

Commentary

Shades of Grey: A Continuum of Biodiversity Understanding from Dark to Bright Diversity

Giovanni Bacaro *

Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy

* Corresponding author. E-mail: gbacaro@units.it (G.B.)

Received: 13 July 2025; Accepted: 15 September 2025; Available online: 17 September 2025

ABSTRACT: This commentary introduces a conceptual framework that reinterprets biodiversity assessment as a continuum, spanning from Dark diversity, representing the unobserved or uncolonized potential of species ecologically suited to a system, to Bright diversity, conceived as an aspirational, fully integrated upper bound of biodiversity knowledge. Bright diversity encompasses not only observed components and their intricate interactions, but also a profound understanding of the reasons for species' presence or absence, including the inferred insights from Dark diversity across taxonomic, functional, phylogenetic, and genetic facets. Situated in between is Grey diversity, which characterizes the predominant state of partial knowledge and inherent uncertainty in real-world ecological assessments as an epistemic gradient. By delineating this epistemological gradient, the framework offers a heuristic tool for ecologists and conservationists to critically evaluate the clarity, completeness, and uncertainty embedded in biodiversity data, and an operational basis for “epistemic cartography”, *i.e.*, the spatial mapping of knowledge sufficiency and uncertainty. It facilitates the identification of knowledge gaps, guides research priorities, and informs conservation actions, especially under conditions of incomplete information, through a compact workflow and transparent indicators. This conceptual spectrum serves as both an epistemological reflection and a practical guide for advancing biodiversity science, while outlining a forward-looking agenda that leverages multi-faceted “bands of biodiversity knowledge” to support robust biodiversity planning.

Keywords: Bands of biodiversity knowledge; Biodiversity; Bright diversity; Dark diversity; Ecological knowledge; Epistemological gradient; Grey diversity; Uncertainty mapping



© 2025 The authors. This is an open access article under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Biodiversity is a foundational concept in ecology, encompassing the variability of life forms at genetic, species, and ecosystem levels [1]. Its pivotal role in ecosystem functioning and stability is increasingly recognized, with different diversity aspects offering complementary information vital for maintaining healthy ecosystems and their services [2]. However, despite decades of conceptual development and methodological refinement, achieving a complete and accurate assessment of biodiversity remains a persistent and formidable challenge [3,4]. The inherent complexity of biological systems makes their comprehensive measurement extraordinarily difficult. Biodiversity is not a static entity: it is a dynamic, multi-scalar phenomenon, influenced by intricate ecological processes, evolutionary histories, and constant interactions across diverse spatial and temporal scales [5,6]. Factors such as species rarity, cryptic diversity, specialized ecological niches, and the sheer vastness of unexplored habitats contribute to the elusive nature of a truly complete inventory [7]. Furthermore, while continuously improving, our observational tools, theoretical models, and sampling efforts possess intrinsic limitations. These constraints often lead to fragmented and incomplete understandings, making it difficult to grasp the full extent of life's variability and underlying drivers [8]. Traditionally, much of our global biodiversity knowledge has focused predominantly on taxonomic diversity (e.g., species richness), often overlooking equally crucial aspects such as species' evolutionary history and functional structure [9,10]. This single-dimensional focus can lead to significant biases and misinterpretations. For instance, two sites with identical species richness might differ dramatically in their functional diversity (the range of traits present) or phylogenetic diversity (the evolutionary relatedness of species), which are far better indicators of ecosystem resilience and functioning [11]. Ignoring these complementary facets means that our conservation strategies might inadvertently miss critical components of biodiver-

sity that underpin ecosystem services, or misallocate resources to areas that appear rich in species but lack evolutionary distinctiveness or functional redundancy [12]. Accordingly, an explicitly multi-faceted knowledge architecture is required to prevent single-dimension biases and to reveal patterns relevant to ecosystem functioning and resilience.

Indeed, integrating multiple diversity facets is an overarching and urgent issue for effective conservation [13]. Each facet offers unique insights, and relying on a single dimension risk underestimating critical patterns, obscuring vital determinants of biodiversity, and ultimately compromising conservation outcomes. Recent advancements, such as the development of synthetic indices that weight species richness by their functional and phylogenetic counterparts, demonstrate a significantly higher sensitivity in describing complex species diversity patterns and capturing broad-scale ecological gradients than species richness alone [14]. This synergistic evaluation can highlight hidden patterns and disclose the role of potential determinants that might otherwise remain underestimated, emphasizing the need for conservation programs to move beyond a focus on specific aspects of diversity. Despite the growing volume of biodiversity data, often made freely accessible through global information networks and facilities, inherent issues of data incompleteness, spatial and temporal biases, and varying quality persist [15]. These knowledge shortfalls, if not properly addressed, severely limit the utility of biodiversity information for robust biogeographical research and informed conservation decision-making [16]. The challenge therefore lies not only in collecting more data, but also in developing frameworks that explicitly acknowledge and integrate the inevitable uncertainty inherent in our understanding of biodiversity. From this perspective, uncertainty is not peripheral but constitutive to biodiversity knowledge; it varies across space and time and can be diagnosed with explicit indicators and reported transparently. This motivates an epistemic cartography that maps knowledge sufficiency and uncertainty, rather than assuming homogeneous data quality across regions or taxa.

