,300 studies, yielding more than 9,400 monetary value
871 estimates, found that subterranean ecosystems accounted for only 0.08% of the
872 sample¹². Similarly, ref. ²⁴⁹ reported negligible research effort toward subterranean
873 ecosystems when analyzing the correlation between ecological and economic
874 assessments of 15 regulating services across 32 ecosystem types. While ecological
875 roles such as nutrient cycling, soil formation, and groundwater provision are well-
876 documented, their economic valuation remains limited, with groundwater being the
877 most studied²⁴⁹.

878 In subterranean ecosystems, most valuation efforts focus on provisioning
879 services, particularly groundwater. Methods include market prices, replacement
880 costs, and production functions that measure the marginal impact of water on
881 economic outputs like agricultural crops²⁵⁰. However, market prices often fail to
882 capture the full social value of groundwater due to distortions like subsidies, requiring
883 adjustments to reflect true economic value²⁵¹. Replacement cost methods, which
884 estimate the expenses needed to restore lost services, offer an alternative
885 approach²⁵².

886 Regulating services, though frequently reported for subterranean ecosystems,
887 are rarely valued economically. For example, studies on erosion control, flood
888 protection, and water quality regulation typically focus on surface ecosystems rather
889 than subterranean ones^{253,254}. Similarly, cultural services like geo- and ecotourism
890 are gaining attention, with examples including the recreational value of mining
891 heritage and willingness-to-pay estimates for geo-guided tours^{255–258}.

892 **Outlook: Communicating the value of subterranean ecosystems**

893

894 Although still emerging, research on subterranean ecosystem services is likely to
895 expand rapidly²⁸. We now have reasonable estimates of the global distribution and
896 volume of certain types of subterranean ecosystems^{44,45}, a growing understanding of
897 subterranean biodiversity patterns^{259,260}, and insights into how much of these
898 ecosystems and their biodiversity are protected^{32,261}. Increasingly available open
899 data²⁶² and emerging technologies—from omics tools²⁶³ and environmental DNA²⁶⁴ to
900 terrestrial laser scanning²⁶⁵ and computer simulations⁴²—enable us to map and
901 quantify subterranean ecosystems at unprecedented resolutions. Simultaneously,
902 state-of-the-art economic theory provides a set of approaches to quantify the socio-
903 economic relevance of these services at meaningful scales (Box 2). If harnessed
904 effectively, these tools could bridge critical knowledge gaps in subterranean
905 ecosystem services research.

906 Yet the importance of subterranean ecological processes to support surface
907 ecosystems and human societies often goes unnoticed. Why do we celebrate
908 climbing the highest mountains, yet overlook the exploration of the deepest caves?
909 Why are so many unaware of the remarkable biodiversity thriving underground? And
910 why do we study distant galaxies while Earth's subterranean environments may hold
911 solutions to today's ecological and societal challenges?

912 Considering the importance of communicating these findings to inform real-
913 world decision-making, this review aims to equip researchers and practitioners with a
914 comprehensive *vade mecum* of examples, concepts, and ideas for conveying the
915 importance of subterranean ecosystems. Effective communication requires tailoring
916 messages to specific target audiences, using the right metaphors and psychological
917 triggers. For some, subterranean biodiversity can be framed as a form of “life
918 insurance,” emphasizing its role in maintaining ecosystem stability and resilience².
919 Others may respond to economic metaphors, recognizing the monetary value of
920 services like water filtration, carbon sequestration, and raw material provision (Box
921 2). At the same time, indigenous cultures, which have depended on subterranean
922 ecosystems for centuries, offer invaluable traditional ecological knowledge and
923 biocultural values that can enrich natural resource management strategies²⁴¹ These

924 perspectives often tap into metaphors related to the spiritual connection with these
925 places, whereas the aesthetic allure and sense of mystery inherent to subterranean
926 ecosystems can captivate audiences drawn to the unknown²⁶⁶.

927 By integrating these diverse perspectives, we can foster a deeper
928 appreciation for subterranean ecosystems and their role in sustaining life on Earth.
929 Subterranean biodiversity is not just a scientific curiosity—it is a cornerstone of
930 planetary health, a source of resilience in the face of environmental change, and a
931 testament to the interconnectedness of all ecosystems. With this knowledge, we can
932 transform awkward questions about subterranean ecosystems into opportunities for
933 inspiration and advocacy. As the world rallies to address environmental change and
934 biodiversity loss, acknowledging and valuing the vital services provided by nature is
935 essential to driving meaningful progress toward a more sustainable future.
936 Ultimately, ensuring that subterranean ecosystems receive the attention and
937 protection they deserve begins with one simple act: shifting the attitude of the next
938 listener from indifference to appreciation.

939

940 **Author contribution**

941 SM, CG, and PC conceived the main idea, with suggestions by all authors. All
942 authors contributed to the classification of services. SM and AB analyzed the data.
943 SM wrote the first draft. All authors contributed to the writing of specific sections, and
944 provided suggestions and additions to the overall text.

945

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983

984 **Conflict of Interest**

985 None declared.

986

987 **Data and code availability**

988 Data and code to reproduce the analysis is available in Github
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990

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