



Land and deep-sea mining: the challenges of comparing biodiversity impacts

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Abstract

The term ‘biodiversity,’ while casually used in practice, is a complicated subject to measure, interpret, contextualize, and compare. Yet the possible advent of deep-sea mining in the mid-2020’s compels us to compare potential impacts of biodiversity loss across ecologically distant realms, a formidable task. Supplying the world’s green infrastructure is expected to lead to shortages of nickel, cobalt and other metals; meanwhile polymetallic nodules sitting atop the abyssal plains of the Clarion-Clipperton Zone (CCZ) of the Pacific Ocean contain billions of tons of nickel, cobalt, copper and manganese, enough to solve the supply issues. Implicit in society’s decision of whether to exploit this resource is a trade-off of harm to biodiversity in the CCZ’s abyssal seafloor and its overlying water column, versus intensification of harm to rainforests and other terrestrial mining habitats. Here we frame the challenges of comparing biodiversity impacts across such different realms, spanning the gamut from normative to fundamental: ambiguities in definitions, lack of protocol standardization, physical challenges in measurement, difficulties to integrate measures among different taxonomic groups, profound differences between ecologically distant realms, contextual necessity to attribute value to mathematical index results, and constraints of current knowledge about species, ecosystems and system level impacts of biodiversity change. Quantitative biodiversity measures alone cannot rank one system above the other; measures must be supplemented with qualitative judgements of the tangible and intangible values of species and habitats to natural systems and to humans, along with consideration of other threats that they and we face.

Keywords Clean energy transition · Critical mineral demand and supply · Mining · Clarion-Clipperton Zone · Species values · Ecosystem services · Anthropocentric values

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Abbreviations

ABNJ	Area Beyond National Jurisdiction
CBD	Convention on Biological Diversity
CCZ	Clarion-Clipperton Zone
DSM	Deep-sea mining
EBV	Environmental biodiversity variable
GWP	Global warming potential
ISA	International seabed authority
LCA	Life cycle assessment
MSFD	Marine strategy framework directive
UNCLOS	United Nations Convention on the Law of the Sea

Introduction

Biodiversity issues are frequently central to environmental permitting disputes for activities that affect habitats. This applies to activities on land (e.g., agriculture, logging, construction, mining) and at sea (e.g., fishing, dredging, offshore oil and gas, offshore wind). With the possible advent of deep-sea mining (DSM) in the mid-2020s, specifically the collection of polymetallic nodules containing nickel, cobalt, copper and manganese¹ from the abyssal seafloor of the Clarion-Clipperton Zone (CCZ), an Area Beyond National Jurisdiction (ABNJ) in the eastern North Pacific Ocean, concerns (e.g., Van Dover et al. 2017; Niner et al. 2018; Miller et al. 2021) have fueled organizational calls for a moratorium, either temporary or permanent (Greenpeace 2019; Chin and Hari 2020; FFI 2020; IUCN 2022a). Some moratorium support is seen in the private sector, with BMW, Google, Patagonia, Phillips, Volkswagen, Volvo and Samsung backing a 2021 World Wildlife Fund call for a *Business Moratorium on Deep-Sea Mining* until risks are fully understood and all alternatives exhausted (Haro 2021; Reuters 2021).

Given the centrality of biodiversity impacts to these concerns, it is crucial to understand the meaning and limitations of the term ‘Biodiversity.’ This includes perceptions of the term by the public, in addition to the role it plays in decisions made by the International Seabed Authority (ISA), the entity empowered by the UN Convention on the Law of the Sea (UNCLOS) to regulate and monitor any exploration or exploitation of ABNJ mineral resources, including setting standards for acceptance of proposed polymetallic-nodule collection projects (UN 2020). To that end, this paper seeks to clarify and expand public understanding of the meaning, significance and limitations of the concept of biodiversity—particularly in evaluating DSM risks.

The time sensitivity of this discussion is driven in part by the urgency to transition away from fossil-fuel dependence and mitigate climate change. Building a renewable-energy infrastructure will require hundreds of millions of tons of metals and other minerals for solar panels, wind turbines, electric motors and batteries, and more (IEA 2021; Hund et al. 2020; Valckx et al. 2021). Swiss investment bank UBS predicts severe shortages of 170,000 tons of cobalt (42% of the market), 10.9 megatons of copper (~50% of current global mined production), 2.1 megatons of lithium (~50% of the market), and 2.2

¹ We refer to nickel, cobalt, copper and manganese as ‘battery metals’ because they are currently important constituents of many batteries for electric vehicles; though they also have other significant industrial uses.

megatons of nickel (~37% of the market) by 2030 (Mills 2022). Prices of lithium, cobalt and nickel could rise several hundred percent above 2020 levels if societies pursue net-zero emissions (Boer et al. 2021), or if geopolitical conflicts threaten supplies—as witnessed when Russia’s invasion of Ukraine put its ~20% global share of high-quality nickel at risk, causing an unprecedented short squeeze and a 250% price surge to its all-time high price of \$101,365 per metric ton (Chin et al. 2022; Burton et al. 2022).

The polymetallic nodules sitting atop the CCZ seafloor contain more nickel and cobalt than the entire global terrestrial resource bases (i.e., proven reserves plus marginally economic and subeconomic deposits) of those metals (Hein et al. 2012, 2020), creating a tempting option to relieve the coming market pressures. Yet their removal would undoubtedly cause some biodiversity harm (Levin et al. 2020; Weaver and Billett 2019). This may include mortality to nodule-obligate organisms; disruptions to food web integrity (Stratmann et al. 2021), sediment structure (Gausepohl et al. 2020), microbial communities (Vonnahme et al. 2020), and benthic fauna (Simon-Lledó et al. 2019a, b); creation of sediment plumes that impact water-column fauna (Robison 2009; Drazen et al. 2019, 2020; Christiansen et al. 2020; Muñoz-Royo et al. 2021); and impacts to ecosystem services (Armstrong et al. 2012; Thurber et al. 2014; Le et al. 2017).

At the same time, producing metals from CCZ nodules would reduce requirements on terrestrial mining and relieve price pressures. Without enough metal stocks available for recycling to relieve the anticipated supply gap (Hund et al. 2020), a moratorium on DSM would force the predicted shortages of nickel, cobalt and copper to be met by increased terrestrial mining, leading to intensified environmental and anthropogenic impacts on land ecosystems (Valenta et al. 2019; Koschinsky et al. 2018; Sonter et al. 2018). Known risks from terrestrial mining include polluting air, water and soil (Agboola et al. 2020; Sergeant and Olden 2020); degrading or fragmenting habitats and harming biodiversity (Sonter et al. 2018); causing morbidity and mortality in humans (Mucha et al. 2018; Nkulu et al. 2018; Lyu et al. 2019; Cornwall 2020); disrupting indigenous cultures and societies (Tolvanen et al. 2018; Bainton 2020); and harming their traditionally-used sacred sites, habitats and biota (BBC 2013; FIDH-KontraS 2014; Aborigin Forum 2020; Cultural Survival 2018).

Such a sourcing decision, made at the scale of hundreds of millions of tons of metal, implies aggregate tradeoffs that affect environments and societies in tangible ways. Broad system level studies, such as life cycle analyses (LCA) of metals obtained from either source, can help frame a comprehensive tradeoff of the environmental, economic and social impacts of either option (Koschinsky et al. 2018; Ali and Katima 2020). Few studies comparing terrestrial mining and DSM are yet available. Koschinsky et al.’s (2018) review introduces some of the potential environmental, legal, economic and societal issues of DSM. Initial life cycle analyses (LCA) reported that nodule-sourced metals could substantially lower greenhouse warming potential (GWP) impacts (Paulikas et al. 2020a,b; Alvarenga et al. 2022), waste quantities and severities (Paulikas et al. 2022), and acidification (Alvarenga et al. 2022) when compared to use of land ores. However, concerns about the impacts to biodiversity and habitats of the abyssal seafloor remain paramount. This is among the first papers to explore the process of comparing biodiversity impacts of sourcing battery metals from land ores vs. polymetallic nodules in the CCZ. The only other such investigation of which we are aware is Pr at et al.’s (2021) prototype framework for assessing anthropogenic impacts to deep-sea biodiversity, based on existing methods applied in terrestrial and coastal habitats, which includes a case study for DSM in the CCZ.

Pr at et al. (2021) identify many data gaps and assumptions affecting such an analysis. Among them is the concern about which ecosystems, whether intact or disturbed, should be more protected, alluded to by the question, “Which is worse: mining in the pristine deep

sea or in vulnerable environments such as the Atacama Desert?” They noted that such a decision must be considered when interpreting results on global biodiversity impact, but that it was beyond the scope of their study. Beginning to grapple with questions like that raised by Pr eat et al. (2021) is a goal of this paper.

As Pr eat et al. imply, such comparisons of biodiversity and ecosystems are challenging for a number of reasons. These range from fundamental complexities of the ecosystems involved and the limits of current science, to normative and pragmatic difficulties in making such comparisons. Terrestrial ecosystems being mined are themselves distinct, geographically dispersed, and span a broader spectrum of ecological differences than the CCZ. Comprehensive species knowledge is lacking for both land and ocean ecosystems, with an estimated 91% and 86% of eukaryotic species expected yet to be discovered in the ocean and on land, respectively (Mora et al. 2011; Costello et al. 2012). Uncertainties about whether sampled genetic sequences represent different species or intraspecific variation underlie large variances in species estimates. Differences abound in experimental and research methods and classification processes, including applications of species accumulation curves (Appeltans et al. 2012; Costello et al. 2012; Deng et al. 2015; Bevilacqua et al. 2018), research periods and assumptions, ways of accounting for rare (unseen) species (Chao and Shen 2003) and species criteria. Perhaps most importantly, profound differences between the two realms and their inhabitants confound comparisons, with plants dominating terrestrial landscapes and biomass, whereas light attenuation limits living vegetation in the water to ~200 m,²; and observations of non-fish vertebrates are more frequent on land than in the deep open ocean.

Against the context of urgency to understand the tradeoffs involved in DSM, specifically for polymetallic nodules in the CCZ, we discuss factors that perplex comparison of mining’s biodiversity impacts on land and in the deep sea and show why results should be interpreted cautiously to avoid fostering misleading conclusions. We begin by addressing the ambiguities inherent in the definition of biodiversity. Next, we analyze the process of biodiversity measurement and comparison, noting inherent challenges present in each step. Third, we address various ways value can be derived from biodiversity, whether explicitly or implicitly, and we highlight the case of nematodes, whose context-dependent biodiversity value cannot be determined from computed indices. Fourth, given the above context we present specific issues that confound comparison of biodiversity on land versus in the deep sea. Finally, we integrate the presented frameworks into a discussion, then conclude.