This commentary aims to provide a novel conceptual framework for understanding biodiversity assessment. It envisions our ecological knowledge as a gradient, spanning from Dark diversity (the unobserved potential, reflecting species ecologically suited but currently undetected or uncolonized) to Bright diversity (comprehensive clarity, representing a fully observed and understood state). Situated between these two poles is Grey diversity, which captures the vast conceptual middle ground of partial knowledge and inherent uncertainty that characterizes most real-world ecological assessments. By structuring our understanding this way, the framework serves as a heuristic tool for positioning ecological knowledge along a continuum of observability, certainty, and uncertainty. It encourages a critical reflection on the scope and limitations of biodiversity assessments and advocates for a more explicit engagement with uncertainty in biodiversity science. By reframing uncertainty not merely as a limitation to be dismissed, but as a core property of ecological inquiry, we can better study, manage, and, where possible, reduce it, thereby advancing ecological theory and practical conservation decision-making. Within this gradient, Bright diversity is conceived as an aspirational, fully integrated upper bound that explicitly includes observed components and ecologically compatible yet unobserved potential (*i.e.*, the domain of dark diversity) across taxonomic, functional, phylogenetic, and genetic facets; Grey diversity is framed as an epistemic gradient that captures degrees of knowledge sufficiency and uncertainty. Building on prior work on knowledge shortfalls and the mapping of ignorance, this synthesis unifies these strands into a single, operational continuum and introduces practical transparency layers (what is known, unknown, and uncertain) together with a compact workflow and indicators for decision support. Finally, it outlines a multi-faceted “bands of biodiversity knowledge” view that enables consistent reporting and benchmarking across regions and management contexts. This commentary’s contribution is thus threefold: it formalizes Bright diversity as an aspirational, integrative upper bound that explicitly merges observed and ecologically compatible (dark) components across taxonomic, functional, phylogenetic, genetic, and interactional facets; it reframes Grey diversity as an epistemic gradient equipped with measurable indicators and a Knowledge Completeness Index; and it operationalizes “epistemic cartography” to make knowledge sufficiency and ignorance spatially explicit for conservation decisions and ecosystem-service assessments.

2. Colors of Diversity: An Epistemological Gradient

In this commentary, biodiversity knowledge is framed along an epistemological gradient by leveraging three distinct “colors” of diversity: Dark, Bright, and Grey. While the concept of Dark diversity is well-established and formalized within ecological literature [17,18], its existence inherently points to the need for a more comprehensive understanding of the full spectrum of biodiversity knowledge. Consequently, it appears a natural progression to define the conceptual extremes to which Dark diversity compares and the nuanced space that lies between them. In this logical progression, Bright and Grey diversity are explored, synthesizing existing ideas into a coherent continuum. This framework provides an alternative lens for contextualizing current biodiversity measures and knowledge, from the unobserved

potential to comprehensive understanding. It offers a practical approach for guiding future assessment strategies, particularly through methods akin to established mapping systems used in many scientific disciplines.

2.1. Dark Diversity: The Unseen Potential

The concept of Dark diversity is well-established in ecological theory, clearly defined as the assemblage of species that are ecologically compatible with a community but remain currently unrecorded or uncolonized due to biogeographical, historical, or biotic constraints [18]. Initially formalized by Pärtel et al. [17], this concept critically reframes absence not as an ecological void but as significant latent potential. Paradoxically, inferring dark diversity often demands a sophisticated understanding of a site's ecological compatibility, environmental filters, and biogeographical history. Dark diversity thus shifts the focus from solely observed assemblages to potential ones, prompting a rethinking of community completeness, ecosystem resilience, and restoration capabilities [19]. It represents the minimum potential of diversity in a given site, pointing to what could exist under suitable conditions, thereby setting a crucial baseline for ecological assessment that extends beyond mere observation [20]. Dark diversity is derived from the regional species pool, filtered through abiotic conditions and biotic interactions [14]. Its identification requires comparative and model-based methods (e.g., Beals smoothing, co-occurrence models, or habitat suitability frameworks) [20–23], often relying on species–environment relationships inferred from broader datasets. While inherently uncertain in its precise composition, understanding dark diversity holds significant value in ecological restoration (identifying candidates for species reintroduction), biogeographic theory, and predictive ecology [21]. Dark diversity can be impacted by natural processes such as dispersal limitations [24,25] and competitive exclusion [26], or anthropogenic effects like species invasion [27] or landscape fragmentation [28]. In conservation contexts, it has been used to prioritize sites or species for conservation [29,30] and reveal species responses to climate change [21].

The concept of dark diversity aligns with Whittaker's classic alpha–beta–gamma diversity framework [31]. While alpha diversity represents the number of species at a site and gamma diversity comprises all species in the surrounding region, dark diversity is taxon-oriented, considering the suitability of each absent species for a study site. Aggregating alpha and dark diversity constitutes the site-specific species pool, which includes only those species from the region suitable for a given site based on its ecological conditions.

