

1      **The hidden dimensions of biodiversity**

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36  
37

38      **Abstract**

39      Uncovering and describing biodiversity is fundamental to advancing both scientific  
40      understanding and public awareness of nature. While many biodiversity facets are visible and  
41      even in the spotlight, including those biodiversity features we encounter on a daily basis, much  
42      of the world's biodiversity remains hidden. This review addresses the critical questions: What  
43      dimensions constitute hidden biodiversity? Why does such a large fraction remain hidden, and  
44      what factors contribute to these knowledge gaps? Moreover, why is it important to unveil these  
45      hidden facets? To address these questions, we (i) dissect the various dimensions of hidden  
46      biodiversity, including the taxonomic, spatio-temporal, genetic, functional, social, and  
47      methodological dimensions, and (ii) identify prevalent knowledge gaps. Moreover, we (iii)  
48      highlight possible ways forward on how to deal with hidden biodiversity, and (iv) conclude with  
49      the proposal of guiding principles to shape future research in this field.

50  
51      **Key words:** taxonomic, functional, genetic, social, methodological, spatio-temporal, bias

52

53	<b>Contents</b>	
54		
55	I. Introduction .....	3
56	II. What is hidden biodiversity? .....	5
57	(a) Taxonomic dimension.....	5
58	(b) Functional dimension.....	6
59	(c) Genetic dimension .....	6
60	(d) Spatio-temporal dimension .....	7
61	(e) Methodological dimension .....	8
62	(f) Social dimension .....	9
63	III. Why is hidden biodiversity relevant?.....	11
64	IV. How to proceed?.....	13
65	(a) Taxonomic dimension.....	13
66	(b) Functional dimension.....	14
67	(c) Genetic dimension .....	15
68	(d) Spatio-temporal dimension .....	15
69	(e) Methodological dimension .....	16
70	(f) Social dimension .....	17
71	V. Conclusions .....	18
72	VI. Acknowledgements .....	18
73	VII. Author contributions .....	19
74	VIII. Tables.....	20
75	IX. References.....	23
76		

77 **I. Introduction**

78  
79 Biodiversity refers to the variety and variability of life on Earth, encompassing genetic, species,  
80 community, and ecosystem-level diversity. We have gained an impressive knowledge of  
81 taxonomic diversity, yet we have to acknowledge that this amounts to an estimated share of  
82 merely 10 % of the total richness (Leibniz Research Network Biodiversity 2024; Larsen *et al.*,  
83 2017; Johnson *et al.*, 2016; Eisenhauer, Bonn & Guerra, 2019) or even significantly less  
84 (Overmann, Abt & Sikorski, 2017). New species are constantly being described (with daily  
85 updates available at <https://tb.plazi.org/GqServer/static/newToday.html> or  
86 <https://lpsn.dsmz.de/>), especially in some understudied taxonomic groups, often referred to as  
87 “dark taxa” with e.g. about 1,000 new prokaryotic species being discovered per year (Parte *et*  
88 *al.*, 2020; <https://lpsn.dsmz.de/statistics/figure/15>). Given that the vast majority of biodiversity  
89 remains “hidden”, an important question arises: how do we define hidden biodiversity, and for  
90 whom is it concealed? Here, we define hidden biodiversity as either (i) unknown biodiversity  
91 that we have yet to uncover, or (ii) known biodiversity that is underexplored or understudied  
92 despite its documented presence (Lindken *et al.*, 2024).

93  
94 The general perception is that the hiddenness of a given species is often linked to its body  
95 size, i.e. smaller organisms such as microbes, insects, and even small mammals may be often  
96 overlooked. Yet, there are notable exceptions to this rule, even to the extent that the public’s  
97 scientific knowledge about a particular small-sized organism might be better studied than many  
98 large-bodied ones. For instance, the common ladybug (*Coccinella septempunctata*), the  
99 common tick (*Ixodes ricinus*), or even deep-sea tardigrades of the genus *Coronarctus* may be  
100 well known to the public, and even better studied than large freshwater organisms, such as the  
101 redtail catfish (*Phractocephalus hemiliopterus*), Malaysian giant turtle (*Orlitia borneensis*), or  
102 Sunda gharial (*Tomistoma schlegelii*). This pattern emerges because certain traits can elevate  
103 a small species’ profile: the ladybug, for instance, charms children with its appealing  
104 appearance and helps gardeners by preying on aphids; the tick draws attention due to its role  
105 in transmitting diseases; and the tardigrade fascinates researchers with its remarkable ability  
106 to thrive under extreme conditions. Hence, on the one hand, a taxon’s hiddenness is influenced  
107 not only by size, but also by its abundance, visibility, habitat, and relevance to humans, where  
108 it occurs (e.g. species living below the water surface or in remote areas are more likely to be  
109 overlooked), the difficulty of differentiation from other species, its role or service provided to  
110 humans, its threat to humans or connection to other features that may contribute to its  
111 awareness level. On the other hand, the diversity and variability of abundant and visible  
112 species may be equally hidden, because different species of rodents or dipterans may be  
113 collectively referred to as “mice” or “flies”, respectively.

114  
115 Each realm is characterised by its distinct habitat types and harbours varying degrees of  
116 biodiversity. A simple Web of Science search using the terms “biodiversity + *realm*” reveals  
117 that environments such as forests (i.e., “biodiversity + forest”, 87496 publications as of  
118 21.05.2025), grasslands (17206), and coral reefs (6072) have attracted more research  
119 attention than less accessible habitats like caves (2478), groundwater (2531) or deep-sea  
120 ecosystems (5847). Freshwater ecosystems can be considered isolated while promoting  
121 species isolation and the potential for diversification (Grosberg, Vermeij & Wainwright, 2012).  
122 Similarly, a taxonomic bias towards certain taxa contributes to knowledge gaps, and thus  
123 contribute to hiddenness of biodiversity (Troudet *et al.*, 2017). For instance, vertebrates,  
124 particularly mammals and birds, have been extensively studied and are well-represented in

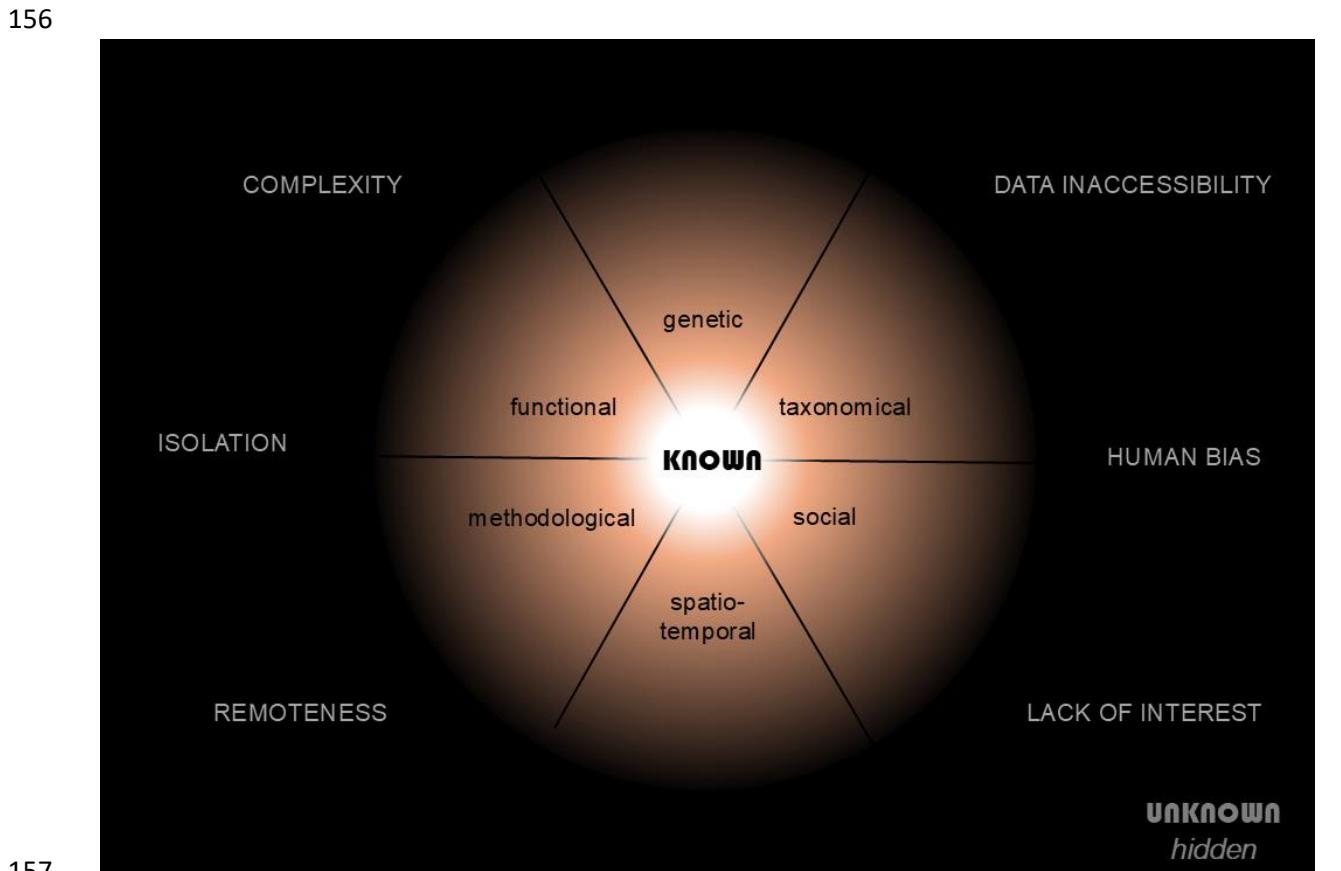
125 public consciousness, while invertebrates and microbial life (insects, fungi, bacteria, and  
126 archaea, among others) are often overlooked despite their vast diversity and ecological  
127 importance; (Eisenhauer *et al.*, 2019; Eisenhauer & Hines, 2021). In addition, cryptic species,  
128 i.e. organisms that are morphologically similar but genetically distinct, are inherently hidden,  
129 particularly among microorganisms. For plankton, genetic delimitation has received less  
130 attention than morphological classification (Morard *et al.*, 2024; Marrone, Fontaneto & Naselli-  
131 Flores, 2022; Van den Wyngaert *et al.*, 2022). The same holds for aquatic plants although  
132 many large genera are prone to hybridisation (e.g. *Potamogeton*: Kaplan & Fehrer, 2013)  
133 which challenges their morphological determination (Espinosa Prieto *et al.*, 2023). Li & Wien  
134 (2023) even estimate that for every insect species described based on morphology, there are  
135 on average 3.1 cryptic species.