Biodiversity definitions

Biodiversity

As Harper and Hawksworth (1994) observed, “it is clear that the concept of ‘Biodiversity’ can mean all things to all people.” ‘Biodiversity,’ a contraction of ‘biological diversity,’ appears frequently in the media and in public discourse, but without an agreed-upon, pragmatically quantifiable definition of the term.

² The current depth record is held by an undescribed crustose red alga (Rhodophyta) growing down to 268 m on a Bahamian seamount where light intensity was ~0.0005% of peak surface irradiance (Littler et al. 1985).

In common parlance, the term connotes the ‘richness’ or ‘variety’ of life within an area. Scientifically, it has been used to describe diversity of species, families, classes or phyla; genetic diversity within and among species; and diversity among sample plots, communities or ecosystems (Harper and Hawksworth 1994; Caro 2010).

The complexity of this definition is maintained in the current working definition of biodiversity, dating to 29 December 1993, when the 196-State Convention on Biological Diversity (CBD) entered into force as a global commitment to the conservation of biological diversity, its sustainable use and equitable sharing of its benefits. They defined biodiversity as: *The variability among living organisms from all sources including inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*

Biodiversity loss

Loss of biodiversity could signify reduction in the number of species (or in the evenness of their relative abundance) within an area, but most often it signifies species loss—at best, local reduction of species richness resulting from local extirpation or migrations to another area, and at worst, global extinction. A species is extinct when no living individual is known to survive, but there is often a delay between the death of that individual and the event(s) that caused it (Nic Lughadha et al. 2020) as well as that last individual’s death and its public or official recognition. Once habitat disturbance, environmental change, invasive species, disease, hunting or other factors reduce demographic structure or habitat size or suitability to a state that cannot sustain population growth, extinction becomes inevitable, with the last individuals eventually dying from stochastic events (e.g., storms, disease, poaching) or old age. This extinction delay may be long for (or not applicable to) species that undergo dormancy (e.g., Morono et al. 2020) or for large species with lifetimes of decades (e.g., white rhinoceros, Northern Right Whale), centuries (e.g., giant redwood [*Sequoiadendron giganteum*]) or longer. For culturally salient animals, a final stage (‘societal extinction’) may occur as cultural experience and collective memory fade, thereby contributing to a shifting baseline of biodiversity, reducing awareness of the severity of anthropogenic impacts and true extinction rates, and eroding cultural heritage (Jarić et al. 2022). Preserving species native to ecosystems is a general goal common to all conservation efforts, but increasingly challenging, as 40,000 of the 142,500 species globally assessed are threatened with extinction, including 41% of amphibians, 37% of sharks and rays, 33% of reef building corals, 26% of mammals and 13% of birds (IUCN 2022b). Additionally, 43.7% of globally assessed vascular plants with sufficient data (roughly 10% of known species) are considered threatened (i.e., categorized as Vulnerable, Endangered, or Critically Endangered). They include 40% of gymnosperms counting 34% of conifers (IUCN 2022b) and 62% of cycads, 44% of ferns and fern allies and 46% of flowering (Nic Lughadha et al. 2020). Thirty percent (30%) of the world’s 58,497 tree species are threatened with extinction, with at least 142 species now extinct in the world (Antonelli et al. 2020). Overall, IBPES (2010) estimated that one million species worldwide are threatened with extinction.

Rounsevell et al. (2020) suggested using extinction reduction as an easily communicated primary measure of progress toward biodiversity goals, with a near-term target of keeping extinctions of described species to well below 20 per year over the next 100 years across all major groups (fungi, plants, invertebrates, and vertebrates) and ecosystem types (marine, freshwater, and terrestrial). For comparison, in 2021, 22 animal species (11 birds,

8 freshwater mussels, two fish and one bat) as well as one plant species were declared extinct in the US alone (USFWS 2021).

Indicators, composite indicators, and indices

Evaluating an area's biodiversity requires construction of an 'indicator'. An indicator is a scientifically verifiable measure whose data can convey information about something other than itself (Biodiversity Indicators Partnership 2011), such as to summarize and communicate key aspects of an ecosystem state (McQuatters-Gollop et al. 2019). For example, trends in annual counts of the population of an animal or plant species have frequently been used to indicate aspects of an area's ecological condition, integrity or biodiversity (Sissig et al. 2016).

Combining such information with results from similar surveys of other species can create a 'composite indicator,' often called an 'index' (the names are used interchangeably), to provide a broader gauge of ecological state in a simplified manner. Assessing biodiversity at regional or global scales typically involves aggregation of numerous indicators. Each incorporated indicator may have idiosyncratic inherent measurement inconsistencies or features, often related to decisions made during design, aggregation, and weighting of sub-indicators, as well as data availability or cost, and treatment of data gaps; hence, index behavior may incorporate biases that hamper utility (Watermeyer et al. 2021).

After CBD ratification, a broad set of composite indicators was assembled for tracking progress toward 20 specific global biodiversity targets (Aichi targets) (Biodiversity Indicators Partnership 2010). The most recent draft indicator review (CBD 2020) includes the Living Planet Index (WWF 2020), which tracks abundance of ~21,000 populations of nearly 4,400 species of mammals, birds, fish, reptiles and amphibians; and the Biodiversity Intactness Index (Scholes and Biggs 2005; Martin et al. 2019), which measures the average current abundance of wild species relative to pre-modern times. The CBD's overall goals include reducing extinction rates tenfold, halving the risk of species extinctions by 2030, maintaining at least 90% of genetic diversity within all species maintained, and protecting at least 30% of the world's oceans and land by 2030 (CBD 2020).

Biodiversity measurement and its challenges

The 'raw material' of biodiversity comprises individual eukaryotic and prokaryotic organisms. Individual eukaryotes belong to ~1.8 million to 8.7 million species, ~0.3 million to 2.2 million of which are marine (Mora et al. 2011; Costello et al. 2012; Appeltans et al. 2012), with an estimated 91% and 86% remaining to be discovered in the ocean and on land, respectively (Mora et al. 2011; also see Costello et al. 2012). In addition, there are approximately ~0.8 to 1.6 million identified prokaryote 'species,' or operational taxonomic units [I] of bacteria and archaea with 16S rRNA gene clusters sharing >97% similarity, roughly corresponding to species (Louca et al. 2019). Most prokaryotes are globally distributed terrestrially or in the ocean such that forms can be recovered from a single land (Ramirez et al. 2014) or marine (Gibbons et al. 2013) location; local populations are determined by differential responses to environmental factors (light, temperature, etc.) rather than presence or absence—suggesting that in contrast to larger organisms, local disturbances or rapid climatic shifts are unlikely to cause extinction of a large fraction of prokaryotic species (Louca 2021).

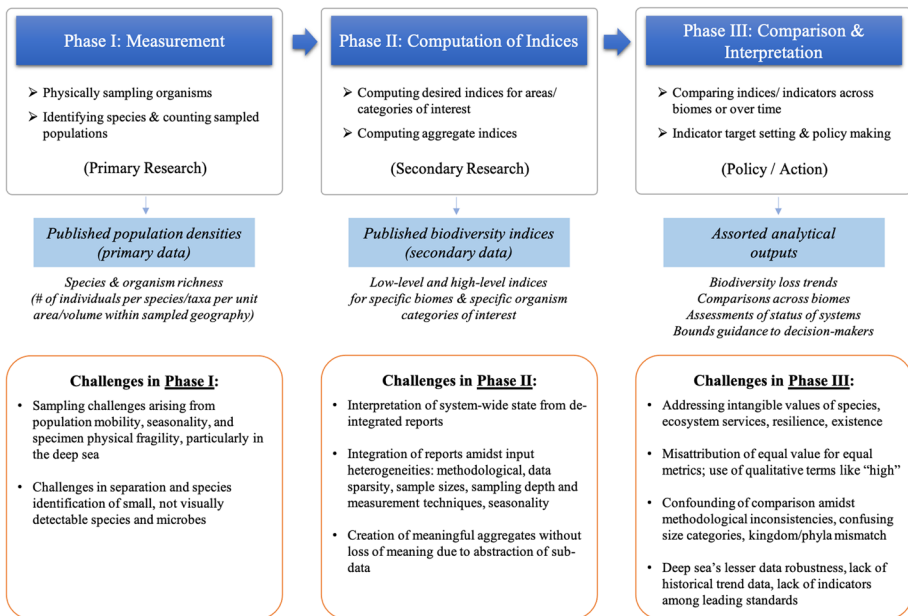


Fig. 1 Process challenges in biodiversity measurement, computation and comparison. Illustrated are the main tasks, outputs, and challenges in biodiversity measurement, computation, interpretation and comparison, grouped by process phase

The fundamental indicator of biodiversity, α diversity, expresses the distribution of individuals among the various species present within a sampled area or volume. It involves three conceptual process phases (Fig. 1). Ideally all entail robust primary data, consistent methodologies, and integrated results, but challenges exist for each phase.

Phase I: measurement

In this phase, primary data for biodiversity estimation are captured as numbers of individuals per species, per unit area or volume within a sampled geography, and typically sequestered into separate taxon- or size-specific analyses. Each separate analysis describes the diversity within a particular category, e.g.,

- (a) For land, e.g., diversity of trees, mosses, soil organisms, amphibians, reptiles, birds or mammals;
- (b) On the deep seafloor, e.g., diversity of nematodes, echinoderms, coelenterates, polychaete worms or fish;
- (c) By size spectrum: e.g., diversity of megafauna, macrofauna, meiofauna (mesofauna), microfauna.

Challenges

The taxonomic variety and broad size spectrum of organisms present in communities typically requires division of labor, both in collection of organisms and analysis of results. As

a result, different investigators and specialists focus on different topics. This often leads to different taxon-specific or size specific methods being used across investigations. Methodological differences can bias the number of species and individuals detected, thereby confounding later comparisons of species diversity or report integration efforts (e.g., Stratmann et al. 2021). Differences among investigators include types of sampling apparatus, sampling season, sieve mesh size (Gage et al. 2002; Zelnio 2009; Lins et al. 2021), size of area sampled, depth of soil or sediment sampled, and analytical techniques.