2.2. Bright Diversity: Comprehensive Clarity

At the opposite end of this knowledge spectrum is “Bright diversity”: an idealized and aspirational state representing the maximum achievable knowledge of biodiversity within a system. In this conceptual realm, biodiversity in a given area is comprehensively assessed across its multiple dimensions (e.g., taxonomic, functional, phylogenetic, and genetic) and over relevant temporal scales. Crucially, this understanding extends beyond the merely observed. It incorporates and integrates the potential diversity of species that are ecologically compatible with the system but currently absent, unseen, or extinct (*i.e.*, dark diversity). This means that Bright diversity encompasses not just what is present, but also what could be present, thereby providing a complete informational landscape of a site's biodiversity potential. These diverse facets, including species' roles, interactions (e.g., within complex food webs), and the dynamics of these relationships across scales, are integratively measured and profoundly understood. Bright diversity serves as an ideal benchmark where the clarity, completeness, and depth of biodiversity data enable precise ecological modeling, robust predictions of ecosystem functioning and stability, and highly informed conservation planning. It defines the upper limit of the conceptual framework, representing the ultimate, albeit largely utopian, goal of comprehensive biodiversity understanding. Achieving this level of knowledge would necessitate an exhaustive, multi-temporal assessment, extending to a detailed comprehension of biotic interactions, trophic links, and all other definable elements of diversity, including the full extent of a site's latent potential.

While achieving a truly complete state of Bright diversity is arguably an unreachable aspiration for most ecosystems, given their inherent complexity and the amount of data required, its pursuit provides a clear directional goal for biodiversity science. As an example, progress towards Bright diversity involves a multi-pronged and integrated approach, involving, among others:

- (1) **Multidimensional Integration:** This goes beyond simply compiling species lists. It entails actively bridging diverse datasets, for instance, linking detailed species occurrence records with comprehensive trait databases to understand functional roles, or integrating genetic data to unravel cryptic diversity and population connectivity [32]. It also critically involves incorporating the inferred components of dark diversity, derived from ecological niche models or co-occurrence patterns, to build a complete picture of a site's potential biodiversity [17].

- (2) **Deep Ecological Characterization:** Beyond mere biodiversity components, a Bright diversity assessment demands a profound understanding of the intricate organismal interactions that define an ecosystem. This includes mapping complex food web structures, identifying key predator-prey relationships, mutualisms, and competitive dynamics [33]. For instance, knowing the full network of plant-pollinator interactions in a meadow or the cascading effects of top predator reintroduction in a wilderness area is crucial for this level of understanding. This also extends to evaluating the equilibrium and stability of the ecosystem, understanding how resilient it is to disturbances and how quickly it can recover, often reflected in the redundancy of functional traits or the robustness of interaction networks [34].
- (3) **Methodological Rigor and Technological Advancement:** Progress towards Bright diversity relies on combining extensive field observations with cutting-edge technologies and analytical methods. This includes sophisticated remote sensing for mapping habitat structure and productivity across vast scales [35–37], advanced molecular data analysis (e.g., environmental DNA for detecting elusive species or assessing microbial diversity) [38], and complex ecosystem modeling that can simulate ecological processes and predict responses to environmental change [39]. When applied across appropriate temporal scales, from short-term monitoring to long-term ecological research, these methods offer increasingly granular and comprehensive data.
- (4) **Interdisciplinary Synthesis:** Realizing Bright diversity necessitates merging ecological data with broader biogeographic, socio-environmental, and management perspectives. This involves understanding the historical human impacts on biodiversity [40], the influence of land-use change [41], and the socio-economic drivers affecting conservation efforts [42]. It means integrating data on ecosystem services [43], functional ecosystem processes (e.g., primary productivity, nutrient cycling) [44], and measures of ecosystem stability [45] to gauge the overall health and functionality of the system.

In practical terms, progress towards Bright diversity is evidenced by decision-relevant outputs: AI-assisted detection and identification pipelines (e.g., camera-trap image analysis and automated plant recognition) that broaden taxonomic coverage and quantify classification uncertainty; big-data integration from citizen science and remote sensing that increases spatial and temporal resolution while correcting sampling bias; and explicit linkages to ecosystem-service appraisals (carbon storage, pollination, water-flow regulation) in which knowledge sufficiency is reported alongside service estimates and used to guide no-regret actions and precautionary rules where uncertainty is high.

The “Bright diversity” concept, thus, suggests not only that the components of biodiversity are known but also that their roles, interactions, and dynamics across scales are comprehensively understood. While constrained by significant logistic, epistemic, and financial barriers, Bright diversity assessments remain essential for guiding systematic conservation planning, developing robust monitoring frameworks, and informing natural capital accounting. Even if never fully achieved, the pursuit of Bright diversity provides a clear directional goal for biodiversity science, pushing the boundaries of what is known and understood.

2.3. Grey Diversity: The Domain of Partial Knowledge

In between the unseen potential of Dark diversity and the comprehensive clarity of Bright diversity falls the vast conceptual middle ground termed Grey diversity. This critical zone represents the reality of most real-world ecological assessments: the diversity that can be observed and quantified, but only partially and often with considerable uncertainty. Grey diversity captures the fragmented understanding that arises from inherent data limitations, methodological constraints, and incomplete theoretical integration. The crucial bridge connects the theoretical minimum to the aspirational maximum of biodiversity knowledge. While Zinchenko et al. [46] formalized Grey Diversity as species observed with low habitat suitability, a broader and more comprehensive interpretation is proposed here. In this framework, Grey Diversity is precisely that epistemological gradient extending from the inability to detect or observe certain diversity components (approaching Dark Diversity) to complete, integrated knowledge (approaching Bright Diversity). It is the domain of partial knowledge: species that are known but poorly understood, habitats that are sampled but inadequately characterized, and ecological interactions that are recognized but not fully quantified. This zone of uncertainty signifies where knowledge is fragmented, incomplete, or primarily inferred rather than directly observed, and crucially, where the absence of comprehensive data should never be mistaken for an absence of diversity. This expanded view of Grey diversity allows for effectively mapping and contextualizing biodiversity information across landscapes.