136  
137 Despite remarkable progress in documenting biodiversity at both global (e.g., Dirzo & Raven,  
138 2003) and national (e.g., Wirth *et al.*, 2024) scales, a large fraction of biodiversity remains  
139 unknown or hidden. This raises several fundamental questions: What exactly constitutes  
140 hidden biodiversity? Why does it remain hidden, and what are the underlying factors  
141 contributing to its hiddenness? Moreover, is it critical to understand and address this hidden  
142 fraction? Here, we discuss possible ways to uncover the different dimensions of hidden  
143 biodiversity, that is, to which extent could hidden biodiversity entities be disentangled from their  
144 ecosystem functions, if at all possible? In other words: should all (hidden) biodiversity be  
145 uncovered, or should the emphasis lie on critical ecosystem functions that deserve the spotlight  
146 and hence targeted resources?

147

148 **II. What is hidden biodiversity?**

149  
150 Scientific knowledge gaps in biodiversity span multiple dimensions (Fig. 1). These include the  
151 primary unknown in taxonomic, functional and genetic biodiversity, which correspond to the  
152 so-called shortfalls in biodiversity knowledge (Hortal *et al.*, 2015). In addition, they relate to  
153 spatio-temporal, methodological and social dimensions which altogether provide a scaffold to  
154 help disentangle the complexity of hidden biodiversity, as discussed in the following sections  
155 and supported by examples in Table 1.



166 The taxonomic dimension is the prevalent one, with 18,000 new species found and described  
167 annually (Zamani *et al.*, 2020), highlighting the knowledge gaps characterised by the Linnean  
168 shortfall (Hortal *et al.*, 2015). In general, our knowledge of taxonomic diversity is skewed  
169 toward larger and charismatic organisms, which tend to be described earlier than smaller  
170 organisms (Collen, Purvis & Gittleman, 2004; Jones *et al.*, 2009). Yet the vast diversity of  
171 multicellular organisms is allocated to invertebrates that represent 75% of all described species  
172 on Earth (Eisenhauer & Hines, 2021). Diversity estimates of *Bacteria* and *Archaea* range from  
173 10 million species (Louca *et al.*, 2019) to 1.7 billion species (Larsen *et al.*, 2017), with estimates  
174 for fungal species ranging between 1 and 11 million (Hyde, 2022) to 160 million species, and

175 an estimated 160 million protist species (Larsen *et al.*, 2017) on land, in marine (Clerissi *et al.*,  
176 2018), and freshwater environments (Metz *et al.*, 2022). A significant knowledge gap exists in  
177 insect biodiversity, with an estimated 80% of species diversity still undescribed (Stork, 2018).  
178 For example, the number of undescribed species of Hymenoptera and Diptera even in a  
179 temperate country like Germany – with a long tradition of taxonomy as a discipline – amounts  
180 to a few thousands (Buchner *et al.*, 2025). Little is known about parasite diversity (Carlson *et*  
181 *al.*, 2020). The striking discrepancy between available knowledge and gaps in the taxonomic  
182 dimension can be exemplified with one of the largest biodiversity databases, the Global  
183 Biodiversity Information Facility portal (GBIF, [www.gbif.org](http://www.gbif.org)): two third of the records pertain to  
184 birds, though they represent only 0.2% of the described diversity (Eisenhauer & Hines, 2021;  
185 Srivathsan *et al.*, 2023).

186

### 187 **(b) Functional dimension**

188 Functional diversity refers to “the value and the range of those species and organismal traits  
189 that influence ecosystem functioning” (Tilman, 2001). In recent decades, research on  
190 functional diversity has expanded (Naeem, 2002), but the proliferation of definitions and  
191 measurement methods (Petchey & Gaston, 2006) has made it challenging to obtain accurate  
192 estimates. We lack substantial knowledge on organismic functional diversity in almost every  
193 habitat on Earth, a gap coined also as the Raunkiær shortfall (Hortal *et al.*, 2015).  
194 Consequently, multiple levels of functional diversity remain hidden, i.e., regarding individuals,  
195 populations, communities, and entire biomes or individual-level traits such as behavioural  
196 variation (Grimm *et al.*, 2025). With the rise of OMICS tools, i.e., shotgun metagenomics,  
197 transcriptomics, proteomics, and metabolomics, or other high-resolution methodologies such  
198 as high-resolution biotelemetry to track behavioural diversity (Nathan *et al.*, 2022), functional  
199 diversity can be assessed even in the absence of sufficient species information. However,  
200 several studies (Basile, 2022; Petchey & Gaston, 2006; Mouillot *et al.*, 2013) suggested that  
201 rare species play a disproportionately important role in functional diversity. Though unknown  
202 and rare species can be extremely important for ecosystem functioning including  
203 biogeochemical cycles and climate feedback (Jousset *et al.*, 2017), they are often being  
204 neglected due to methodological limitations. Thus, it is key to bear the limits of our knowledge  
205 in mind when addressing conservation measures aiming to counteract the current loss of  
206 functional diversity (Mouillot *et al.*, 2013).

207

### 208 **(c) Genetic dimension**

209 Genetic diversity within species has long been overlooked due to the assumption that its effect  
210 could be ignored compared to interspecific differences (Violle *et al.*, 2012; Bolnick *et al.*, 2011).  
211 However, genetic diversity forms the basis for (rapid) evolution to occur, even on ecologically  
212 relevant time scales, resulting in dynamical interactions between ecological and evolutionary  
213 processes (Schoener, 2011; Hendry, 2017). The importance of genetic diversity is given by its  
214 potential to increase the resilience of populations and communities by enabling adaptive  
215 responses to changing environments (Diaz *et al.*, 2013). Moreover, genetic diversity can have  
216 ecological effects comparable to those of species diversity and influence primary productivity,  
217 population recovery from disturbance, interspecific competition, community structure, and  
218 chemodiversity as well as fluxes of energy and nutrients (Des Roches *et al.*, 2018; Hughes *et*  
219 *al.*, 2008).

220 With the increasing availability of molecular tools and advances in high-throughput sequencing  
221 technologies, we are now able to produce high-quality reference genomes of an increasing  
222 number of species (Lu *et al.*, 2025) and can reveal the genetic diversity of species populations  
223 as well as adaptive processes (Satam *et al.*, 2023; Lu *et al.*, 2025). Yet, until now, a large

224 fraction of the genetic diversity still cannot be interpreted or remains uncovered. Even though  
225 DNA sequencing is conducted in high throughput, the entire diversity of microbial populations  
226 remains largely unknown, and most genome sequences comprise genes with unknown  
227 functions (Vanni *et al.*, 2022; Overmann *et al.*, 2017).