Physical limitations and sampling challenges can also bias results. Organism rarity, movements, catchability, diurnal rhythms, migrations and seasonalities, as well as inherent difficulties of sampling some communities (e.g., tree canopy or deep-sea habitats), complicate biodiversity measurements based on traditional methods. Marine sampling methods, including remotely operated vehicles, drop cameras, trawls and other devices, differ in effectiveness at sampling different types of benthic epifauna or habitats (Mendonça and Metaxas 2021). Nets may also destroy delicate oceanic organisms, such as jellyfish, salps, appendicularians and others, so accurate counts must rely on videography from underwater vehicles or similar technology.

Additionally, very small or rare organisms and cryptic species are difficult, time-consuming, and expensive to sample and study using morphology-based taxonomy (Le et al. 2021). An increasingly used cost-effective method to detect such variety of present life forms is through analysis of samples of short, specified micro-sequences of DNA or RNA directly from the environment (eDNA, eRNA) such as water, soil, feces or air (Thomsen and Willerslev 2014; Laroche et al. 2020; Lejzerowicz et al. 2021; Clare et al. 2021). Such sampled sequences can be sorted into higher taxa (e.g., kingdom, phylum, order) but usually not to species (except if matched to a genetic sample from a previously morphologically described species, i.e., ‘bar-code’) (Hebert et al. 2003). eDNA thus yields general information on richness of life and the relative abundance of types, though not whether sequences represent species or varieties, or their absolute abundance, population structure or biomass (Le et al. 2021); unless referred to bar-coded species, e-DNA does not provide information on morphology, physiology, behavior or ecosystem functions of the host organism, other than by inference. However, as more species are described and bar-coded, particularly as both techniques are utilized together, current difficulties in resolving morphological and eDNA study results will decrease, thereby improving biodiversity estimates by detecting diversity hidden in cryptic species (e.g., Sheikh et al. 2022), parasites (e.g., Barčák et al. 2021) and even supposedly well-known groups such as corals (Bongaerts et al. 2021).

Phase II: indicators and indices

In this phase, investigators assemble multiple primary and secondary data inputs into quantitative numerical indicators or indices to estimate biodiversity or track its trends. All rely on integrating the number of species present (‘species richness’) with the distribution of individual organisms among them (Peet 1974). Biodiversity is regarded as highest when individual organisms (or genetic samples) are evenly distributed among species (or morphotypes) (‘evenness’). The techniques are applicable for any scale of study area or habitat type, size range (e.g., macrofauna), taxon (e.g., Annelida), etc., and resulting indices of diversity are expressed as dimensionless numbers regardless of the system being evaluated.

One of the most frequently used measures, Simpson’s indicator of biodiversity (Simpson 1949), ranges from 0 (when all individuals belong to one species) to 1 (when every

individual is a different species and diversity is ‘infinite’) and is calculated as $1 - \{\sum n(n-1) / N(N-1)\}$, where n =number of individuals of a particular species and N =number of individuals across all species. Numerous alternative techniques are also available (Ardron et al. 2019; Hayek and Buzas 2010), and there is no single best or true biodiversity index. Instead, the type of indicator(s) used is ideally selected based on the specific ecological question to be addressed (Gorelick 2011). Albeit simplistic, our discussion focuses on species richness as the most common and easily understood measure of ‘biodiversity,’ mentioning aspects of genetic or phyletic diversity where appropriate.

Challenges

Whether and how to integrate results from heterogeneous taxon- or size-specific studies to form an overall biodiversity assessment is not clear cut. The absence of measurement process uniformity in Phase I can lead to ambiguity, inconsistency, incompleteness, or bias in composite indices. Additionally, some ecosystems and taxa are much better studied than others—e.g., birds and mammals, in which nearly every species is described—while the overwhelming majority of systems, organisms and clades are under-studied (Sigwart et al. 2018), including microorganisms and many invertebrate groups, leading to (unintentionally) biased evaluations of their species diversity.

Integration of results using heterogeneous techniques also remains a challenge, especially since patterns of species richness vary among taxa, as in Ritter et al. (2019) who compared morphologically based results for Amazonian trees and birds with meta-barcode-based results for microorganisms. Both sets of results shared a declining west-to-east gradient at large spatial scale, but significant differences at smaller scales and inconsistencies across taxa indicated that at a regional scale, the diversity distribution of one taxonomic group should neither be used as a general proxy for the diversity of another nor as an indication of overall patterns of richness; and that at small spatial scales, idiosyncrasies of each taxonomic group and peculiarities of each environment appeared to be more important than general diversity patterns, which differ among organism types.

Phase III: comparison and interpretation

In this phase, compiled indicators and indices are used and interpreted to some end, often for policymaking or driving action. This could entail comparing indices across biomes and/or time, as well as interpreting the quantitative values qualitatively.

Challenges

Quantitative comparison of species richness measured at different scales requires access to site-specific species-area discovery functions, which are not always available. Additionally, comparable results for the same category (e.g., taxonomic group, size class, etc.) may not be available, especially if the different biomes have not been quantitatively sampled in the same way.

Without an integrated picture, policy makers with varying levels of technical proficiency may be encumbered in their analyses, restricted to system comparisons of taxon- or size-class-specific reports that incorporate the methodological inconsistencies mentioned above. Though some of the more mechanical challenges can be resolved (Lins et al. 2021), the compared indices still do not capture the relative values of their component species.

Overall, the way to integrate siloed results to describe inclusive community diversity is not entirely clear.

Interpreting the relative value of different biodiversity measurements may also be challenging, because there is no unequivocal mapping of the benefits that biodiversity confers. Although areas with ‘high’ biodiversity are typically regarded as ‘better’ than ones with ‘low’ biodiversity, a higher biodiversity index by itself does not necessarily confer greater importance on an ecosystem. Other factors, such as existence values, ecosystem services and resilience may carry greater weight, as described below.

Value considerations in biodiversity

Do identical biodiversity index scores for two different systems imply equal value? Should a high biodiversity measure of an ecosystem’s parasites (Gómez and Nichols 2013) or pathogens be valued equally with the high biodiversity measure of, e.g., its echinoderms or amphibians? Gómez and Nichols (2013) answer affirmatively.³ Velland (2017) too suggested that quantification of biodiversity should be value-free to safeguard scientific credibility, but he noted that such measures may not always correspond with anthropocentric values. Such considerations add complexity to tasks of comparing biodiversity across regions, such as discussing mining’s biodiversity impacts on land versus the deep sea.

Existence value beyond a single index

To begin, and separate from the fact that biodiversity measurements treat them all equally (Magurran 2004), individuals and species share ‘intrinsic value.’ This represents the equal inherent worth that emanates directly from themselves and the fact of their existence (Francis 2015; de Vere et al. 2018; Katona et al. 2021).⁴ However, they differ in ‘existence

³ Gómez and Nichols (2013) contend that arguments advanced to conserve free-living species apply equally well to parasites, and that ignoring parasites in efforts to conserve biodiversity would constitute neglecting critical components of patterns and processes that form natural ecosystems. They describe parasitism as perhaps the most widespread animal trophic strategy, noting that 31 of the 42 broadly recognized phyla are entirely or predominantly parasitic, while others contain multiple parasitic clades; and that parasitic biomass can equal or exceed free living biomass in some groups. Lovejoy’s (1994) discussion of weevils is also of interest.

⁴ It is difficult to conceive of intrinsic value absent humans (or other sentient beings) to appreciate it. Hence, ‘existence value’ is often used in reference to the psychological benefits people receive from knowing that a species or natural feature exists, even though they may never see it (Harvard Law Review 2016). Species may gain psychological traction and value to humans through fictional representation (e.g., Melville’s “Moby Dick”, London’s “Lobo”, Disney’s “Nemo”), documentary literature (Joy Adamson’s “Elsa”), or through particularly well-known representatives, such as individuals of great age (the “Methuselah” bristlecone pine or the Japanese koi “Hanako”), notable reproductive success (Laysan albatross “Wisdom”), noteworthy intelligence (western lowland gorilla “Koko”, orca “Namu”, African gray parrot “Alex”), touristic importance (African lion “Cecil”) or symbolic importance of the last remaining individuals (passenger pigeon “Martha” or Sumatran rhinoceros “Tam”). Few deep-sea species have gained such iconic status, with the possible exception of the giant squid (perhaps originally intended as an octopus) introduced to the public in 1870 by Jules Verne in 20,000 Leagues Under the Sea. However, photographs of newly discovered deep-sea species in the CCZ (Davis 2020) and elsewhere (e.g., Schmidt Ocean Institute 2020) have gained public attention, including xenophyophores, the sea-anemone-like *Relicanthus*, a polychaete worm *Ophelina nunnallyi*, a strange bulbous worm *Travisia zieglerae*, as well as the first live photographs of some species discovered by the Challenger Expeditions of 1872–1876 such as the “gummy squirrel” sea cucumber (Théel 1882) and some “Dumbo” octopuses (Jamieson and Vecchione 2020). In time, some deep-sea

value’, which represents their value to biological communities, humans or perhaps to the world as a whole (Harper and Hawksworth 1994).

Such differences may influence judgements of what rights to well-being different species (or individuals) have or ought to possess, as well as human decisions to conserve them and/or use their habitats. They also influence interpretation of biodiversity measures.

How might we evaluate differing biodiversity scores for a forest bird community and a deep-sea echinoderm or fish community? It is at least clear that, as Feest et al. (2009) recognized, a single measure of biodiversity cannot definitively answer such value-comparison questions. Instead, they proposed simultaneous use of a range of biodiversity-related indices, such as species richness, evenness/dominance, biomass, population and rarity/intrinsic value, as a more satisfactory description of ‘biodiversity quality.’

Whether a comprehensive multidimensional index of biodiversity quality could (or ought to be) created as a stand-alone measure for comparing ecosystems still remains to be seen. Indicator trends in different areas can reveal where biodiversity loss is fastest or greatest, but not which area might have most value to humans, other natural communities, or the planet.

Resilience values

Two values often associated with biodiversity are ecological resistance and ecological resilience. Resistance describes a community’s ability to absorb the effects of internal or external disturbance without noticeable change in function or structure; while resilience describes the ability and rate of recovery from disturbance (Gollner et al. 2017; Meredith et al. 2018). Biodiversity, encompassing variation from within species to across landscapes, may be crucial for resistance and longer-term resilience of ecosystem functions and the services they underpin (Oliver et al. 2015). In theory, the presence of more species, traits and genotypes can help ecosystem functions resist or recover more rapidly from environmental perturbations. Note that regional rather than local diversity appears to be more closely linked to macrosystem stability (Patrick et al. 2021).