3. Grey Diversity as Spatial Epistemology: Operationalizing Uncertainty

The concept of Grey Diversity represents the pervasive state of partial knowledge in biodiversity assessment, bridging the unseen potential of Dark Diversity with the comprehensive clarity of Bright Diversity. This critical middle ground, where information is fragmented, incomplete, or inferred rather than directly observed, constitutes the primary domain for practical ecological inquiry and conservation action [15]. To effectively navigate this complex informational landscape, it is essential to operationalize Grey Diversity, transforming its inherent uncertainties into actionable insights. In practical terms, operationalization entails making the status of knowledge itself measurable and comparable across space and taxa, so that uncertainty becomes a mapped attribute rather than an implicit assumption.

A powerful analogy for understanding Grey Diversity in an operational context can be found in the domain of remote sensing, particularly in the interpretation of digital numbers (DNs) recorded by satellite sensors. A DN is not a direct measurement of a biophysical variable but a relative value reflecting electromagnetic energy [47]. The transformation of these raw values into actionable information (e.g., Normalized Difference Vegetation Index (NDVI), land cover classification) requires sophisticated modeling, calibration, and ground truthing [48]. Similarly, in biodiversity science, raw species records, functional traits, and phylogenetic data are often akin to DNs: they are raw, relative, and context-dependent. For instance, a region with few but exceptionally well-studied taxa may possess a higher epistemic resolution than one with many recorded species but scarce ecological or contextual data. Thus, Grey Diversity, much like DNs, represents a potentiality, or, in other words, a space for transformation, interpretation, and inference, enabling the mapping of knowledge and its limitations. Extending the analogy, just as radiometric/atmospheric corrections and field validations convert DNs into biophysically meaningful products, Grey Diversity requires explicit preprocessing of biodiversity evidence, e.g., quality metadata, calibration against independent data, and transparent modelling choices, to yield interpretable knowledge layers. Accordingly, a synthetic Knowledge Completeness Index can summarize the sufficiency of evidence for each cell or site, while preserving the underlying components for scrutiny and replication.

Adopting this expanded definition of Grey Diversity allows for the conceptual and practical development of epistemic cartographies [49]. These are spatial representations that visualize not only the extent of our biodiversity knowledge but also its intensity, reliability, and the distribution of remaining uncertainties across landscapes. Such cartographies can incorporate several complementary dimensions of ecological information, each contributing to a more nuanced understanding of knowledge gaps. Key diagnostic indicators include sampling coverage, the temporal “vintage” of records, spatial bias diagnostics (e.g., distances to sampling nodes or accessibility proxies), taxonomic/identification uncertainty, and model-based uncertainty; together, these indicators define positions along the Grey-diversity gradient and can be reported as standalone layers and as part of the Knowledge Completeness Index. In parallel, transparency layers that explicitly label what is known, unknown, and uncertain make the evidentiary basis auditable for management purposes. At present, AI and machine learning, together with globally available datasets spanning multiple facets of biodiversity, contribute substantially at three complementary levels: (i) data intake (de-duplication, taxonomic reconciliation, automated quality flags); (ii) inference (ensemble models with calibrated probabilistic outputs and explicit uncertainty quantification); and (iii) bias correction (effort-aware sampling models and synthetic-data augmentation), each of which feeds the Knowledge Completeness Index and enhances the reliability of epistemic cartography.

The development of these epistemic maps of Grey Diversity must systematically account for the inherent uncertainties in biodiversity data, which fundamentally stem from nature’s complexity and dynamics. Just as measuring any complex phenomenon with absolute precision is impossible [50], every biodiversity measure carries an associated, often unknown, measurement error [51,52]. Therefore, mapping biodiversity distributions necessitates quantifying and visualizing this uncertainty [15]. These key sources of uncertainty include the inherent complexity of species distributions, where biodiversity patterns are outcomes of dynamic ecological, evolutionary, and historical processes varying across scales [53], such as population dynamics, environmental adaptations, dispersal capacity, and landscape complexity [54–56]. While challenging to quantify directly, models attempting to capture these complexities inherently produce uncertainty that can be effectively mapped [57]. Crucially, uncertainty should be propagated through the entire inferential chain—from data acquisition to modelling and prioritization—so that decision outputs carry explicit ranges and sensitivity to modelling choices. Another significant source of uncertainty stems from the quality of available data: biodiversity information, particularly from natural history collections and global networks, often exhibits patchy distributions, incompleteness, and spatial or temporal biases [58–61]. These biases manifest as inaccuracies, such as incorrect taxonomic identifications or incomplete labeling, which can lead to erroneous distribution predictions [62]. Spatial biases are also common, as survey efforts have historically concentrated in easily accessible areas, politically stable regions, or near research centers, resulting in high inventory completeness in some locales but severe under-sampling elsewhere

[16,59,63,64], often creating a “distance-decay” of knowledge from well-sampled regions [63,65]. Furthermore, temporal biases from older specimens may misrepresent current distributions due to recent landscape, land cover, or climate changes [66]. Finally, limitations of the measurement system itself contribute to uncertainty: field surveys and taxonomic identifications, despite their critical role, are subject to biases influenced by data collectors’ preconceived views or experience [52,67]. To mitigate these issues, a structured audit and quality-weighting of data sources is required prior to modelling or prioritization, integrating multiple streams of evidence (occurrence records, traits, phylogeny, remote-sensing proxies, targeted surveys, citizen-science repositories, and eDNA datasets) while documenting assumptions and reliability.