228

#### 229 **(d) Spatio-temporal dimension**

230 The taxonomic dimension is closely linked to the spatial and temporal dimensions of detecting  
231 species, characterised by the Wallacean and Prestonian shortfalls (lack of knowledge in  
232 species distributions and abundance, respectively; Hortal *et al.*, 2015). Life on our planet is  
233 subject to geophysicochemical boundaries captured as “Nature’s envelope” (Patterson, 2022):  
234 biodiversity occurs inside the envelope of spatial and temporal scales relevant for life. Species  
235 rarity contributes to being hidden, considering either spatially restricted occurrences,  
236 regardless of abundance, or low occurrence numbers, regardless of the distribution (Kunin &  
237 Gaston, 1993; Crisfield *et al.*, 2024), both of which reduce its detection probability (McCarthy  
238 *et al.*, 2012; Royle *et al.*, 2012). The latter is often accompanied by a patchy distribution,  
239 particularly evident in soil or benthic flora and fauna, necessitating extensive sampling to  
240 achieve accurate detection and counts within a given area and timeframe.

241 The temporal dimension is another aspect to measure the “unknown”, and can be split between  
242 short-term dynamics such as diel behaviour, i.e. day- or night-time activity, and long-term, such  
243 as seasonal changes or multi-year life cycles. Biases in biological research, historically  
244 favouring daytime studies, have led to significant data gaps in understanding nocturnal species  
245 (Gaston, 2019). For instance, over 80% of mammalian species listed as data-deficient on the  
246 International Union for Conservation of Nature (IUCN) are listed as nocturnal (Bennie *et al.*,  
247 2014). Likewise, the majority of insect activity is nocturnal (Wong & Didham, 2024), and the  
248 best studied insect groups are — on top of being charismatic — all diurnal, such as butterflies,  
249 dragonflies and damselflies, and bees. In a similar vein, certain ecosystem functions such as  
250 pollination have mostly been studied during the day, despite nocturnal pollination being almost  
251 equally important (Fijen *et al.*, 2023). Consequently, only recently the disruptive impact of  
252 artificial light at night on nocturnal pollination and other night related ecosystem services has  
253 been brought to attention as a significant concern (Buxton *et al.*, 2022; Cox & Gaston, 2024;  
254 Knop *et al.*, 2017; Höller *et al.*, 2010).

255 Combined, the spatio-temporal dimension includes species life cycles and migration patterns  
256 where a given species may occupy different parts of the spatial and / or temporal continuum  
257 during its lifecycle impacting also its detection probabilities. For example, inactive life stages  
258 during events such as droughts may not be detected, leading to an underestimation of  
259 abundances if species observations are limited to periods of activity. This issue is also evident  
260 in species with multi-year life cycles, such as certain insects, where not all stages are active  
261 at the same time (Tauber & Tauber, 1981; Heliövaara, Väistönen & Simon, 1994). Aquatic  
262 insects with a freshwater larval stage may be challenging to identify or study in their natural  
263 environment and remain overlooked, likewise leading to an incomplete understanding of their  
264 full life cycles (Dijkstra, Monaghan & Pauls, 2014). Species thus may occupy specific  
265 environmental conditions and their niche may shift spatio-temporally, for example when  
266 crossing ecosystem boundaries, as in the case of such insects or migratory fish. The gaps in  
267 knowledge of species’ ecological niches are described as the Hutchinsonian shortfall (Hortal  
268 *et al.*, 2015). Reasons contributing to this shortfall are seasonal migration but also long-term  
269 adaptation patterns due to climate change, leading to shifting baselines in species  
270 distributions, further challenging the analysis of species niches and biotic interactions.

271 A special case of the temporal dimension is non-native / invasive species, which may remain  
272 unnoticed in their newly colonised environment for a long time during their initial lag phase  
273 before possible population explosions (Kelly *et al.*, 2021). Similarly, odd multi-year cycles such  
274 as El Niño and La Niña affect spatial distributions through temporal climatic contingencies  
275 (Ávila-Jiménez, Gutiérrez & Altamiranda-Saavedra, 2024).

276

### 277 **(e) Methodological dimension**

278 Given methodological shortcomings and challenges in sampling procedures, entire  
279 ecosystems may be considered hidden. Isolated habitats and areas are hard to access, such  
280 as caves, high mountain sites, tropical rainforest, deep ocean, and extreme environments in  
281 general (Mammola *et al.*, 2019; Basnet *et al.*, 2019; Schultz *et al.*, 2023). Biodiversity in soils  
282 and aquatic habitats remains “below the surface” and has a low detection probability. In fact,  
283 soils are among the most concealed terrestrial habitats, even though they have long been  
284 recognised as exceptionally biodiverse (Anthony, Bender & van der Heijden, 2023). The low  
285 accessibility of soil organisms requiring different extraction methods depending on the  
286 organism group, high numbers of (cryptic) species and low number of taxonomic experts for  
287 some groups of organisms combined lead to a high disparity in estimated *versus* undescribed  
288 species in every group of soil meso- and microfauna (Geisen *et al.*, 2019). Likewise, in the  
289 marine realm, two-thirds of all species are estimated to be described, and especially the deep-  
290 sea encompassing 95% of the ocean’s volume can be considered the least explored  
291 environment on Earth (Danovaro *et al.*, 2017; Costello & Chaudhary, 2017).

292 The habitat or ecosystem accessibility relates to sampling and extraction procedures specific  
293 to respective organisms (Flocco, Mac Cormack & Smalla, 2019; Hughes *et al.*, 2021). In  
294 addition, geographical bias induced by the location of researchers, safety issues in several  
295 regions, as well as differences in the implementation of the Nagoya Protocol impede  
296 systematic biodiversity assessments in entire geographic regions (Prathapan *et al.*, 2018;  
297 Overmann & Scholz, 2017; Heinrich *et al.*, 2020). Many of these aspects contribute to the so-  
298 called “biodiversity blindspots” proposed by Ball *et al.* (2025). In addition, sampling biases are  
299 often caused by selective perception, collector bias, species body size, as well as species and  
300 location attractiveness (Phillips *et al.*, 2017). Size is a human factor explaining the skewed  
301 distribution of species knowledge: the smaller an insect body size, the later the year of  
302 description (Stork *et al.*, 2015). Similarly, inconsistent sampling protocols, lack of  
303 standardisation, and limited technological access can hinder biodiversity detection, for  
304 example, molecular methods may miss rare taxa that require deep sequencing. In addition, a  
305 lack of data contributes to a limited awareness – an issue across realms and ecosystems,  
306 including a lack of open and Findable, Accessible, Interoperable and Reusable data (FAIR;  
307 Wilkinson *et al.*, 2016). While most notions of diversity are centred around the presence of  
308 certain taxa in a given context, the concept of “dark diversity” (Pärtel, Szava-Kovats & Zobel,  
309 2011) captures information about the absence of such taxa in spatio-temporal contexts for  
310 which comparable data and ecological models would suggest that they are present. The  
311 combination of species absence and presence data can be further combined into more  
312 complete biodiversity measures like the Community Completeness Index (Pärtel, Szava-  
313 Kovats & Zobel, 2013).

314 Finally, some groups of organisms actually have been studied, yet the information gathered  
315 about them is not prevalent in the scientific community. This phenomenon can be referred to  
316 as “dark knowledge” (Jeschke *et al.*, 2019). This can be due to either highly specialised  
317 scientific publications which do not address the larger community, or so-called “forgotten  
318 results” given published but neglected research due to inaccessibility e.g. non-English (Amano  
319 *et al.*, 2023) or non-digitised publications.