Recognized value categories

The assumption of species equality within a biodiversity index obscures the fact that some species may be particularly ‘valuable’ to a biological community. These may include ‘*Structural species*’ that provide its physical architecture—trees, giant kelp, mangroves, reef-forming corals, oysters, mussels (Huston 1994), xenophyophores (Ashford et al. 2014; Simon-Lledó et al. 2019a, b), stalked glass sponges (Stratmann et al. 2021); ‘*Ecosystem engineers*’ that actively alter it—beavers, earthworms, termites,⁵alligators, hippopotamus; and ‘*Keystone species*’ which are disproportionately connected to more species in a food

Footnote 4 (continued)

species, including species that have not yet been discovered, could become iconic and serve as flagship or umbrella species for deep-sea conservation.

⁵ As one example, in northeastern Brazil, a single species, the litter-feeding termite, *Syntermes dirus*, has constructed an array of 200 million interconnected mounds, each ~2.5 m tall and 9 m in diameter, that covers 230,000 km² and has persisted for 4000 years (Martin et al. 2018). The largest animal-made structure, the 344,468 km² Great Barrier Reef (NOAA 2022) was built over the past ~600 ± 280 ka by many species of corals and other calcifiers (Alexander et al. 2001).

web (Menge and Freidenburg 2013) or have essential functional roles in creating or maintaining a habitat or ecosystem's structure and functions—redwood trees, prairie dogs, elephants, beavers, wolves, sea otters.

Other species may be particularly valuable as strategic assets for conservation efforts, such as '*Indicator species*' (Sissig et al. 2016) or '*Sentinel species*' used as proxies for a habitat or ecosystem's status and health—spotted owl, river otter, frogs, parrot fish, sharks; '*Umbrella species*' with extensive areal needs, such that protecting them also benefits other organisms in their habitat or ecosystem—tigers, jaguars, grizzly bears, whales; and '*Flagship species*' iconic or symbolic of particular habitats or ecosystems and sufficiently fascinating to galvanize public support for their conservation, and, if well chosen, to inspire actions that protect background species and biodiversity (McGowan et al. 2020)—whales, tigers, gorillas, orangutans, great pandas elephants, seahorses (Barua et al. 2012; Verissimo et al. 2011).

We note that, with the exception of structural contributions of stalked xenophyophores and glass sponges, lack of knowledge about abyssal seafloor ecosystems has thus far prevented public acknowledgement of Indicator, Sentinel, Keystone, Umbrella or Flagship species. (The amount of popular-press coverage of the discovery of pale invertebrate 'ghost octopuses' nicknamed 'Casper' at great depths in the Pacific Ocean, though not yet found in the CCZ (Purser et al. 2016), could make them a candidate for Flagship status.) Notably, despite their foundational importance in soils and on the abyssal seafloor, microbes have not yet been included in such categories, with the exception of macroaggregated foraminiferans (xenophyophores) on the deep seafloor.

Ecosystem services benefits

Existence values of different species reflect their various benefits to humans. Greater biodiversity may offer the potential for more such benefits, termed 'ecosystem services', to be delivered or available to people (Lovejoy 1994). Ecosystem services are direct and indirect, tangible and intangible contributions to human well-being. Among others, they include (De Groot et al. 2010):

1. Provisioning Services: food, water, raw materials, and genetic and medicinal resources;
2. Regulating Services: maintaining air quality, climate, water flow, moderating extreme events, maintaining soil fertility and reducing erosion, waste treatment, pollination and biological control;
3. Supporting Services: primary production, nutrient cycling, habitat or nursery areas for residents or migrating species, maintenance of genetic diversity;
4. Cultural Services: aesthetic or spiritual opportunities, opportunities for recreation and tourism, inspiration for culture, arts and design, and information for cognitive development.

Neither biodiversity quantification nor the amount of ecosystem services provided is alone sufficient to rank one ecosystem 'better' than another. Both must be considered. For example, tropical rainforests on land and coral reefs in the shallower ocean harbor the highest biodiversity and broadest array of ecosystem services in their respective spheres (Wagner et al. 2020); but lower-diversity systems may also be important by providing large quantities of fewer ecosystem services—e.g., carbon sequestration and lumber from

northern forests (Gauthier et al. 2015), or water purification and nursery habitat for commercially harvested whelks from horse mussel reefs (Kent et al. 2016).

Ambiguous value of high biodiversity indices (case: nematodes)

Some value issues are complex. Nematodes offer a prime example where detailed ecological context is necessary for determining the value of high biodiversity. Given the range of niches filled by nematodes and the many species harmful to plants, animals and people, high nematode biodiversity cannot simply be valued as ‘better’ or ‘good.’ A more nuanced evaluation of nematode biodiversity is needed—one that considers the roles, benefits and harms associated with the various species (or major groups) present in an ecosystem. The same can likely be said for many other taxa.

The ubiquity of nematodes inspired Cobb’s (1915) memorable reflection that if everything but nematodes were swept away, the shape of our world and all that had lived in it would still be dimly recognizable as represented by a film of nematodes. The $\sim 4.4 \times 10^{20}$ individuals in soil alone make nematodes Earth’s most abundant metazoan organisms (van den Hoogen et al. 2019). They are also extremely abundant in fresh and marine waters, representing approximately 90% of the metazoan animals on or in the CCZ seafloor. Their ranks include detritivores, bacterivores, fungivores, herbivores, omnivores, predators and parasites (Schratzberger et al. 2019).

On the ‘bad’ side, more than 4000 species parasitize plants, causing annual average losses of $\sim 12\%$ of crops and ~ 215 billion USD to global agriculture; and more than 300 species parasitize animals, causing billions of dollars of losses to livestock, fish, and expenses for prevention, extermination and treatment as they also infect 24% of the global human population (Bernard et al. 2017; Salikin et al. 2020). On the ‘good’ side, ‘beneficial’ predatory or parasitic nematodes that kill species-specific types of agricultural pests are sprayed on fields and gardens to control slugs, snails, thrips, grubs, beetles, earworms, moths and others, all with no harm to people or wildlife (Askary and Abd-Elgawad 2017). Furthermore, regardless of its messiness, high nematode biodiversity appears to enhance the rates and efficiency of ecosystem processes. In the CCZ, this would include bioturbation and redistribution of food within the sediment, detrital processing and composition, biodiversity enhancement through predation on larvae of other organisms, and stimulation of growth, activity and carbon production by bacteria and other microorganisms (Danovaro et al. 2007; Schratzberger et al. 2019). Thus, from an ecosystem perspective, high nematode biodiversity likely benefits the CCZ seafloor community, even if future research reveals examples of parasitism.

From a human-centered utilitarian perspective, the situation is also nuanced. On land, nematodes are geographically and temporally closely connected to humans and to the ecosystem services supporting us. There, high nematode biodiversity is not unequivocally beneficial, but both positive and negative effects of nematodes are felt. In contrast, the CCZ seafloor’s great depth reduces the contributions of its inhabitants to Provisioning Services, and it slows delivery time for any others. Hence, while in shallower coastal and pelagic systems higher nematode biodiversity is correlated with higher ecosystem services delivered (e.g., fisheries productivity, nursery habitat, ecotourism, water filtering capacity, resilience to disruptive events) (Worm et al. 2006), in the CCZ the near-term human impacts of benthic nematodes—whether beneficial or not—are likely far less significant (with further research necessary to reveal any longer-term impacts). The value of ‘high’ biodiversity is thus both context and knowledge dependent.

As a further example of this, vector-transmitted diseases demonstrate the need for nuanced interpretations of biodiversity. Using mosquitoes as an example, on the ‘good’ side, mosquito adults of the 3400 known species are important food for insectivorous bats, birds, dragonflies, carnivorous plants (e.g., some pitcher plants, sundews, venus fly traps and bladderwort (Król et al. 2012; Scherzer et al. 2019) and predacious mosquitoes. Mosquito larvae are eaten by the larvae of damselflies and aquatic beetles as well as some tadpoles and young turtles. Both sexes feed on nectar, pollinating small flowers during the process. On the ‘bad’ side, females seek blood meals from vertebrates before they make eggs. About 10% of species are efficient vectors of human and animal disease, including life-threatening illnesses such as malaria, dengue fever, yellow fever and others. The net result can be a conflict between mosquito ecosystem services to biota and to humans (Manguin and Boëte 2011). Similarly, on the ‘bad’ side, high vertebrate biodiversity can provide a negative ecosystem service to humans by serving as a source pool for new pathogens. On the ‘good’ side, it can also reduce human incidence, to the extent that mosquitos or other vectors have non-human vertebrates available to feed on that are less competent hosts for pathogens. Conversely, low vertebrate biodiversity can have the opposite effect: reductions in the biodiversity of birds, small mammals and plants have increased the infectivity of West Nile virus, hantavirus and fungal rust, respectively (Keesing et al. 2010).

Comparing biodiversity between land and the deep sea

Given the above biodiversity definitions, measurement challenges, and nuances in value determination, we now turn to several issues that specifically confound comparisons between biodiversity on land and in the CCZ or other deep-sea areas.

Microbes

Quantification of the abundance, diversity and function of microbes is a mandatory part of the application process for commercial exploration for CCZ nodules (Sec. 36(d) ISA 2013). In contrast, microbes are not usually considered during review of terrestrial projects that disturb soil. In fact, despite their known ecological importance to soil and plant ecology, they rarely receive attention in land mining (Pugnaire et al. 2019). This discrepancy in biodiversity measurement standards for microbes during environmental impact assessments can hinder scientific comparison of the two realms, as well as public discussion about them.

Microbes (bacteria, archaea, protista, fungi and viruses) are very small organisms that are vitally important within all terrestrial and marine ecosystems. They act variously as primary producers, decomposers, chemoautotrophs, dissolved carbon assimilators, food sources, parasites, pathogens and symbionts. However, estimating their abundance and diversity is difficult (Corinaldesi 2015) and how to include them in biodiversity assessments is problematic.