Collectively, these tools enrich traditional biodiversity mapping by introducing a critical and often overlooked dimension: the sufficiency and quality of underlying data. By doing so, they support more informed and cautious conservation planning, which acknowledges not only what is empirically known but also what remains hypothetical, uncertain, or entirely unexplored. In this light, Grey Diversity emerges as a strategic and epistemological framework for guiding research priorities, optimizing biodiversity monitoring, and identifying locations where protective actions are urgently needed, even in the absence of complete data. In these areas where undetected potential may conceal richness, conservation efforts may yield the greatest returns. Operationally, this translates into a coherent flow that begins by defining objectives and governance constraints and proceeds through the auditing and weighting of data, the computation of epistemic indicators and the derivation of an epistemic cartography, before integrating these layers with observed diversity, expectations about dark diversity, pressures and risks, and ecosystem-service stocks and flows, ultimately supporting deliberation with uncertainty-aware outputs that are periodically updated as new evidence accrues. At each step, confidence intervals and data provenance are recorded, enabling ecosystem-service models to weight inputs by knowledge sufficiency and to flag areas where precautionary rules or additional monitoring are warranted.

4. Towards a Full Spectrum of Biodiversity Knowledge Colors

The “Shades of Grey” framework presented in this commentary offers an alternative lens through which to view biodiversity assessment, defining a continuum from the unobserved potential of Dark diversity to the comprehensive understanding of Bright diversity, with Grey diversity embodying the pervasive state of partial knowledge that characterizes most real-world ecological data [68]. This epistemological approach provides a powerful heuristic tool for evaluating the clarity, completeness, and uncertainty inherent in biodiversity information, thereby supporting more strategic research and conservation actions. Beyond a heuristic, it also serves as an operational scaffold for making knowledge itself observable: uncertainty can be rendered explicit, located, and compared through transparent indicators and spatial layers, so that decisions are informed not only by what is known but also by how well it is known. However, further research is essential to deepen the understanding of this framework and its future direction. This includes a more rigorous definition of the specific elements and metrics that contribute to assessing and evaluating each of the “colors” of diversity across various contexts. Developing standardized methods for quantifying the boundaries and transitions within the Dark-Grey-Bright spectrum will be crucial for its practical application.

Further extending the remote sensing analogy previously defined, the current epistemological approach outlined here provides a ‘panchromatic’ view of biodiversity knowledge [69]. This generalized perspective spans different dimensions, indicating where our understanding is limited or robust. However, much like a panchromatic image provides high spatial detail across a single, broad spectral range but no distinct spectral (color) differentiation [70], this initial framework offers a foundational, albeit unified, perspective. The true usefulness of this framework will emerge when we can define distinct “bands of biodiversity knowledge”, analogous to the multispectral bands in remote sensing. For instance, one could develop separate measures of knowledge for phylogenetic diversity, functional diversity, ecosystem diversity, or genetic diversity. Once these individual knowledge layers are precisely defined and quantifiable, it will be possible to combine these various “bands” to create an entire spectrum of knowledge colors for biodiversity.

Operationalizing multispectral view of biodiversity knowledge has immediate consequences for applied conservation and impact assessment: in Environmental Impact Assessments and biodiversity offsetting, for example, mapping Grey diversity can help in avoiding the false equivalence between “absence of evidence” and “evidence of absence”, strengthens baselines under the mitigation hierarchy and No Net Loss/Net Gain policies, and prioritizes monitoring or restoration where knowledge is most incomplete and dark diversity suggests latent potential [71]. In this sense, distinct bands of biodiversity knowledge, rather than generic “bands of diversity”, can be combined to create a spectrum of biodiversity-knowledge colors that makes the evidentiary basis auditable and comparable across regions. This advanced approach would yield a truly multidimensional understanding, revealing not just the overall “shade of grey” for a given area, but the specific “colors” that define the depth and type of our knowledge across the myriad facets of life. In

conclusion, policy and management should be accompanied by maps of knowledge alongside maps of biodiversity; Grey diversity should therefore be recognized not as a flaw but as the natural substrate of decision-making under partial information; and progress toward Bright diversity can be tracked with measurable markers—such as facet coverage, interaction knowledge, and temporal depth—underpinned by transparent reporting and periodic updates as new evidence accrues.

Ethics Statement

Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

Not applicable.

Funding

This research received no external funding.