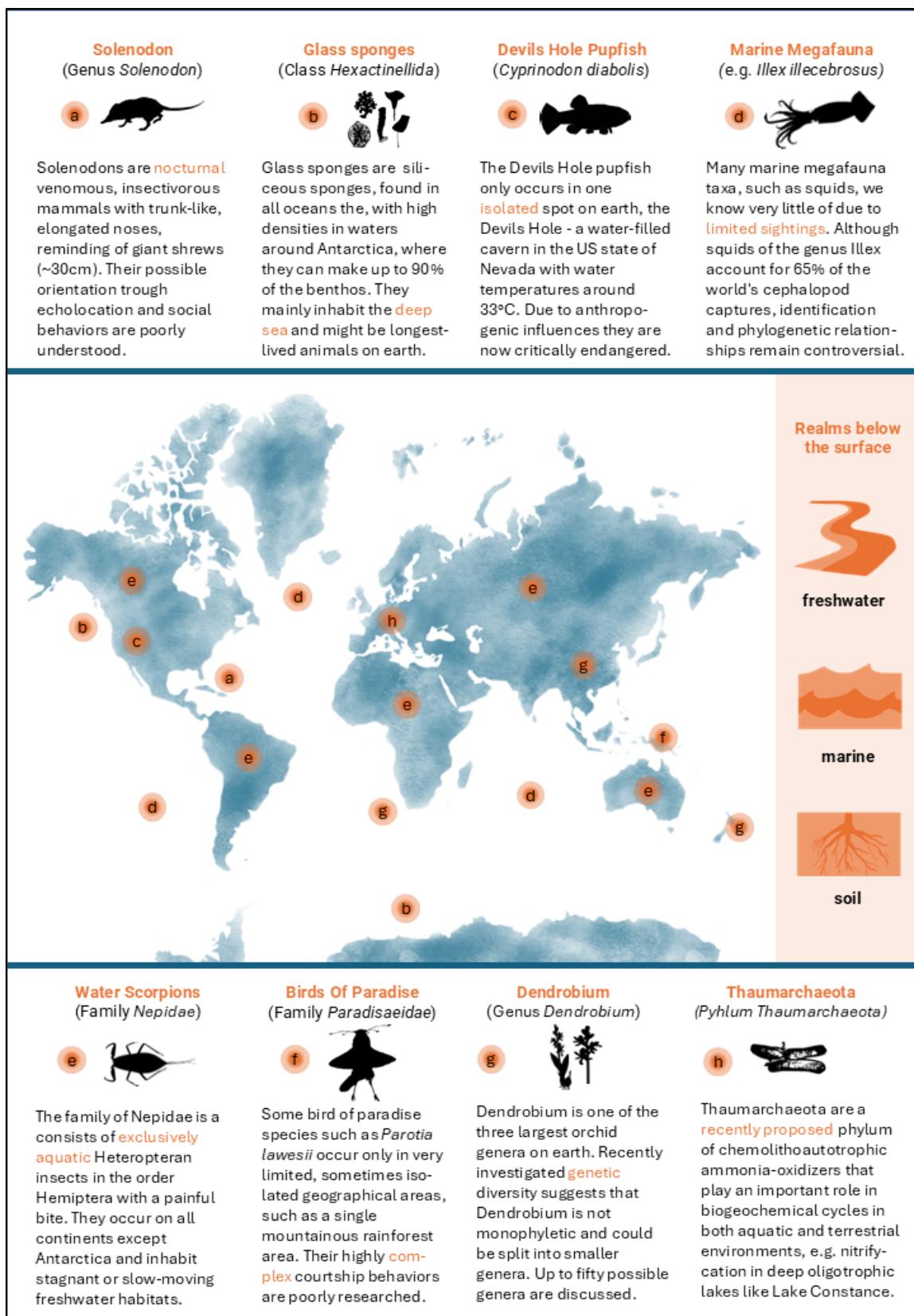
320     **(f) Social dimension**

321     The degree of “hiddenness” also includes social dimensions as it is often related to the cultural  
322     background of different human societies, economic practices, and experiences. Many  
323     important human-driven environmental changes and their impacts on biodiversity remain  
324     surprisingly underexplored (Heger *et al.*, 2019). Moreover, ecological effects of specific facets  
325     of global change have been examined, but we lack knowledge on their combined effects and  
326     their complexity (e.g., Pendleton *et al.*, 2016; Vos *et al.*, 2023; Orr *et al.*, 2024). This notion  
327     results in a large degree of hiddenness for scientists as understanding and projecting  
328     ecological complexity such as synergistic, additive, and antagonistic effects of multiple drivers  
329     on organisms and ecosystems demands coordinated cross-disciplinary research (Heger *et al.*,  
330     2019).

331     Human bias is a major driver of imbalanced biodiversity knowledge, as it influences how  
332     research is conducted and communicated and thus affects all other dimensions (Mazor *et al.*,  
333     2018; He *et al.*, 2021). A prominent example is the diurnal bias in our society in perceiving  
334     nocturnal processes and issues (Kyba *et al.*, 2020). In addition, a lack of knowledge creates  
335     lack of the awareness, or knowledge can be unintentionally biased (e.g., introduced species  
336     being considered native, Kochalski *et al.*, 2019). These gaps often result from methodological  
337     challenges and the undersampling of certain areas, due to a lack of research focus and  
338     sufficient fieldwork, which also mirrors temporal and spatial biases in scientific efforts, or  
339     challenges in communicating scientific results to the public. Being it a lack of interest, funding,  
340     or due to societal, political or regional aspects – such human induced biases unfortunately  
341     continue despite better knowledge. Troudet *et al.* (2017) showed that taxonomic biases in  
342     biodiversity data have remained broadly the same since the 1950’s although the problem has  
343     been known since several decades (Bonnet, Shine & Lourdais, 2002).

344

345



346

347 **Fig. 2 |** Examples of hidden biodiversity across the world, including a) Solenodons, b) Glass sponges,  
 348 c) Devils Hole Pupfish, d) marine megafauna, e) water scorpions, f) Birds of Paradise, g) *Dendrobium*  
 349 and h) *Candidatus Thaumarchaeota*, along with their approximate distribution. In addition, different  
 350 realms that are beneath the surface, such as freshwater, marine and soil environments, can be  
 351 considered hidden. See Table 1 for more examples and <https://hiddenbiodiversity.org/> for an interactive  
 352 visualisation.

353     **III. Why is hidden biodiversity relevant?**

354

355     Hidden biodiversity has its intrinsic value, similar to the known biodiversity, however with a  
356     major caveat: it is challenging to consider something relevant, or attribute a given process or  
357     function to a taxon which is not yet known or described as such. Hidden biodiversity is likely to  
358     contribute to many ecosystem functions and services which for humans still remain in the dark,  
359     and in this regard, the precautionary paradox is relevant for maintaining ecosystem stability  
360     and resilience.

361     Ecosystem functions may remain hidden but can be considered critical biological entities  
362     (Emmett Duffy, Paul Richardson & Canuel, 2003; Lynch *et al.*, 2023; Anthony *et al.*, 2023;  
363     Bahram *et al.*, 2018; Hooper *et al.*, 2012; Bell *et al.*, 2005). The biodiversity–ecosystem  
364     function (BEF; Schulze & Mooney, 2012) relationship is often explained by niche partitioning,  
365     positive interactions, or asynchronous population dynamics of the coexisting species (Barry *et*  
366     *al.*, 2019), which reduce competition, but increase productivity and ecosystem resilience  
367     (Tilman, Isbell & Cowles, 2014; Cardinale *et al.*, 2012; Barry *et al.*, 2019). Notably, ecosystem  
368     functions can be compromised already by decreases in species abundance opposed to  
369     complete species extinctions (Isbell *et al.*, 2017; Spaak *et al.*, 2017). This is relevant, especially  
370     in the case of microorganisms which, due to their very large population sizes (Morris *et al.*,  
371     2002; Miller *et al.*, 2005) and their potentially broad or even global geographical distribution  
372     (Casamayor *et al.*, 2023), have a low extinction risk, in contrast to many metazoa. The same  
373     applies to the vectors of microorganisms: while individual insect species may not be threatened  
374     with extinction, their dwindling abundance can silently undermine ecosystem resilience. For  
375     example, Mata *et al.* (2015) found knowledge gaps regarding ground and bark-dwelling beetles  
376     and insects with an aquatic phase, and revealed hundreds of new insect species delivering  
377     ecosystem functions for the metropolitan area. Such knowledge gaps are critical as changes  
378     in biodiversity can affect ecosystem functions with considerable delays, where e.g. plant  
379     richness can impact belowground processes even after several years (Eisenhauer *et al.*,  
380     2024b; Bongers *et al.*, 2021; Guerrero-Ramírez *et al.*, 2017; Weisser *et al.*, 2017; Reich *et al.*,  
381     2012).