Broadly, microbial groups include the following:

- *Bacteria* Terrestrial bacteria build and maintain soil by decomposing organic matter and mineralizing nutrients. They assist plants by fixing nitrogen, aiding uptake of nutrients and water, synthesizing needed substances, and stimulating production of chemical defenses against herbivory. They also influence plant growth, physiology and palatabil-

ity, and both protect against and cause various plant diseases (Hayat et al. 2010; Heinen et al. 2018). Oceanic bacteria include Earth's most abundant photosynthetic organisms, the marine cyanobacteria, *Prochlorococcus spp.*, and communities in abyssal sediments (Bienhold et al. 2016), on nodules (Wear et al. 2021) and at hydrothermal vents and cold seeps that help power the benthic food web through chemoautotrophic and heterotrophic production (Sweetman et al. 2018).

- **Archaea** A kingdom first described in 1977, archaea include 30 phyla and numerous taxa at all levels of classification. They inhabit both extreme and common habitats in soil and aquatic and marine waters and sediments. Archaea contribute important functions in the global carbon cycle, methanogenesis, sulfur cycling and nitrification (Adam et al. 2017; Zou et al. 2020) including in CCZ waters and sediments.
- **Protista** Between 60,000 to 200,000 Protistan species are thought to exist, occupying any environment where liquid water is present. They include photosynthetic, heterotrophic, saprophytic, predatory and pathogenic types. Numerically important in the marine water column, they may comprise 50% of microbial abundance there, but their numerical abundance is much lower on the abyssal seafloor (though giant agglutinated foraminiferan protists—xenophyophores—are a key component of the abyssal seafloor megafauna, with important structural significance) (Gooday et al. 2020).
- **Fungi** Fungal species estimates range from ~611,000 (Mora et al. 2011) to 2.2–3.8 million (Hawksworth and Lücking 2017) to ~5 million (Blackwell 2011). On land, many species connect and help nourish nearly every terrestrial plant through complex mycelial networks (Steidinger et al. 2019; Sheldrake 2020), though quantifying their diversity is a challenging task (Feest et al. 2009). On the other hand, parasitic fungi destroy one third of global food crops annually (Fausto et al. 2019), and about 300 of the ~148,000 fungal species described as of 2020 (Cheek et al. 2020) are harmful to humans (McKenna 2021). Identification and classification of deep-sea fungi are still in their infancy (Vargas-Gastélum and Riquelme 2020), though some species have been proposed as a potential source for bioactive molecules (Arifeen et al. 2020). The well-known metal-scavenging abilities of terrestrial fungi have potential utility for treating mining wastes, reclaiming mine sites and extracting metals from nodules (Dusenge-mungu et al. 2021; Beolchini et al. 2020). Because fungal ubiquity on land particularly coevolved with vascular plants, it will be interesting to learn the extents of their roles and associations in the deep sea where no plants exist.
- **Viruses** Though not technically 'alive,' viruses are the ocean's most abundant and genetically diverse entities. Each day they lyse an estimated 20% of the phytoplankton, bacteria and other microbes that make up 90% of the ocean's biomass, releasing carbon and other nutrients to pelagic and benthic marine food webs (Suttle 2007). Filter feeders, including crabs, cockles, oysters and sponges (Welsh et al. 2020), as well as *Oikopleura* (Lawrence et al. 2017) and presumably other appendicularians, remove viruses from the water column, but their dietary importance is not known. Decomposition of bacteria lysed in seafloor surface sediments, as well as the protein coats and nucleic acids of the viruses themselves, may also be a primary source of nutrients to seafloor productivity (Suttle 2005; Dell'Anno et al. 2015).

Whether and how to include microbes in an overall description of ecosystem biodiversity (as opposed to function) remains unclear, in part because microbial significance is not always correlated with their diversity. Single-species or single-genus populations can have enormous import, e.g., via invasive impacts (Thakur et al. 2019), disease (Bayliss et al. 2017; Baker et al. 2021) or health maintenance in humans (e.g., dominance of

Lactobacillus spp. in vaginal microbiota, Witkin and Linhares 2016) or animals (e.g., *Termitomyces* spp. in termite fungal farms—probably the most complex colony and mound structures formed by any terrestrial invertebrate group (Aanen et al. 2002). Also unclear is the relationship between microbes' diversity and the diversity of organisms in larger size classes or taxa.

The relationship between microbial genetic diversity and traditionally measured biodiversity is not always straightforward either. The very small sizes of these organisms make them extremely difficult to count and identify. Studies of microbial communities and diversity are typically conducted independently from studies of multicellular organisms, with each microbial group (e.g., viruses versus bacteria) typically studied separately due to the need for specialized techniques. Microscopy rarely permits visual identification to species, so eDNA or eRNA is increasingly used to distinguish unique sequences present. Whether the sequences represent species or varieties can be inconclusive, especially since the definition of species is problematic for bacteria, archaea and viruses (Fig. S3, Bar-On et al. 2018), at least.

Vascular plants

Current biodiversity comparisons between land and the deep-sea focus exclusively on animals. Such analyses fail to express the high species richness of vascular plants in land biomes disrupted by traditional mining. Kingdom Plantae comprises 80% of Earth's biomass (Bar-On et al. 2018) and includes about 391,000 known species of vascular plants, of which 21% are in danger of extinction (RBG Kew 2016) from conversion of forests and other land to agriculture, development, or mineral extraction, among others. Terrestrial metal mining has caused extinction of metallophyte plants, which evolved where metal accumulations extend to the Earth's surface. Remaining metallophyte refugia are under acute threat as previously uneconomic deposits of metals are targeted for extraction, particularly in biodiverse tropical areas. For example, hundreds of endemic copper metallophyte species are among the most critically endangered plants in the world due to increased copper mining in the Democratic Republic of Congo (Erskine et al. 2012).

In contrast, no vascular plants exist in the CCZ water column or on its abyssal seafloor (e.g., Assis et al. 2020) and plants in the water column are limited to microscopic phytoplankton in the photic zone—about 0 to ~200 m in the CCZ. We found no overall estimate of the number of phytoplankton species there, but Zinssmeister et al. (2017) reported 66 species of dinoflagellates (Dinophyceae), said to be an unexpectedly high number, of which up to 7 could be new. If mining-related impacts are engineered out of at least the top 1000 m of the water column by deep discharge, disturbance to phytoplankton or other near-surface life would be limited to factors typical of ship operation such as noise (Martin et al. 2021), light (Miller et al. 2018), airborne engine exhaust, wastewater discharge and metal pollution from bottom paint (Richir et al. 2021). Nevertheless, finding ways to compare the biodiversity of one realm whose biomass is dominated by plants and fungi with another dominated by animals and protists (Bar-on et al. 2018) is troublesome.

Phylogenetic diversity

Phylogenetic diversity differences between terrestrial and deep-sea habitats confound efforts to measure baselines and establish priorities for conservation. Despite covering only 30% of Earth's surface and containing vastly less volume than the ocean, land is inhabited

by many more species than exist in the ocean, thereby leading to many land regions with greater species diversity than the CCZ. However, the situation is reversed at the levels of eukaryote phylum and class: 34 phyla live in the marine realm, 17 in freshwater, and only 15 on land; similarly, 77 classes occur in the sea, 35 in freshwater, and 33 on land (Briggs 1995). Terrestrial biodiversity measures are heavily skewed by the extraordinary number of species in one phylum, Arthropoda, whose estimated 7 million species (including 5.5 million insects and 1.5 million beetles) comprise 90% of all terrestrial species (Stork 2018). In contrast, 8 phyla, led by Nematoda and Mollusca, are needed to cover the same proportion (90%) of marine species (Briggs 1995). Moreover, the CCZ seafloor and water column contain many phyla that have no presence on land or in its adjacent freshwater systems: Ctenophora, Chaetognatha, Echinodermata, Sipuncula, Echiura, Brachiopoda, among others.

Inhabitants of both ecological realms face growing numbers and intensities of stressors, i.e., natural or anthropogenic environmental changes that decrease organismal fitness (Boyd and Hutchins 2012). Current stressors to deep pelagic and benthic biodiversity are climate change, fishing (although most occurs at shallower depths) and chronic or episodic pollution that degrades habitat quality, such as noise from military activities, shipping or others. Stressors added by DSM would especially include noise (Martin et al. 2021, Williams et al. 2022), habitat loss, sediment disruption and turbidity. Meanwhile, biotic communities on land face numerous and increasing pressures as the growing human population demands more food, water and materials, stimulating conversion of natural landscapes to rangeland, intensive agriculture, urbanization and industrialization accompanied by accelerating habitat loss, pollution by synthetic pesticides and fertilizers, spread of pathogens, exotic species and other biological factors, and contributing to climate change. These stressors have already caused dramatic declines in plant and animal populations (as well as indigenous cultures) globally, such that an estimated 40 percent of species could become extinct within coming decades (Sánchez-Bayo and Wyckhuys 2019).

Consequently, a measure of biotic richness on the CCZ seafloor would likely have higher phyletic diversity, but lower species diversity, than a measure on land. Meanwhile conservation efforts on land could protect more species, while conservation in the deep ocean could protect more phyla and classes; but under most circumstances, other criteria for protection would be more useful than taxonomic level.

Inconsistent criteria for size classification

Criteria for names given to size classes of organisms—megafauna, macrofauna, meiofauna (or mesofauna in soil science), and microfauna—vary among research studies. Even within habitats, methodological sampling differences and categorical transgressions by ontological life stages complicate size class descriptions, such as for macrofauna and meiofauna (Lins et al. 2021). Terrestrial and marine scientists use mostly the same names for size classes, but with very different size criteria for identically named categories on land versus on the seafloor (see Fig. 2).⁶ We highlight ‘megafauna’ as a prime example.