Declaration of Competing Interest

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

References

- Chiarucci A, Bacaro G, Scheiner SM. Old and New Challenges in Using Species Diversity for Assessing Biodiversity. *Philos. Trans. R. Soc. B-Biol. Sci.* **2011**, *366*, 2426–2437. doi:10.1098/rstb.2011.0065.
- Olmo V, Petruzzellis F, Alberti G, Sigura M, Balbi S, Bacaro G. Assessing Ecosystem Services in Protected Areas: Trade-Offs and Hotspots in Friuli Venezia Giulia Region (Northeastern Italy). *Biodiversity* **2025**, *26*, 143–156. doi:10.1080/14888386.2025.2460759.
- Ricotta C. A Semantic Taxonomy for Diversity Measures. *Acta Biotheor.* **2007**, *55*, 23–33. doi:10.1007/s10441-007-9008-7.
- Magurran AE. Measuring Biological Diversity. *Curr. Biol.* **2021**, *31*, R1174–R1177. doi:10.1016/j.cub.2021.07.049.
- Kissling WD, Ahumada JA, Bowser A, Fernandez M, Fernández N, García EA, et al. Building Essential Biodiversity Variables (EBVs) of Species Distribution and Abundance at a Global Scale. *Biol. Rev. Camb. Philos. Soc.* **2018**, *93*, 600–625. doi:10.1111/brv.12359.
- Correia AM, Lopes LF. Revisiting Biodiversity and Ecosystem Functioning through the Lens of Complex Adaptive Systems. *Diversity* **2023**, *15*, 895. doi:10.3390/d15080895.
- Botella C, Joly A, Monestiez P, Bonnet P, Munoz F. Bias in Presence-Only Niche Models Related to Sampling Effort and Species Niches: Lessons for Background Point Selection. *PLoS ONE* **2020**, *15*, e0232078. doi:10.1371/journal.pone.0232078.
- Kühl HS, Bowler DE, Bösch L, Bruelheide H, Dauber J, Eichenberg D, et al. Effective Biodiversity Monitoring Needs a Culture of Integration. *One Earth* **2020**, *3*, 462–474. doi:10.1016/j.oneear.2020.09.010.
- Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, et al. Biodiversity Change Is Uncoupled from Species Richness Trends: Consequences for Conservation and Monitoring. *J. Appl. Ecol.* **2018**, *55*, 169–184. doi:10.1111/1365-2664.12959.
- Gatüzère P, O'Connor L, Botella C, Poggiato G, Münkemüller T, Pollock LJ, et al. The Diversity of Biotic Interactions Complements Functional and Phylogenetic Facets of Biodiversity. *Curr. Biol.* **2022**, *32*, 2093–2100.e3. doi:10.1016/j.cub.2022.03.009.
- Paz A, Crowther TW, Maynard DS. Functional and Phylogenetic Dimensions of Tree Biodiversity Reveal Unique Geographic Patterns. *Glob. Ecol. Biogeogr.* **2024**, *33*, e13877. doi:10.1111/geb.13877.
- Le Bagousse-Pinguet Y, Soliveres S, Gross N, Torices R, Berdugo M, Maestre FT. Phylogenetic, Functional, and Taxonomic Richness Have Both Positive and Negative Effects on Ecosystem Multifunctionality. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 8419–8424. doi:10.1073/pnas.1815727116.
- Pollock LJ, O'Connor LMJ, Mokany K, Rosauer DF, Talluto L, Thuiller W. Protecting Biodiversity (in All Its Complexity): New Models and Methods. *Trends Ecol. Evol.* **2020**, *35*, 1119–1128. doi:10.1016/j.tree.2020.08.015.
- Tordoni E, Carmona CP, Toussaint A, Tamme R, Pärtel M. Global Patterns and Determinants of Multiple Facets of Plant