382     The majority of studies on BEF relationships have so far focused on terrestrial plant  
383     communities and their productivity, and the BEF of other communities only recently gained  
384     attention. Aquatic fungi take a key role in ecosystems, carbon and nutrient cycling and energy  
385     flow, producing essential organic compounds and dynamic food-webs (Vatova *et al.*, 2022).  
386     Soil biodiversity is a key regulator in soil ecosystem multifunctionality (Delgado-Baquerizo *et*  
387     *al.*, 2020; Wu *et al.*, 2025; Schultdt *et al.*, 2018; Wagg *et al.*, 2014), and herbivorous insects  
388     and microbial decomposers are important promoters of grassland ecosystems (Soliveres *et*  
389     *al.*, 2016). Likewise, many ecosystem services rely biodiversity, such as crop, fish, and timber  
390     production, or the regulation of pests and prevention of diseases (Brooks *et al.*, 2016; Isbell *et*  
391     *al.*, 2017; Duffy *et al.*, 2016; Liang *et al.*, 2016; Keesing *et al.*, 2010; Barnes *et al.*, 2020; Lynch  
392     *et al.*, 2023). Management of ecological systems might go wrong if hidden biodiversity is  
393     ignored. In fisheries management, for instance, many well-intended actions fail because the  
394     behavioural diversity and responses of fishes were not taken into account (Pine *et al.*, 2009).  
395     Growing evidence shows that biodiversity is generally positively associated with plant, animal,  
396     and human health (Banerjee & van der Heijden, 2023; Flandroy *et al.*, 2018; Haahtela, 2019;  
397     Rillig *et al.*, 2018), and hidden biodiversity is likely to play an equally important role. On a  
398     different note, there are also unknown species that pose considerable health risks to animals  
399     and humans. One example is the recently described cyanobacterium *Aetokthonos hydrillicola*  
400     (Wilde *et al.*, 2014) that occurs associated with submerged plants and produces potent  
401     neurotoxins that can be fatal to herbivores and birds of prey (Breinlinger *et al.*, 2021).

402 In most ecosystems, small organisms constitute a major fraction of the hidden biodiversity not  
403 only by the number of species but also by their sheer biomass. Microorganisms constitute the  
404 second most dominant biomass fraction in soils after plant roots (Bar-On, Phillips & Milo, 2018)  
405 and can amount to > 1 ton of biomass carbon per hectare (Fierer, 2017), being equally  
406 dominant and important also in marine sediments (Hoshino *et al.*, 2020). The fact that hidden  
407 biodiversity is most prominent among small organisms has important implications for its  
408 functional relevance, since the mass-specific metabolic activity of organisms is increasing with  
409 decreasing size. This is exemplified by biomass-specific respiration rates, which are up to five  
410 orders of magnitude higher for bacteria than for multicellular organisms ranging from copepods  
411 to elephants (up to 100,000 versus 1-100 mmol O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>). As a consequence, the composition  
412 of microbial communities is a major driver of carbon sequestration, nutrient cycling, or  
413 greenhouse gas emissions, and is relevant for key ecosystem services like pathogen control  
414 and pollutant degradation (Azam & Malfatti, 2007; Täumer *et al.*, 2021; Bardgett & van der  
415 Putten, 2014; Deubel & Merbach, 2005; Harms, Schlosser & Wick, 2011; Kandeler, Stemmer  
416 & Gerzabek, 2005; Falkowski, Fenchel & Delong, 2008; Delgado-Baquerizo *et al.*, 2020; Abs,  
417 Chase & Allison, 2022). For example, the metabolic activity of bottom sediment bacteria  
418 contributes to the transformations and mineralisation of organic matter, and in certain  
419 conditions to the release of regenerated nutrients to near-bottom waters (Lewicka-Rataj *et al.*,  
420 2024).

421 The persisting knowledge gaps of hidden biodiversity, particularly those of functional  
422 biodiversity, not only have high relevance for the understanding of these ecosystem functions  
423 and services, or aggravate the uncertainties in predicting the consequences of biodiversity  
424 change (Burian *et al.*, 2024; Dornelas *et al.*, 2023), but also impede the development of  
425 mitigation strategies for the preservation of key ecosystem functions during environmental  
426 change (Pereira *et al.*, 2024; Oliver *et al.*, 2015; Hong *et al.*, 2022; Averill *et al.*, 2022). In  
427 general, ecosystem functions provided by biodiversity play a key role in, e.g., climate change  
428 mitigation and adaptation (Cavicchioli *et al.*, 2019; Aben *et al.*, 2022; He *et al.*, 2010; Weiskopf  
429 *et al.*, 2024; Shin *et al.*, 2022; Oliveira, Moore & Dong, 2022; Jansson, 2023), and this can be  
430 expanded likewise to hidden biodiversity (Table 1).

431 Beyond ecosystem functions, hidden biodiversity is likely to offer new and innovative solutions  
432 for biotechnology, agriculture, and human or veterinary medicine. For instance, genome  
433 sequences of understudied microbial lineages have been found to contain novel biosynthetic  
434 gene clusters or metabolic pathways (e.g., Cuadrat *et al.*, 2018; Overmann *et al.*, 2017). Given  
435 that bacterial phyla without any cultured representatives contain the highest fraction, up to 85%  
436 of unknown genes, dark taxa appear particularly promising targets for future biodiscovery. In  
437 a large, comparative metabolomic study across four bacterial phyla, thousands of mostly  
438 unknown different metabolites were detected, of which only 12% occurred in all four phyla  
439 while up to 107 unique metabolic features were observed in just a single bacterial strain,  
440 including an entire novel compound family (Fiorini *et al.*, 2022). More broadly, hidden  
441 biodiversity is likely to have manifold so-called Nature Contributions to People (NCPs; IPBES,  
442 2019; Díaz *et al.*, 2018). For instance, (Gascon *et al.*, 2015) review many ecosystem services  
443 provided by species, including several of unexpected value to humans.

444 Taken together, hidden biodiversity has, beside its intrinsic value, far-reaching impacts on  
445 ecosystem functions and services as well as management of aquatic ecosystems. There are  
446 some fundamental issues to solve, e.g., if a global policy goal is to protect all biodiversity, how  
447 do current policies do when a major portion of biodiversity remains hidden? Our insufficient  
448 understanding of hidden biodiversity severely impedes our ability to comprehensively (i)  
449 elucidate the biological basis (taxa, phenotypic traits, genes, and gene regulation) of specific

451 ecosystem functions (Overmann *et al.*, 2017; Zoccarato *et al.*, 2022), (ii) identify drivers and  
452 feedback mechanisms of ecosystem functions during environmental change (Eisenhauer &  
453 Hines, 2021; Eisenhauer *et al.*, 2024a), (iii) assess biological interactions, functional similarity  
454 and ecosystem resilience (Bishop *et al.*, 2022; Kost *et al.*, 2023; Rousk, Brookes & Bååth,  
455 2009; Philippot *et al.*, 2013), (iv) develop appropriate, state-of-the-art monitoring and  
456 management approaches (Mammola *et al.*, 2020; Guerra *et al.*, 2021; Singleton *et al.*, 2024),  
457 (v) comprehensively assess the effects of conservation measures (Waldron *et al.*, 2020), and  
458 (vi) exploit the full potential of biodiversity for future applications in sustainable agriculture,  
459 fisheries, bioeconomic development and ecosystem restoration, or human and veterinary  
460 medicine (He *et al.*, 2024; Overmann *et al.*, 2017; Krause *et al.*, 2022; Humphries & Winemiller,  
461 2009).

462

#### 463 **IV. How to proceed?**

464

465 Given the challenges in the different dimensions of hidden biodiversity, the question arises:  
466 what could be done regarding this so-called known unknown? Targeted research to uncover  
467 hidden biodiversity may be perceived as a tension zone in comprehensive *versus* purpose-  
468 driven biodiversity research, with the latter reflecting the importance to accumulate *sufficient*  
469 knowledge. However, what should be considered sufficient? One approach could be to focus  
470 on the major NCPs and develop incentives for society to invest into biodiversity research and  
471 protection linked to these NCPs. This approach is, however, at the risk of being circular, since  
472 we would focus on aspects that are already known. We also have to ask ourselves: how much  
473 has the “uncovering of hidden biodiversity” in the past decades contributed to, e.g., biodiversity  
474 protection, restoration, and the understanding of NCPs? While valuable examples of beneficial  
475 impacts exist (see Table 1), the detrimental anthropogenic impacts on biodiversity outweigh  
476 these positive examples, as shown e.g., by the negative trend in population abundance of  
477 monitored vertebrates globally (He *et al.*, 2019; WWF, 2024). While this does not mean that  
478 interest-driven efforts to uncover hidden biodiversity should be neglected, we have to be  
479 mindful of our limited resources regarding time, labour and funding. In addition, raising  
480 awareness for hidden biodiversity is essential, and we aim to support this by collating examples  
481 from the larger community using our newly-developed interface at  
482 <https://hiddenbiodiversity.org/>. [Note to reviewers: this is a first prototype and more  
483 functionalities will be added, and we are happy to implement possible suggestions].  
484 We call for a balance between addressing interest-driven and purpose-driven biodiversity  
485 research. However, the emerging questions are evident: how do we prioritise the efforts?  
486 Which are the critical ecosystem functions? Which realms, ecosystems, and habitat types  
487 should ‘deserve’ being on the fast-track? The circularity of hidden biodiversity where  
488 insufficient knowledge might impede the establishment of an appropriate restoration baseline,  
489 raises the question: what is the ultimately desired *versus* realistic status of biodiversity? We  
490 discuss important trends and opportunities in biodiversity research and methodological  
491 developments across the dimensions, concluding in seven principles for future research on  
492 biodiversity sustainability.