⁶ The ‘mega’ prefix accretes further ambiguity through use in the public arena, particularly advertising, where it typically connotes great, large, huge, very big, greatly surpassing others of its kind, or very good—as in megastars, megastores, Mega Pokémon®, Mega Bloks® building toys, and Mega Variety Snack Packs, but also in public dictionary entries that typically include ‘megafauna’ as organisms of large mass or size, but without precision, such that Google search results carried out on 21 February 2020 for ‘definition of megafauna’ yielded “in terrestrial zoology ...comprises the large or giant animals of an area, habitat, or geological period extinct or extant” (Wikipedia.com); “animals (such as bears, bison, or mammoths) of particularly large size” (Merriam-Webster.com); “animals with adults larger than a threshold size, originally

In physical science, the prefix ‘mega-’ specifies one million times the stated unit (e.g., megaton). Biological scientists use it differently, describing terrestrial, freshwater and pelagic marine ‘megafauna’ on the basis of mass, but categorizing benthic marine and soil invertebrate ‘megafauna’ by length (Moleón et al. 2020). On land, ‘megafauna’ originally designated animals > 45 kg (Martin 1967); but Malhi et al. (2016) used consumption and predation patterns to categorize large herbivores (45–999 kg), megaherbivores (≥ 1000 kg), large carnivores (21.5–99 kg), and megacarnivores (≥ 100 kg). Additionally, some soil scientists reappropriate the term to describe small vertebrates and earthworms. In coastal and pelagic systems, criteria generally resemble Malhi et al.’s (2016) (Pimiento et al. 2020), but on the abyssal seabed, ‘megafauna’ denotes organisms longer than 2 cm, or sometimes longer than 1 cm (e.g., Simon-Lledó et al. 2019a, b). Hence, depending on its habitat and a researcher’s specialty, a hypothetical 1 or 2 cm organism may be classified as:

- (a) Megafauna, if resident on the abyssal seafloor;
- (b) Macrofauna, if resident in a coastal system and classified by a marine ecologist;
- (c) Either megafauna or macrofauna, if found in soil;
- (d) Macrofauna, if found in a non-soil land habitat.

In Moleón et al.’s (2020) systematic literature review, only 26% of scientists using the term ‘megafauna’ defined it, and definitions were often idiosyncratic. While encouraging authors to unambiguously define how they use ‘megafauna’ and present the logic underpinning their definition, Moleón et al. (2020) also proposed consideration of functional significance and size as potential definitional components.⁷

Such varied connotations and understanding of the ‘mega’ prefix may bias ecosystem-use communications or decision making that involves public forums (e.g., DOSI 2021), activist groups (e.g., *Deep Sea Conservation Coalition*, *Deep Sea Mining Campaign*) or discussion groups (e.g., World Economic Forum’s *Deep Sea Minerals Dialogue*). In such settings, discussion may include organisms labeled as ‘megafauna’ at risk from CCZ nodule collection—sponges, cnidarians, xenophyophores, echinoderms (e.g., Jones et al. 2019a, b; Simon-Lledó et al. 2019a, b)—but may exclude the much larger fauna or ‘megafauna’ potentially at risk from terrestrial mining of battery metals—Sumatran tigers, orangutans, rhinoceros, bears in Indonesia, wolf and lynx in Minnesota, Indri lemur in Madagascar, Nubian ibex in Jordan. Clarifying and standardizing terminology could thus have policy implications beyond the academic sphere.

Footnote 6 (continued)

100 lb (45.3 kg)” (Malhi et al. 2016); “large or relatively large animals of a particular region, period, or habitat: Pleistocene megafauna; crabs and other aquatic megafauna” (Your Dictionary.com); “big (mega) animals (fauna)” (Ermanga Natural History Museum, <https://www.enhm.com.au>).

⁷ The term ‘charismatic megafauna’ may introduce further semantic confusion. It is typically applied to large (Berti et al. 2020), terrestrial, and exotic mammals and has been useful in conservation campaigns and marketing (Albert et al. 2018). It has also been used for large aquatic animals, e.g., cetaceans, elasmobranchs and groupers (Mazzoldi et al. 2019), but could similarly be applied to ‘less attractive’ or smaller organisms depending on the target public and campaign objectives (Luque et al. 2018). Thus Smith et al. (2018) noted that “the enormous diversity of seafloor invertebrates [on the CCZ seafloor] offers many candidates as charismatic megafauna” including the 60 cm ‘gummy squirrel’ holothurian *Psychropotes laungicauda*.

The significance of megabiota, including large trees, terrestrial megaherbivores (elephant, hippopotamus, bison, elk), megaplanktivores and piscivores (basking sharks, whale sharks, whales), and megacarnivores (sharks, large reptiles, large cats, wolves) in delivering ecosystem services and maintaining system function at landscape, seascape, biome and earth scales is well known (Malhi et al. 2016). Conservation strategies that promote large trees and animals will have significant impacts on biodiversity, ecosystem processes (fertility, biomass, heterotrophic metabolism) and climate mitigation (Enquist et al. 2020). Past and ongoing loss of many of their populations and habitats (Malhi et al. 2016) underlies an appeal for a new global initiative for their conservation (Norris et al. 2020), including terrestrial and aquatic systems plus the linkages between them (e.g., Doughty et al. 2016).

The extent to which the much smaller seafloor ‘megafauna’ may have such broad ecological significance requires further investigation, especially if deep-sea megafauna are used as the benchmark to monitor biodiversity impacts, as suggested by Pr eat et al. (2021).

Dearth of indicators or historical data for the deep sea

A rich array of indicators and indices is available for terrestrial, freshwater, coastal and pelagic regions. Those employed to measure regional or global progress toward the 20 Aichi biodiversity targets include studies of trends in wild populations, the ecological footprint of the human population on the uses of land, water and net primary production, changes in areas of different habitat types, percentage of land or sea in protected status, number of species on the IUCN Red List, citizens’ awareness of biodiversity concepts and concerns, number of countries with biodiversity-relevant charges, fees, subsidies or taxes, trends in nitrogen deposition, and others. A dashboard of indicators and indices used for each Aichi target may be explored at <https://www.bipindicators.net> or <https://bipdashboard.natureserve.org/>. Additional measures in development include Environmental Biodiversity Variables (EBVs) and large-scale satellite-based identification of plant species and traits, community composition, ecosystem structure and function as possible aids to management and mitigation (Pennisi 2021). In contrast, few indicators and indices are available for the deep sea. Some of the 600 marine biodiversity indicators cataloged by Teixeira et al. (2016) for use in implementing the Marine Strategy Framework Directive (MSFD) in European waters could be used as models for deep-sea indicators. Although none focus on the CCZ region, lessons from the MSFD process can be useful for creating Integrated Environmental Assessment frameworks for deep-sea areas (Orejas et al. (2020).

Similarly, ecosystem services provided by deep-sea ecosystems have been less studied and are harder to identify, understand and evaluate than those on land (Armstrong et al. 2012; Thurber et al. 2014; Le et al. 2017). There are some indications that DSM has less impact on ecosystem services than terrestrial mining (Koschinsky et al. 2018). For example, the CCZ seafloor currently provides no immediate Provisioning Services, mainly because it is so isolated from human communities and activities by depth and geography, but future supply of metals or genetic resources for medical or commercial use would qualify as such. Regulating (climate regulation, carbon sequestration) and Supporting (habitat, nutrient cycling, chemoautotrophic primary production) Services are provided by the CCZ’s seafloor, although its great depth, geographic distance from human populations and the slow tempo of deep currents cause delivery to be slower than in terrestrial or coastal systems.

Indicators and appropriate metrics are essential for the ISA to fulfill its required responsibility to detect and prevent “serious harm to the marine environment,” defined as “any

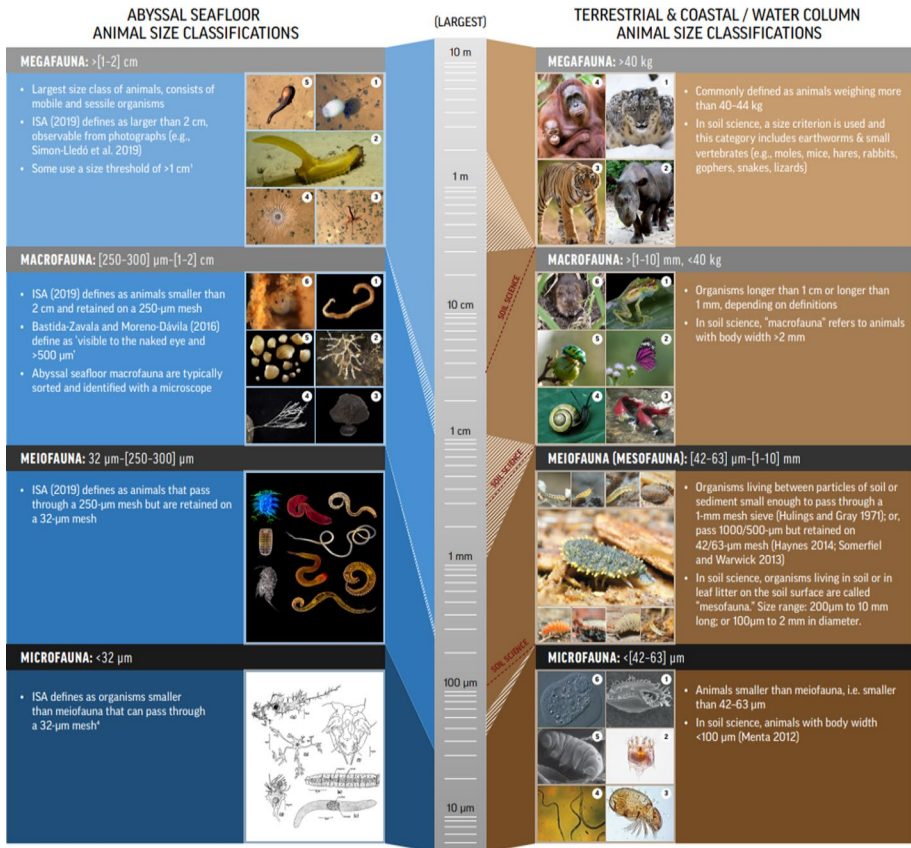


Fig. 2 Inconsistent size class definitions for animals on the abyssal seafloor vs. in terrestrial or coastal habitats. Complete photo credits available in Supplementary Information. Abridged photo credits: *Seafloor Mega fauna*: Photos 1,3,4,5. Courtesy D.O.B. Jones, National Oceanographic Center, Southampton, UK. Photo 2. Courtesy CD Smith, J. Durdon, IFREMER. *Seafloor Macrofauna*: Photos 1,2,4,5,6. Courtesy A. Glover, UK Seabed Resources Baseline Survey. Photo 3. The Metals Company. *Seafloor Meiofauna*: Dominant meiofauna groups from CCZ. Left: tardigrade, kinorhynch and harpacticoid copepod. Middle and right: six different nematode species. Copyright: Gilles Martin/French Institute for Ocean Science (IFREMER). *Seafloor Microfauna*: Drawings of abyssal microfauna (amoeba, sporozoan trophozoite, suctorian ciliate, wormlike metazoan, cyclopoid copepod nauplius) in deep waters offshore from California. Figure 1 from Burnett (1973), [https://doi.org/10.1016/0011-7471\(73\)90065-X](https://doi.org/10.1016/0011-7471(73)90065-X), courtesy Elsevier. *Terrestrial Mega fauna*: Photo 1. Snow leopard. Stock photo. Photo 2. Sumatran rhinoceros. Rahmadi Rahmad/Mongabay Indonesia. Photo 3. Bengal tiger Aditya Singh/Getty. Photo 4. Orangutans, Sumatra. Stock photo. *Terrestrial Macrofauna*: Photos 1. Glass frog, *Nymphargus balionotus*, Ecuador. Photo: Jaime Culebros/Photo Wildlife Tours. Photos 2–6. iStock photo. *Terrestrial Meiofauna (Mesofauna)*: Soil mesofauna from soil and leaf litter. Andy Murray, A Chaos of Delight, <https://www.chaosofdelight.org/overview>. *Terrestrial Microfauna*: Photo 1. Ciliate. Photo 2. Rotifer (iStock). Photo 3. Mite. Photo 4. Nematode, courtesy Soil and Water Conservation Society. Photo 5. Tardigrade Photo 6. Amoeba (Photos 1, 2, 3, 5, 6 from European Commission (2016))