- Diversity. *Glob. Ecol. Biogeogr.* **2024**, *33*, e13823. doi:10.1111/geb.13823.
15. Rocchini, D.; Hortal, J.; Lengyel, S.; Lobo, J.M.; Jiménez-Valverde, A.; Ricotta, C.; Bacaro, G.; Chiarucci, A. Accounting for Uncertainty When Mapping Species Distributions: The Need for Maps of Ignorance. *Progress. Phys. Geogr. Earth Environ.* **2011**, *35*, 211–226. doi:10.1177/0309133311399491.
 16. Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ. Seven Shortfalls That Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **2015**, *46*, 523–549. doi:10.1146/annurev-ecolsys-112414-054400.
 17. Pärtel M, Szava-Kovats R, Zobel M. Dark Diversity: Shedding Light on Absent Species. *Trends Ecol. Evol.* **2011**, *26*, 124–128. doi:10.1016/j.tree.2010.12.004.
 18. Pärtel M, Szava-Kovats R, Zobel M. Community Completeness: Linking Local and Dark Diversity within the Species Pool Concept. *Folia Geobot.* **2013**, *48*, 307–317. doi:10.1007/s12224-013-9169-x.
 19. Carmona CP, Pärtel M. Estimating Probabilistic Site-Specific Species Pools and Dark Diversity from Co-Occurrence Data. *Global Ecol. Biogeogr.* **2021**, *30*, 316–326. doi:10.1111/geb.13203.
 20. Gavriel T, Azzurro E, Benedetti-Cecchi L, Bertocci I, Cai LL, Claudet J, et al. Using Dark Diversity to Disentangle the Effects of Protection and Habitat Quality on Species Diversity. *Biol. Conserv.* **2025**, *305*, 111096. doi:10.1016/j.biocon.2025.111096.
 21. Trindade DPF, Carmona CP, Reitalu T, Pärtel M. Observed and Dark Diversity Dynamics over Millennial Time Scales: Fast Life-History Traits Linked to Expansion Lags of Plants in Northern Europe. *Proc. Biol. Sci.* **2023**, *290*, 20221904. doi:10.1098/rspb.2022.1904.
 22. Fujinuma J, Pärtel M. Decomposing Dark Diversity Affinities of Species and Sites Using Bayesian Method: What Accounts for Absences of Species at Suitable Sites? *Methods Ecol. Evol.* **2023**, *14*, 1796–1807. doi:10.1111/2041-210X.14109.
 23. Paganeli B, Fujinuma J, Trindade DPF, Carmona CP, Pärtel M. A Roadmap to Carefully Select Methods for Dark-Diversity Studies. *J. Veg. Sci.* **2024**, *35*, e13264. doi:10.1111/jvs.13264.
 24. Riibak K, Ronk A, Kattge J, Pärtel M. Dispersal Limitation Determines Large-Scale Dark Diversity in Central and Northern Europe. *J. Biogeogr.* **2017**, *44*, 1770–1780. doi:10.1111/jbi.13000.
 25. Riibak K, Reitalu T, Tamme R, Helm A, Gerhold P, Znamenskiy S, et al. Dark Diversity in Dry Calcareous Grasslands Is Determined by Dispersal Ability and Stress-Tolerance. *Ecography* **2015**, *38*, 713–721. doi:10.1111/ecog.01312.
 26. Fløjgaard C, Valdez JW, Dalby L, Moeslund JE, Clausen KK, Ejrnæs R, et al. Dark Diversity Reveals Importance of Biotic Resources and Competition for Plant Diversity across Habitats. *Ecol. Evol.* **2020**, *10*, 6078–6088. doi:10.1002/ece3.6351.
 27. Paganeli B, Toussaint A, Bueno CG, Fujinuma J, Reier Ü, Pärtel M. Dark Diversity at Home Describes the Success of Cross-Continent Tree Invasions. *Divers. Distrib.* **2022**, *28*, 1202–1213. doi:10.1111/ddi.13522.
 28. de Oliveira Gonçalves-Araújo MD, de Carvalho CE, Pequeno PACL, Trindade DPF, Hughes F, de Araújo FS, et al. Observed and Dark Diversity of Plants' Life-Forms Are Driven by Climate and Human Impacts in a Tropical Dry Forest. *Biodivers. Conserv.* **2024**, *33*, 759–773. doi:10.1007/s10531-023-02771-z.
 29. Lewis RJ, de Bello F, Bennett JA, Fibich P, Finerty GE, Götzenberger L, et al. Applying the dark diversity concept to nature conservation. *Conserv Biol.* **2017**, *31*, 40–47. doi:10.1111/cobi.12723.
 30. Moeslund JE, Brunbjerg AK, Clausen KK, Dalby L, Fløjgaard C, Juel A, et al. Using Dark Diversity and Plant Characteristics to Guide Conservation and Restoration. *J. Appl. Ecol.* **2017**, *54*, 1730–1741. doi:10.1111/1365-2664.12867.
 31. Pärtel M, Tamme R, Carmona CP, Riibak K, Moora M, Bennett JA, et al. Global Impoverishment of Natural Vegetation Revealed by Dark Diversity. *Nature* **2025**, *641*, 917–924. doi:10.1038/s41586-025-08814-5.
 32. Heuertz M, Carvalho SB, Galindo J, Rinkevich B, Robakowski P, Aavik T, et al. The Application Gap: Genomics for Biodiversity and Ecosystem Service Management. *Biol. Conserv.* **2023**, *278*, 109883. doi:10.1016/j.biocon.2022.109883.
 33. Bascompte J, Jordano P. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **2007**, *38*, 567–593. doi:10.1146/annurev.ecolsys.38.091206.095818.
 34. Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, et al. Anticipating Critical Transitions. *Science* **2012**, *338*, 344–348. doi:10.1126/science.1225244.
 35. Torresani M, Rossi C, Perrone M, Hauser LT, Féret J-B, Moudry V, et al. Reviewing the Spectral Variation Hypothesis: Twenty Years in the Tumultuous Sea of Biodiversity Estimation by Remote Sensing. *Ecol. Inform.* **2024**, *82*, 102702. doi:10.1016/j.ecoinf.2024.102702.
 36. Beccari E, Pérez Carmona C, Tordoni E, Petruzzellis F, Martinucci D, Casagrande G, et al. Plant Spectral Diversity from High-Resolution Multispectral Imagery Detects Functional Diversity Patterns in Coastal Dune Communities. *J. Veg. Sci.* **2024**, *35*, e13239. doi:10.1111/jvs.13239.
 37. Gillespie TW, Rogers M, Robinson C, Rocchini D. Biodiversity of the World: A Study from Space. In *Remote Sensing Handbook*, 1st ed.; CRC Press: Boca Raton, USA, 2024; Volume 4, p. 16. ISBN 978-1-003-54117-2.
 38. Çevik T, Çevik N. Environmental DNA (eDNA): A Review of Ecosystem Biodiversity Detection and Applications. *Biodivers. Conserv.* **2025**, *34*, 2999–3035. doi:10.1007/s10531-025-03112-y.
 39. Schuwirth N, Borgwardt F, Domisch S, Friedrichs M, Kattwinkel M, Kneis D, et al. How to Make Ecological Models Useful for Environmental Management. *Ecol. Model.* **2019**, *411*, 108784. doi:10.1016/j.ecolmodel.2019.108784.
 40. Keck F, Peller T, Alther R, Barouillet C, Blackman R, Capo E, et al. The Global Human Impact on Biodiversity. *Nature* **2025**,