##### 493 **(a) Taxonomic dimension**

494 Neglecting the taxonomic diversity of organisms with low charismatic appeal leads to a  
495 distorted view, where neglect increases with diversity and decreases with body size. For  
496 instance, Srivathsan *et al.* (2023) found that insect families contributing more to global insect  
497 communities are those that been most neglected. This neglect, which cascades into the lack

498 of research efforts, could be addressed by identifying and tackling the diversity of hidden taxa  
499 with scalable techniques. One such important tool to detect everyday yet important taxa is  
500 Next-Generation Sequencing (NGS) barcoding. This allows cost-effective high-throughput  
501 generation of short specimen-specific barcodes and yields new barcodes, including some that  
502 are potentially new to science. The method can be implemented by a wide range of  
503 laboratories, accelerating, e.g., invertebrate species discovery and yielding relative abundance  
504 information (Wang *et al.*, 2018). Nowadays, decreasing processing costs enable sequencing  
505 genomes at scale and in projects such as the Darwin Tree of Life for the British fauna  
506 (<https://www.darwintreeoflife.org/>), the Psyche Project for European Lepidoptera  
507 (<https://www.projectpsyche.org/>) or the Ten Thousand Plant Genome Project (Cheng *et al.*,  
508 2018). Similarly, employing machine-learning such as deep clustering has the potential to  
509 support taxonomic identification, as shown by Milošević *et al.* (2025) for Chironomids.  
510 The cost-effective method of identifying taxonomy by DNA leads to a rapid increase of  
511 taxonomic databases, yet also the errors in taxonomic labelling bear huge challenges. Grenié  
512 *et al.* (2023) reviewed this topic and developed a Shiny app in an attempt to solve the puzzle  
513 (<https://mgrenie.shinyapps.io/taxharmonizexplorer/>). They (i) identify the correct treatment of  
514 taxon names as a prerequisite for robust biodiversity research, (ii) suggest the taxonomic name  
515 harmonisation by employing a thorough search for the most suitable (i.e. most reliable and up-  
516 to-date) databases and existing related tools and (iii) propose a typology of widely used  
517 taxonomic databases and extensively reviewed R packages, along with the documentation of  
518 the harmonisation workflow (software versions, functions, parameters and database versions).  
519 To facilitate such efforts, database managers and tool developers need to make their  
520 resources discoverable for all researchers globally and describe them with all necessary meta-  
521 data. Such joint efforts between taxonomists and ecologists could therefore strengthen efforts  
522 across research communities and disciplines for obtaining robust information.  
523 Finally, any new species descriptions and findings must find their way into public knowledge,  
524 but also into backbone taxonomies of national and global databases for taxonomic search  
525 queries. The Freshwater Animal Diversity Assessment (FADA) project  
526 (<http://fada.biodiversity.be/>) mobilises experts and collates information on freshwater  
527 biodiversity and taxonomy globally. These efforts are the prerequisite to query for freshwater  
528 taxa and to address the spatio-temporal dimension of hidden biodiversity.  
529

### 530 **(b) Functional dimension**

531 Addressing the functional dimension provides a complementary perspective to shed light on,  
532 e.g., the community composition and structure given species traits and contributions to  
533 ecosystem functioning, and to identify keystone species which drive community composition  
534 and function irrespective of their abundance. Accordingly, their loss can cause significant shifts  
535 in the structure and function of communities (Banerjee, Schlaepi & van der Heijden, 2018; He  
536 *et al.*, 2024). A promising avenue to identify keystone species are co-occurrence and network  
537 analyses which allow identifying those hub species that are highly interconnected to other  
538 community members. Such network analyses would benefit from moving from exploratory  
539 correlation analyses to testing hypothesised interactions among taxa. However, the identified  
540 keystones need to be also verified, e.g., through experimental removal from / addition to their  
541 communities (Röttjers & Faust, 2019; Weiss *et al.*, 2023) which might be feasible for animal  
542 and plant communities, but challenging for complex microbiomes. As an alternative approach,  
543 microbial keystones may be identified as species that are capable of key or bottleneck  
544 reactions in community-wide metabolic networks (Roume *et al.*, 2015). The caveat is however  
545 the urgent requirement regarding data to uncover their spatio-temporal dimension. Moreover,

546 investments in so far overlooked traits that are likely of fundamental importance for ecology  
547 and evolution and largely overlooked, such as studying the behavioural variation in organisms,  
548 is recommended. Novel tracking technologies can be a stepping stone in the right direction  
549 (Nathan *et al.*, 2022).

550

### 551 **(c) Genetic dimension**

552 Time-series and spatial surveys are important to uncover some of the hidden genetics, i.e. the  
553 role that contemporary evolution plays in species survival and acclimation to environmental  
554 stressors, and how this acclimation affects future generations (Brennan & Logares, 2023).  
555 Large scale, complex genetic and environmental assessments can be customised by focusing  
556 and adding detailed parameters pertinent to specific niches or tackling particular questions.  
557 For instance, in microbiology the assessment of plant rhizosphere communities can be used  
558 to design pest biocontrol or enhanced crop yield strategies (e.g., Syed Ab Rahman *et al.*,  
559 2018). The identification of microorganisms furnishing crops with resistance to environmental  
560 stressors is of particular importance in the context of climate change (Scheben, Yuan &  
561 Edwards, 2016) or the identification of key microbial organisms bound to the occurrence of a  
562 disease (e.g., Milliken *et al.*, 2021). The genetic diversity in wild relatives can be used to protect  
563 the yields by improving the disease and stress resistance in crops and domestic animals  
564 (Andersson & Purugganan, 2022; Zhu *et al.*, 2000). The same applies to sustainable  
565 aquaculture which depends on genetically diverse wild stocks (Yáñez, Newman & Houston,  
566 2015). However, the resources for both terrestrial and aquaculture crops are at threat given  
567 the incentives for farmers to abandon traditional crops (Bellon *et al.*, 2017) and by declines in  
568 wild populations (FAO, 2019). Furthermore, the use of non-native improved strains in  
569 aquaculture can impact the genetic composition and diversity of wild populations (Sanda,  
570 Metcalfe & Mable, 2024). Likewise, efforts towards securing sustainable seafood production  
571 benefit from improved and innovative genetic monitoring schemes to obtain data on the health  
572 state of aquatic ecosystems, and to adjust management decisions accordingly (Bernatchez *et*  
573 *al.*, 2017). For the sustainability of domestic cultures and the conservation of wild species  
574 resources, NGS is a highly useful technology (Bohan *et al.*, 2017).

575

### 576 **(d) Spatio-temporal dimension**

577 It is vital to perform regular and standardised monitoring to detect the spatio-temporal  
578 dynamics in biodiversity. High-resolution long-term records of biodiversity help to detect the  
579 variation in biodiversity which otherwise remains hidden due to a missing baseline to compare.  
580 Examples for long-term biodiversity records include marine prokaryotes and protists (Yeh &  
581 Fuhrman, 2022), fish catches (Froese *et al.*, 2012), harmful marine algal blooms (Wells *et al.*,  
582 2015), marine zooplankton data (Chiba *et al.*, 2018), freshwater invertebrates (Haase *et al.*,  
583 2023; Gillmann *et al.*, 2024), as well as terrestrial and soil organisms (Fischer *et al.*, 2010).  
584 Efforts can build on numerous important ongoing monitoring efforts and networks such as The  
585 Group on Earth Observations Biodiversity Observation Network ([GEO BON](#)) and thematic  
586 BONS (e.g., SoilBON, FWBON), the European Reference Genome Atlas ([ERGA](#)), the Long  
587 Term Ecological Research Network ([LTER](#)), the Global Lake Ecological Observatory Network  
588 ([GLEON](#)), or the World Register of Marine Species ([WoRMS](#)). Likewise, species observation  
589 databases such as [GBIF](#), [speciesLink](#), or [VertNet](#), [FishNet2](#), [Atlas of Living Australia](#) (Belbin  
590 *et al.*, 2021), [observation.org](#), [eBird](#), [iNaturalist](#) (Della Rocca *et al.*, 2024), [Edaphobase](#)  
591 (Burkhardt *et al.*, 2014) provide the basis for addressing the spatio-temporal dimension. Yet  
592 the key issue is that the data collection is not happening where it is most needed: the tropics  
593 (Meier, Lawniczak & Srivathsan, 2025).