effect from activities in the Area on the marine environment which represents a significant adverse change in the marine environment determined according to the rules, regulations and procedures adopted by the Authority on the basis of internationally recognized standards and practices" (I.3.f, ISA 2013). Levin et al. (2016) suggest measures of biodiversity,

abundance, habitat quality, population connectivity, heterogeneity levels, and community productivity as ways to determine whether important ecosystem properties exceed normal ranges of variability. They also suggest extinction, significant decline in abundance, decline in foundation species, reduction below critical reproductive density, loss of source populations and/or loss of critical stepping-stone populations as useful markers of serious harm at the species level, changes of key trophic linkages among species, reduction in species diversity beyond natural levels of variability, and/or regional declines in habitat heterogeneity (e.g., loss of entire habitats or community types) as indicators of serious harm at the community level; and impairment of key ecosystem functions or services (e.g., biomass production, nutrient recycling or carbon burial, fisheries) as indicators of serious harm at the ecosystem level. Tilot et al. (2018) mention the possible use of Indices for Environmental Sensitivity or Vulnerability to identify areas or habitats with highest needs for protection, as well as the development of Management Alert systems to help managers know if or when DSM activities created unacceptable stress.

Until agreed-upon indicators and thresholds of “serious harm” are created, DSM cannot easily be monitored and managed in ways comparable to what is possible on land. Unfortunately, as Levin et al. (2016) note and Christiansen et al. (2022) indicate, years to decades of data may be needed to extract trends in metrics such as they propose from naturally occurring variability.

Casual declarations of ‘high’ biodiversity

‘High biodiversity’ and similar casual descriptors are frequently used without explicit comparison to a scale of reference, causing confusion or misinterpretation. For example, the abyssal seafloor (Paulus 2021), seamounts (Morato et al. 2010; Watling and Auster 2017) and hydrothermal vents of the eastern tropical Pacific (Mullineaux et al. 2018) have all at times been labeled as having ‘high’ or ‘rich’ biodiversity despite significant differences. The abyssal seabed has intermediate numbers of species with relatively few individuals each; seamounts vary significantly with geography, oceanography and depth (McClain 2007; Clark and Bowden 2015) but typically host more species with many individuals each and may also act as pelagic biodiversity “hotspots” for marine predators (Morato et al. 2010); and vent systems host relatively fewer species with many individuals of each per unit area. The abyssal seabed exists in a relatively constant ambient environment; seamounts are relatively stable structurally, but create increase local current flow rate, upwelling and food transport to resident suspension feeders and others; while vent communities are ephemeral owing to variations in the flow of geothermally heated fluids caused by the volcanism, mid-ocean spreading or subduction that creates them (Van Dover 2014; Mullineaux et al. 2018). Casually describing biodiversity at all three sites as ‘high’ or ‘rich’ can be confusing, and it obscures their unique characteristics and differences. At finer scale, the biodiversity of abyssal plains has been described as “high” (Ramirez-Llodra et al. 2011), “distinctive” (Miller et al. 2018), “rivalling rainforests” (Dybas 1996), rich enough “to even out-compete the most blooming and dense rainforests on land” (Myhre 2021) and “beyond those of coral reefs and rainforests” (Hallgren and Hansson 2021). Certainly, deep-sea inhabitants are remarkable in having adapted to extreme conditions of intense hydrostatic pressure, low food availability, low temperature (though high at thermal vents), and perpetual darkness punctuated only by bioluminescent flashes. Their adaptations have included slow metabolic growth, slow maturation, low reproductive potential, low rates of colonization,

and in some cases greater longevity (Tilot et al. 2018). Beyond the abyssal plains' vastness and antiquity, scientists are still trying to understand the reasons for the biodiversity that exists there (Snelgrove and Smith 2002; McClain and Schlacher 2015; Dixon 2019).

However, among the descriptors mentioned above, only 'distinctive' is appropriate. 'High' is ambiguous and lacks a reference point. 'Rivaling' or 'outcompeting' rainforests is misleading, considering the abundance and diversity of life at the abyssal seabed are not quantitatively high when compared to a sampling of tropical rainforests (Fig. 3). Megafaunal (i.e., > 1 or 2 cm) species richness on the CCZ seafloor was recently reported to be 100 species for a 90,000-hectare study area (Smith et al. 2020). We found no directly comparable species richness data for organisms > 1 or 2 cm in tropical rainforests, but an Amazonian tropical rainforest in French Guiana contained 240 bird species per 100 ha (Thiollay 1994), and the 6000 ha rainforest on Barro Colorado Island, Panama contained 306 bird species and 81 mammal species (Basset et al. 2012)—three-fold more species than found in 90,000 hectares of CCZ abyssal seafloor, without even counting its fish, amphibians, reptiles, invertebrates or 1294 species of trees. A single hectare of Barro Colorado Island rainforest was estimated to contain an average of 18,439 species overall (Fig. 2b, Basset et al. 2012).⁸ While species richness in both the CCZ and tropical forests remains incompletely known (e.g., Moura and Jetz 2021), qualitative judgments can be made with existing information alongside knowledge about driving factors that typically promote speciation: physical diversity, primary productivity and geographic barriers to reproduction. The CCZ's physical remoteness, low primary productivity, and low physical diversity support the conclusion that species richness in the CCZ abyssal seafloor (and likely its overlying water column) is not 'high' or 'rivaling' rainforests.

Van Dover's (2014) summary description of biodiversity at hydrothermal vents exemplifies the type of clarity and context most useful to a reader: *Diversity (species richness) at deep-sea hydrothermal vents is relatively low, on a par with that observed in temperate and boreal rocky intertidal systems... with numerical dominance (thousands of individuals per m³) by a small number of species (< 10) and with a large percentage (25%) of rare taxa (occurring as singletons or doubletons) in suites of replicate quantitative samples...* Increased use of precision and contextual definitions in this manner, rather than imprecise use of casual descriptors, can aid in producing clearer discourse and preventing misleading terms from being propagated.

Discussion

Many frustrations were unearthed during our investigation of 'Biodiversity' measurement and comparison. At the highest level, we found 'Biodiversity' used variously. To the lay public, it signifies 'richness of life,' but lacks precision or consistency. To scientists, it connotes more specific mathematical descriptions of biotic richness, but confusion often

⁸ The species richness of trees in other tropical forests suggests a similar conclusion. Values range from 68 to 1171 species per 50 hectares in six study areas in India, Panama, Thailand and Malaysia (Proctor et al. 1983); 89 to 228 species per hectare for eight study areas in Indonesia, Philippines, Australia and Malaysia (Gradstein et al. 2007); and 140 species per 0.1 ha in Australia (Rice and Westoby 1983). Kirmse and Chaboo (2020) reported that an average of 26.35 unique species visited each flowering Neotropical tree species sampled in a 1.4 ha canopy plot of pristine lowland tropical rainforest in southern Venezuela, implying 421,600 beetle species in the estimated 16,000 tree species of the Amazonian rainforest.

results from unresolved methodological and taxonomic differences among investigations, as highlighted by our attempt to compare terrestrial and deep-sea biodiversity in such different habitats and realms. Furthermore, differential investment in genetic- and morphology-based taxonomy and siloing of resulting information have hindered progress, leading to calls for a more integrative taxonomy (Boero 2010). Matters are further complicated by differences in ecosystem services provided by species on land and in the deep sea, as well as their geographic closeness and temporal rate of delivery. Lastly, differences in the intangible (and intrinsic) values recognized for species in those habitats, as well as for the ecosystems themselves, are problematic and profound.

All of this even assumes that the required data is at least available. But biodiversity and related ecosystem services, especially in the deep sea, are still under-characterized and poorly understood. The newly found abyssal species mentioned previously, along with expert comments such as “...the [CCZ] is likely home to more than 1,000 species, 90 percent of which may be new to science” (Craig Smith quoted in Dasgupta 2016), suggest that a high proportion of CCZ seafloor species will be new. Even in terrestrial habitats, a large proportion of new species is still expected, with hundreds of new species being described every year (California Academy of Sciences 2021; Davis 2021). How can one compare the values of two large but still generally unknown assemblages?

Even once direct numerical comparisons of biodiversity indices are obtained from these different realms, it is unclear what can be done. Biodiversity comparisons may be quite valuable in examining changes over time in a particular study area or in ecologically similar areas, and to help direct management attention, but their utility decreases with increasing ecological distance between compared communities. Not only do methodological heterogeneities confound direct biodiversity index comparison, but value attribution challenges make any tradeoff or prioritization questions very difficult to answer. Implicit in deciding whether to collect CCZ nodules is a choice between harming different species and their habitats; and implicit in this choice is a value judgment between them. Many contextual factors may deserve consideration, including the degree of endemism or endangerment, noteworthy morphological or physiological traits, relative value for scientific study, provision or support of ecosystem services, and traditional, aesthetic, spiritual or cultural values.