594 Strengthening scientific networks is essential to enhance monitoring and data exchange, to  
595 avoid redundancies and instead to create synergies, including especially economically weaker  
596 states and those at risk of warfare (Hanson *et al.*, 2009). Credits should be given to how and  
597 by whom data is collected, and to support the diversity of researchers and bridge the Global  
598 North-South divide (Nakamura *et al.*, 2023) and to emphasise biodiversity hotspots (Wentzel  
599 *et al.*, 2023). Bowler *et al.* (2025) discuss weighting techniques to potentially reduce both the  
600 bias and variance of parameter estimates to overcome those gaps in biodiversity monitoring  
601 data. However, reducing such bias critically depends on knowledge and the availability of data.  
602 Addressing the primary cause requires accounting for the distance between researchers and  
603 the study area, supporting local research funding and participation in data-sharing networks  
604 (Meyer *et al.*, 2015). Furthermore, new tools are essential to overcome barriers in sampling  
605 and monitoring of species that are remote or occur in times when we are unable to detect their  
606 behaviour. For instance, nocturnal ecology has recently benefited by new and improved  
607 technologies that allow organisms to be tracked at night under natural conditions (Gaston,  
608 2019; Nathan *et al.*, 2022; Degen *et al.*, 2024). Aquatic research can use Unmanned Aerial-  
609 Aquatic Vehicles capable of performing underwater sampling (Farinha *et al.*, 2022). Remote  
610 sensing is increasingly used for both day and night time observations and to research about  
611 hidden biodiversity functions (Wang *et al.*, 2024; Fu *et al.*, 2024). Spaceborne and airborne  
612 sensors provide information that incorporate wavelengths unperceivable for the human eye.  
613 Moreover, modelling techniques enable research on functional diversity changes over different  
614 spatial and temporal scales (Rocchini *et al.*, 2022).

615

### 616 **(e) Methodological dimension**

617 Missing access to biodiversity data is a major obstacle to adaptive management in the  
618 conservation and management of natural resources. Stephenson & Stengel (2020) have  
619 identified a preliminary list of important data resources, yet many are difficult to find, access or  
620 not easy to use. Enhancing global biomonitoring strategies should leverage existing initiatives  
621 and programs while identifying and addressing gaps. For example, eDNA sampling could be  
622 integrated into existing environmental monitoring stations to enhance data collection and  
623 analysis (Thomas *et al.*, 2018). Often, it is not biodiversity which is hidden but the data  
624 describing it (Kühl *et al.*, 2020). Efforts should address the scattered monitoring data across  
625 administrators, the appropriate format, ensuring that data is centralised, accessible, and that  
626 data is consistently updated. Examples of initiatives that could benefit from such integration  
627 include intergovernmental, national, and regional environmental monitoring programs that  
628 track changes in biodiversity and environmental health. In an attempt to develop a robust  
629 conceptual framework for monitoring, Dalton *et al.* (2023) recommend seven key conceptual  
630 questions related to the broad application and development of effective biodiversity monitoring  
631 programs: “why monitor”, “which indicators” should be included, “where” and “when” monitoring  
632 will occur, “who” will be involved, and “how many” resources are required. The seventh  
633 question of “how” to conduct protocols is the result of the conceptual requirements and is  
634 considered in the implementation phase.

635 Combining biomonitoring with environmental, geographical, and other datasets should further  
636 be emphasised to model trade-off scenarios in the conservation policy arena. For example,  
637 the assessment of ecosystem corridors, areas of connectivity, migration routes, and other  
638 transnational scenarios is of high relevance for the design and implementation of area-based  
639 conservation measures, such as for example the “30 by 30” biodiversity strategy (European  
640 Commission 2024) or the implementation of 25,000 km free-flowing rivers in Europe (Stoffers  
641 *et al.*, 2024) to address the various hidden biodiversity dimensions below the surface.

642 Further, combining data across science, society, and policy will be necessary. As the  
643 catastrophic event in the Oder River in 2022 highlighted, compounded human impacts, like  
644 pollution, habitat alteration, and climate change, destabilised an entire freshwater ecosystem  
645 (Köhler *et al.*, 2024). By integrating datasets from genetic information to environmental and  
646 anthropogenic stressors predictive models should be developed, supporting the assessment  
647 of ecosystem vulnerabilities and resilience, informing conservation strategies and policy  
648 actions, for example limiting pollutants and preventing disruptive engineering projects (IGB,  
649 2020).

650 Shared open-access databases can allow robust analyses on a wide range of questions on  
651 the causes and trends of large-scale biodiversity change (Kühl *et al.*, 2020; Güntsch *et al.*,  
652 2024). This can be achieved in integrating stakeholders within unified networks, which need to  
653 value the diversity of stakeholder motivations, responsibilities, expertise, and knowledge  
654 pathways and the variety of existing biodiversity recording schemes. Thus, high coordinating  
655 efforts to integrate stakeholder groups and provide shared institutional values, rules, and  
656 norms have to be considered.

657

### 658 **(f) Social dimension**

659 Inviting and including “the society” will support, on the one hand, uncovering hidden biodiversity  
660 by reducing the limitations in time and space (i.e., person power) in biodiversity research and  
661 monitoring efforts on a large scale (Fraisl *et al.*, 2022; Belletti *et al.*, 2020; Premke *et al.*, 2022;  
662 Gąsiorek *et al.*, 2024). The combination of classical methods with citizen science can  
663 significantly increase insights and generate new data (Zulian, Miller & Ferraz, 2021; Kimmig *et*  
664 *al.*, 2025; Table 1). In addition, citizen science enhances the stewardship for the value of  
665 biodiversity and its protection (Peter, Diekötter & Kremer, 2019; Merenlender *et al.*, 2016), and  
666 can thus broaden institutionalised science’s horizon and foster innovation in sociological and  
667 political areas of science (Austen *et al.*, 2024). On the other hand, citizen science data also  
668 offers challenges, which can blur the view on hidden biodiversity itself since participants can  
669 introduce variation, bias, and errors into the newly collected datasets given e.g. personal  
670 preference of sampling location and time. Involving the society in biodiversity monitoring  
671 requires developing software, tutorials, and guidebooks, workshops but also software and data  
672 storage solutions for citizen scientists, which are as essential as more quantitative training for  
673 ecologists to align with the more complex and sophisticated analytical approaches increasingly  
674 used for big data in ecology (Johnston, Matechou & Dennis, 2023). Thus, to maximise the  
675 potential for scientific innovation through citizen science, trained scientists should be involved  
676 to strengthen data quality assurance, adapt standardised protocols and ensure adequate  
677 resources (Kosmala *et al.*, 2016; Austen *et al.*, 2024). Only through large interdisciplinary  
678 networks can the whole suite of biodiversity be uncovered because biases and preferences  
679 for specific taxa exists within academia and academic silos are prevalent (e.g., terrestrial vs.  
680 aquatic or marine vs. freshwater).

681 Societies across the globe have to be invited to biodiversity research given that, e.g.,  
682 indigenous cultures provide biodiversity monitoring in everyday life, and nature-centric  
683 indigenous languages exist around the world. These languages are a great source of  
684 biodiversity knowledge, describing organisms and their functions onomatopoeically (Zimmer,  
685 2024). The challenge is, however, that the languages often do not exist in any written form or  
686 are suppressed. So-called “Talking Dictionaries” have been created since 2005  
687 (<https://talkingdictionary.swarthmore.edu/>) to avoid losing the knowledge from these  
688 languages. However, as it is a race against time to capture knowledge about species that will  
689 soon no longer be found described in languages that soon may be extinct, it is of utmost  
690 importance to meet indigenous cultures at eye level and to share knowledge with each other  
691 (Ogar, Pecl & Mustonen, 2020). This also requires addressing the problems of colonialism in

692 biodiversity research, and perspectives from other knowledge traditions should be brought to  
693 the fore using methods that allow multiple voices and perspectives to be heard and assessed  
694 for relevance (Austen *et al.*, 2024; Ogar *et al.*, 2020).

695

## 696 **V. Conclusions**

697 We conclude with seven suggestions and guiding principles aimed at scientists and their  
698 networks designed to strengthen sustainability research by uncovering hidden aspects of  
699 biodiversity:

- 700 1. Promote data that are Findable, Accessible, Interoperable, and Reusable (FAIR) as a  
701 prerequisite for uncovering hidden biodiversity and expanding our collective  
702 knowledge.
- 703 2. Establish regular and standardised biodiversity monitoring, including sampling at night,  
704 in remote locations, and of highly diverse or small-bodied taxa.
- 705 3. Employ a wide range of tools and technologies, including DNA techniques in a  
706 standardised way, especially to explore taxa with high diversity and small body size to  
707 remote sensing for large-scale assessments.
- 708 4. Use key biological entities and abiotic parameters as proxies to model and monitor  
709 biodiversity patterns and changes under different scenarios.
- 710 5. Focus on microbial species that act as metabolic bottlenecks or keystone players in  
711 ecosystem processes and community-wide networks.
- 712 6. Involve society to support monitoring efforts on a large scale, especially addressing  
713 indigenous cultures that can provide their knowledge about organisms and their  
714 functions.
- 715 7. Strengthen cross-border biodiversity research and conservation by combining datasets  
716 and modelling, and by informing governance across jurisdictional boundaries.

717

718 We strongly advocate for research that reveals the diversity of species and biological  
719 dimensions that have been hidden so far. By integrating knowledge on the state and dynamics  
720 of biodiversity in a human-dominated world, biodiversity research can better align with  
721 conservation goals, which maximises benefits to people and nature, and addressing the  
722 complexity of social-ecological systems (Kareiva & Marvier, 2012; Urban *et al.*, 2021; Guerra  
723 *et al.*, 2022).

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725

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737

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739

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743 TM, AP, NS, TS, ST, CGF, JO

744 **Writing review and editing:** SD, SS, SoK, SaK, RA, LDM, ALD, NE, LG, AG, HPG, FH, SH,  
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757 **VIII. Tables**

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759 **Table 1** Examples for the different dimensions of hidden biodiversity (Fig. 1), what specifically  
 760 is hidden, why can be considered hidden, and why is it considered relevant and its relevance.

761 [Note to reviewers: this table could possibly be an online-only table.]

Dimension	What is hidden?	Why is it hidden?	Why is it relevant?	Reference
Taxonomic	Most of arthropod biodiversity is unknown to science.	Taxonomic neglect, with little signs of increasing activities in recent years	Taxonomic families that dominate insect diversity are often 'hidden taxa' particularly from the megadiverse orders Hymenoptera and Diptera; neglect of dark taxa could severely affect our perception of how life on Earth is organized.	Srivathsan <i>et al.</i> (2023); Forbes <i>et al.</i> (2018); Karlsson <i>et al.</i> (2020)
Spatial	Studies about the genus <i>Eurythenes</i> , the largest scavenging deep-sea amphipods (max. 154 mm), have revealed a cryptic species complex	Lives in the remote hadal zone	<i>Eurythenes plasticus</i> sp. nov., recovered between the depths 6010 and 6949 m in the Mariana Trench (Northwest Pacific Ocean) in 2014 presented plastic fiber in its guts, probably from anthropogenic pollution	Weston <i>et al.</i> (2020); Gerringer <i>et al.</i> (2017)
Spatial	Deep-sea: A third of the species and 25% DNA	Lack of accessibility	Underestimated taxa offer the potential of a biological carbon pump by binding atmospheric carbon dioxide to the sea floor	Cordier <i>et al.</i> (2022)
Spatial	Blooms of benthic toxic cyanobacteria: relative proportion of toxic and non-toxic strains	Lack of appropriate monitoring approaches	Health risks, global increase in associated animal poisonings	Wood <i>et al.</i> (2020)
Spatial	Ground water biodiversity	Little number of efforts to assess subsurface ecosystems so far even in research	Unknown impact on quality drinking water in many regions of the world, incl. ESS such as purification of human chemical inputs.	Zhong <i>et al.</i> (2023)
Temporal	Night-time activity by particular species	Lack of human resources at night time	Knowledge about the ecological functions of nighttime organisms and how the evolution of day- and nighttime ecological functions differ, provides a better, more holistic ecological understanding	Gaston (2019); Buxton <i>et al.</i> (2022); Fijen <i>et al.</i> (2023)

Temporal	Long-term time series, e.g. in aquatic ecosystems	Changing methods, discontinuous funding and staff availability	A large fraction of biodiversity can be hidden in the rare biosphere, but that may change at different time points of sampling throughout seasons or several years. Shifts only visible/explainable if time series are sufficiently long with comparable methods	Pilotto <i>et al.</i> (2020); Outhwaite <i>et al.</i> (2020); Haase <i>et al.</i> (2023)
Spatio-temporal	Evolution of diversity in insect species that have a larval freshwater stage	100,000 species from 12 orders spend one or more life stages in freshwater. Little is known about how this remarkable diversity arose.	Insights in aquatic insect diversity may be highly suitable to study ecological diversification.	Dijkstra <i>et al.</i> (2014)
Spatio-temporal	The freshwater pearl mussel ( <i>Margaritifera margaritifera</i> ) larval and juvenile stages	has an obligate parasitic phase, where its larvae (glochidia) develop on specific host fish, like brown trout and Atlantic salmon, relying on their dispersal, before transitioning to juveniles. Juveniles then bury themselves in the hyporheic zone, remaining hidden for years before emerging as long-lived adults, with lifespans exceeding 100 years.	The mussel's survival depends on hydrodynamic conditions without significant sediment movement, and disturbances at any life stage can disrupt the population	Geist (2010); Baldan <i>et al.</i> (2021); Barouillet <i>et al.</i> (2024)
Functional	Plant resilience to habitat loss and fragmentation	Missing research mainly in tropical areas where landscape fragmentation has high impact	A better understanding of the effects of habitat loss and fragmentation on functional diversity will improve predictions of the resilience and resistance of fragmented systems under global change	Zambrano <i>et al.</i> (2019)
Functional	Benthic communities are poorly described	Although the littoral and profundal habitats are full of ecosystem service providers intensive studies about the communities is missing.	The vast majority of fish species feed on profundal or littoral resources	Vadeboncoeur, McIntyre & Vander Zanden (2011)
Functional	The mechanisms and magnitude of interactions mediated by tube-dwelling invertebrates such as chironomid larvae organisms are still poorly understood	The large effects stand in contrast to the conventional limnological paradigm emphasizing predominantly pelagic food webs.	Based on existing research and models, tube-dwelling invertebrates play a central role in controlling water column nutrient pools, hence water quality and trophic state. Furthermore, they influence the thresholds that determine shifts between alternate clear and turbid states of shallow lakes.	Hölker <i>et al.</i> (2015)
Genetic	Genetic diversity of wild plants for resilience against abiotic extremes and subsequent conditions.	Domestication provide genetic bottlenecks as cultivation involves only limited diversification, subsequent conscious or unconscious selection by farmers leads to a further narrowing of the gene pool.	The conservation of a diversity of crops and livestock reproductive material in gene banks constitute only "snap-shots" of the genetic diversity present at the time of collection. Knowledge about the diversity of wild plants is important to ensure long term viability of breeds and varieties.	Bellon <i>et al.</i> (2017)

Genetic	Genetic status of many farmed aquaculture species.	Lack of financial instruments, training and policies.	To monitor farmed types used for aquaculture and their wild counterparts for risk assessment when introducing non-native species and when managing native species including developed farmed types.	Sonesson et al. (2023)
Genetic	Genetic diversity can increase the resilience in ecosystems.	Experimentally increasing the genotypic diversity of the cosmopolitan seagrass <i>Zostera marina</i> has been shown to enhance ecosystem resilience.	A low genotypic diversity within a lake population of the pondweed <i>Stuckenia pectinata</i> was assumed to be the reason for slow recovery of macrophytes from eutrophication.	Reusch et al. (2005); Hilt et al. (2013)
Social	Underestimated extent of existence of the Vinaceous-breasted Parrot ( <i>Amazona vinacea</i> ) with conservative methods for wildlife management.	Conservative estimates used for the IUCN Red List underestimated the occurrence of the endangered bird, suggesting current range estimates being inadequate for planning purposes.	The increasing availability of citizen-science datasets offers a great opportunity to improve species distribution maps. eBird, WikiAves and Xeno-canto jointly produced 1.45 times more parrot detections, from samples that covered 45 times more municipalities, than the researcher-led counts.	Zulian et al. (2021)
Social	Knowledge about organisms and their functions	Missing connection to indigenous cultures	A lot of knowledge about biodiversity and functions is available in indigenous languages. Loss of languages and species leads to the extinction of knowledge.	Zimmer (2024)
Methodological	Insect biodiversity on a Global scale, especially in areas with low funding for biodiversity monitoring.	Access to cost-effective and non-invasive methods for global monitoring. Biodiversity hotspots are often not well equipped in funding and the killing of specimens is prohibited in many protected areas.	Smartphone-macro lens-based setup can enable low cost monitoring of insects. The method can enable researchers of all social backgrounds to contribute to insect monitoring, even in low income states and protected areas.	Riyaz & Ignacimuthu (2023)
Methodological	Habitat-specific eDNA assessments. For example, ponds which are highly diverse, yet understudied systems.	Combined knowledge and expertise to review applications and challenges that must be addressed for the future and consistency of habitat-specific eDNA monitoring.	Robust, comparable, and ecologically meaningful data to enable effective conservation and management	Harper et al. (2020)

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764 **IX. References**

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