The indeterminacy of these value judgments leads to some difficult questions, such as: How do risks of CCZ nodule collection to CCZ seafloor populations (e.g., nematodes, sponges, polychaete worms, sea anemones, nudibranchs and fish, including species that may be undescribed, rare or endemic) compare to risks faced by better-known terrestrial species due to land mining (e.g., the Critically Endangered Bushy-tailed Cloud Rat (Hance 2012) and Vulnerable Dinagat-Caraga Tarsier (Brown et al. 2014) threatened by nickel laterite mining on Dinagat Island, Philippines)? Or, how might one compare the importance of preserving newly-discovered species of xenophyophores (Amon et al. 2016; Gooday et al. 2020), abyssal sponges (Amon et al. 2016; Lim et al. 2017), corals (Amon et al. 2016), isopods (Rieh T and De Smet 2020), ophiuroids (Christodoulou et al. 2020) and others on the CCZ seafloor, with saving two newly described species of manganese-accumulating plants in the Euphorbia family, *Weda fragaroides* Welzen and *W. lutea* Welzen, found at the site of a potential nickel mine on Halmahera Island (North Moluccas), Indonesia (van Welzen et al. 2020)?

Implicit in these questions is a challenge to make system-level value judgments amidst incomplete information and unknown unknowns. Even with decades of more data, complete answers to the above questions may not be available. Not only do they require understanding the direct and indirect consequences of biodiversity loss within a very complex set of ecological systems—a tall order—but they also require that an aggregate societal value

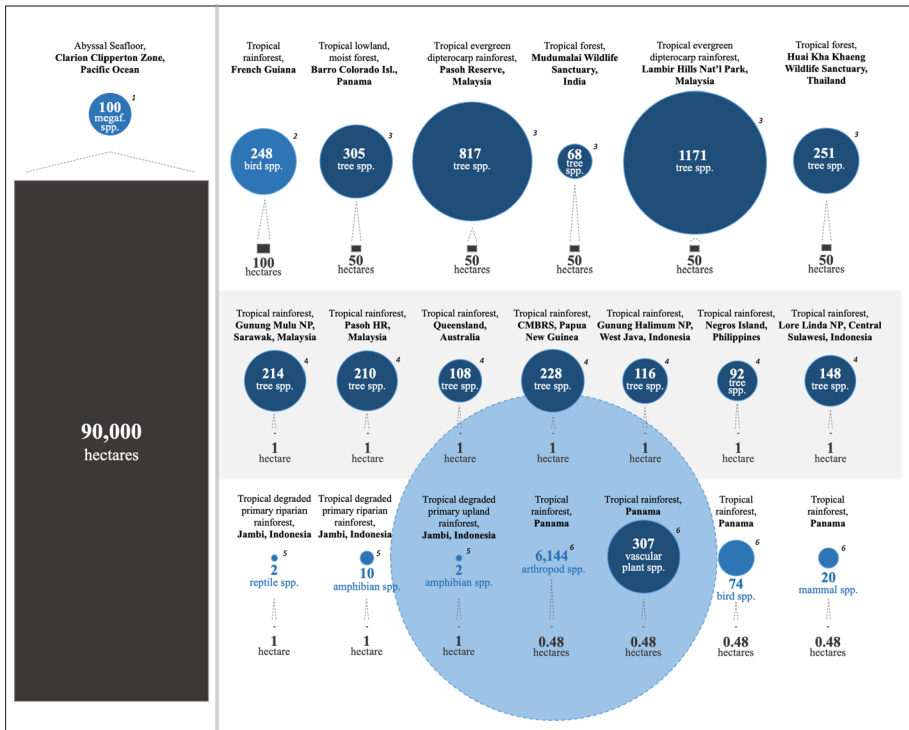


Fig. 3 Comparison of species richness in CCZ and a variety of tropical rainforests. Sizes of sampled area (hectares) are stated numerically and shown graphically as scaled black rectangles if ≥ 1 ha. Numbers of species in sampled areas are stated and shown graphically as scaled circles—light blue for animals, dark blue for plants. Data sources, indicated as superscripts adjacent to species numbers, are: ¹Smith et al. (2020); ²Thiollay (1994); ³Plotkin et al. (2000); ⁴Figure 3 in Gradstein et al. (2007), references cited therein; ⁵Paoletti et al. (2018); ⁶Basset et al. (2012)

judgment be made. How does a society come to such a collective value agreement? One answer may be to seek a balance of minimal anthropocentric impacts, with preservation of all biodiversity equally due to intrinsic value, as Gómez and Nichols (2013) might espouse.

Given the subtleties discussed above, a mathematical formula alone clearly cannot be a sole guide toward the world we want (and need) to see. Evaluating contextual factors, like the absence of an entire kingdom (Plantae) and two vertebrate classes (Amphibia and Aves) from deep-sea measures, or the absence of marine phyla from land measures, is perplexing. Furthermore, the relative values of species represented in a biodiversity index are not stated, and they may also change with time and circumstances. Crises of climate, water and biodiversity may increase values attributed to plants as public awareness grows for their ecological roles in carbon, water, oxygen and soil cycles, and the role of kin recognition and other aspects of sociality in their lives (Anten and Chen 2021; Simard 2021). Biodiversity comparisons will also need to weigh the values of invertebrate (Chen 2021) vs. vertebrate (Severtsov 2013) animals.

An alternative may be to supplement existing quantitative measures with qualitative inputs of values and needs, both human and non-human, current and future. Feest et al.'s (2009) list of quantitative indicators could be extended to include the system's contribution

to tangible and intangible ecosystem services, contextual factors such as its geographic location, the scale and degree of impending systemic threats, and relevant moral and ethical considerations (e.g., harm to sentient species), among others. By providing a richer understanding of the system's gestalt and comparative value, biodiversity loss impacts might be better compared.

Conclusion

The potential development of DSM has raised concerns about possible effects on deep-sea biodiversity, as well as on broader oceanic or atmospheric functions. At the same time, there is growing concern about critical biodiversity decline on land (Bradshaw et al. 2021), in soil (Tibbett et al. 2020; FAO et al. 2020), in fresh water (Tickner et al. 2020) and at sea (O'Hara et al. 2021), along with worldwide concern about climate change and the seriousness of its projected impacts on nature and people (Hoegh-Guldberg et al. 2019). Land-use conversion and its cumulative impacts on habitats, climate and water, among others, threatens the extinction by 2070 of 1700 amphibians, birds and mammals out of 19,400 species examined (Powers and Jetz 2019).⁹ Some of these terrestrial-mining impacts could be relieved by sourcing minerals from the abyssal ocean, in effect trading loss of abyssal biodiversity for maintenance of terrestrial biodiversity.

Therefore, challenging as it may be to execute, comparing the biodiversity in these two realms seems necessary. Whether one community's biodiversity is higher or lower than another's should not alone drive a decision about resource exploitation, but it is one of many factors to consider. In comparing the biodiversity of such ecologically distant realms, consideration not only of species richness or other numerical diversity descriptors, but also of value-based information—including tangible and intangible impact, social and ecological value, ecosystem services and other cultural information—could enable more satisfactory decisions to be made.

From a biological perspective, valuing systems only on the basis of their measured biodiversity makes little sense; ecosystems with lower species richness are no 'worse' than those with higher richness. All play the biophysical hand they were dealt in the best way they can, as biodiversity coevolves with its ecosystem: the existence of patterns in biodiversity related to latitude, altitude, depth, geographic distance from continents, seasonality, freshwater availability and other gradients suggests that each ecosystem does what it can to thrive. Nevertheless, from an anthropocentric perspective, high-biodiversity systems often command increased attention, both for their generally higher variety and for their potentially more diverse flow of ecosystem services, tangible and intangible.

Comparisons of biodiversity data could be greatly improved by increased global standardization of sampling protocols, including screen sizes, sampling depths and quadrat sizes when possible. Standardization of size-class definitions and nomenclature could then improve interpretation and communication of results. Such changes, plus dissemination of a clearer definition of biodiversity and its implications—one that is both acceptable to scientists and understandable by the lay public—would enable higher

⁹ This could be an underestimate, since global land use change between 1960 and 2019 affected 32% of global land area, four times greater than previously estimated (Winkler et al. 2021).

quality, more inclusive discussions of biodiversity-related issues, and more informed decisions for environmental management and conservation.

As sampling protocols and analytical techniques become standardized, so too would it be desirable for environmental impact assessment processes to consistently incorporate a high bar of biodiversity baselining (and impact mitigation planning). For the CCZ, the ISA plays that central role, but on land, biodiversity-related indices and metrics, per se, have not usually factored into the permitting of mines. Similar functions are potentially fulfilled, to some extent, by avoidance of sensitive areas previously designated as protected areas, parks, *World Heritage Sites*, *Key Biodiversity Areas*, Biodiversity Hotspots (Myers et al. 2000) or others; and some measurement, reporting and verification programs being developed to monitor progress toward climate mitigation as part of the *United Nations Framework Convention on Climate Change* may fulfill some functions of a Management Alert system for carbon. However, terrestrial mining companies' progress on the disclosure of impacts on biodiversity, land, water and other areas of natural capital lag by comparison (Bradley 2020).

By calling attention to shortcomings in the standards for sampling and size class nomenclature as well as ambiguities in discussion and comparison of biodiversity results, we intend no disrespect to the scientists and organizations that have assembled the impressive and growing body of information that exists today. We credit these shortcomings to the manner in which biodiversity study organically evolved: inside the silos that exist within academia, the amateur and professional scientific establishment, the conservation community and government agencies.

Indeed, we applaud the remarkable progress that has been achieved in chronicling the ever-more remarkable and complex story of life on Earth. We present the above concerns in hopes that improved standardization and greater collaboration across disciplines, geographies and taxonomic disciplines, both morphological and biomolecular, will steadily minimize them. Doing so can improve the quality of information contributed to, e.g., the *Global Biodiversity Information Facility*, whose Biodiversity Information Standards Working Group develops rules and conventions for describing, recording, structuring and sharing datasets containing hundreds of millions of species occurrence records, from every habitat, contributed by hundreds of institutions worldwide. Thus all stakeholders invested in describing and conserving Earth's biodiversity will benefit from more accurate and comparable data. Equally important is forming effective policies that address biodiversity, climate and human society as coupled systems (Pörtner et al. 2021), including the challenge of how to best meet future metal demands. This would be significantly aided by the development of a more holistic, contextual and nuanced appreciation of 'Biodiversity', the benefits it provides, but also the constraints on its measurement and interpretation.

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Data availability All data presented were obtained or derived from reviewing publicly available literature cited in the text and listed in References.

Declarations

Competing interest MC, EI, GS are employees and shareholders of TMC. DP is a shareholder of TMC. SK holds 2,906 shares of TMC purchased on December 5, 2023 @ 0.858 USD, total investment 2,493 USD. SK and LP are members of TMC's Scientific Advisory Committee. SA and LP declare no competing interests.

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