- 641, 395–400. doi:10.1038/s41586-025-08752-2.
41. Reidsma P, Tekelenburg T, van den Berg M, Alkemade R. Impacts of Land-Use Change on Biodiversity: An Assessment of Agricultural Biodiversity in the European Union. *Agric. Ecosyst. Environ.* **2006**, *114*, 86–102. doi:10.1016/j.agee.2005.11.026.
 42. Wu J, Guo Y, Zhou J. Nexus between Ecological Conservation and Socio-Economic Development and Its Dynamics: Insights from a Case in China. *Water* **2020**, *12*, 663. doi:10.3390/w12030663.
 43. Costanza R, d’Arge R, de Groot R, Farber S, Grasso M, Hannon B, et al. The Value of the World’s Ecosystem Services and Natural Capital. *Nature* **1997**, *387*, 253–260. doi:10.1038/387253a0.
 44. Truchy A, Angeler DG, Sponseller RA, Johnson RK, McKie BG. Chapter Two - Linking Biodiversity, Ecosystem Functioning and Services, and Ecological Resilience: Towards an Integrative Framework for Improved Management. In *Advances in Ecological Research*; Woodward G, Bohan DA, Eds.; Ecosystem Services; Elsevier Ltd.: Amsterdam, Netherlands. 2015; Volume 53, pp. 55–96.
 45. Mitchell RJ, Auld MHD, Le Duc MG, Robert MH. Ecosystem Stability and Resilience: A Review of Their Relevance for the Conservation Management of Lowland Heaths. *Perspect. Plant Ecol. Evol. Syst.* **2000**, *3*, 142–160. doi:10.1078/1433-8319-00009.
 46. Zinchenko TD, Shitikov VK, Rosenberg GS. Assessment of Bottom River Communities in Considering the “Dark and Gray Diversity” of Species: Approaches to a Solution. *Arid Ecosyst.* **2023**, *13*, 527–534. doi:10.1134/S2079096123040200.
 47. Jensen JR. Biophysical Remote Sensing. *Ann. Assoc. Am. Geogr.* **1983**, *73*, 111–132. doi:10.1111/j.1467-8306.1983.tb01399.x.
 48. Chander G, Markham BL, Helder DL. Summary of Current Radiometric Calibration Coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI Sensors. *Remote Sens. Environ.* **2009**, *113*, 893–903. doi:10.1016/j.rse.2009.01.007.
 49. Fairbairn D, Gartner G, Peterson MP. Epistemological Thoughts on the Success of Maps and the Role of Cartography. *Int. J. Cartogr.* **2021**, *7*, 317–331. doi:10.1080/23729333.2021.1972909.
 50. Heisenberg W. The Physical Principles of the Quantum Theory. 1930. Dover Publication Inc.: Chicago, USA. Available online: <https://www.hlevkin.com/hlevkin/90MathPhysBioBooks/Physics/Physics/Heizenberg/2015.166273.The-Physical-Principles-Of-The-Quantum-Theory.pdf> (accessed on 12 July 2025).
 51. Kangas A, Korhonen KT, Packalen T, Vauhkonen J. Sources and Types of Uncertainties in the Information on Forest-Related Ecosystem Services. *For. Ecol. Manag.* **2018**, *427*, 7–16. doi:10.1016/j.foreco.2018.05.056.
 52. Bacaro G, Baragatti E, Chiarucci A. Using Taxonomic Data to Assess and Monitor Biodiversity: Are the Tribes Still Fighting? *J. Environ. Monit.* **2009**, *11*, 798–801. doi:10.1039/b818171n.
 53. Bernardo-Madrid R, González-Suárez M, Rosvall M, Rueda M, Revilla E, Carrete M, et al. A General Rule on the Organization of Biodiversity in Earth’s Biogeographical Regions. *Nat Ecol Evol* **2025**, *9*, 1193–1204. doi:10.1038/s41559-025-02724-5.
 54. Pulliam HR, Dunning JB, Jr., Liu J. Population Dynamics in Complex Landscapes: A Case Study. *Ecol. Appl.* **1992**, *2*, 165–177. doi:10.2307/1941773.
 55. Münkemüller T, Travis MJ, Burton OJ, Schiffers K, Johst K. Density-Regulated Population Dynamics and Conditional Dispersal Alter the Fate of Mutations Occurring at the Front of an Expanding Population. *Heredity* **2011**, *106*, 678–689. doi:10.1038/hdy.2010.107.
 56. Block S, Levine JM. How Dispersal Evolution and Local Adaptation Affect the Range Dynamics of Species Lagging Behind Climate Change. *Am. Nat.* **2021**, *197*, E173–E187. doi:10.1086/714130.
 57. Brugnach M, Pahl-Wostl C, Lindenschmidt KE, Janssen JAEB, Filatova T, Mouton A, et al. Chapter Four Complexity and Uncertainty: Rethinking the Modelling Activity. In *Developments in Integrated Environmental Assessment*; Jakeman AJ, Voinov AA, Rizzoli AE, Chen SH, Eds.; Environmental Modelling, Software and Decision Support; Elsevier Ltd: Amsterdam, Netherlands, 2008; Volume 3, pp. 49–68.
 58. Sastre P, Lobo JM. Taxonomist Survey Biases and the Unveiling of Biodiversity Patterns. *Biol. Conserv.* **2009**, *142*, 462–467. doi:10.1016/j.biocon.2008.11.002.
 59. Rocchini D, Tordoni E, Marchetto E, Marcantonio M, Barbosa AM, Bazzichetto M, et al. A Quixotic View of Spatial Bias in Modelling the Distribution of Species and Their Diversity. *NPJ Biodivers.* **2023**, *2*, 10. doi:10.1038/s44185-023-00014-6.
 60. Wetzel FT, Bingham HC, Groom Q, Haase P, Köljal U, Kuhlmann M, et al. Unlocking Biodiversity Data: Prioritization and Filling the Gaps in Biodiversity Observation Data in Europe. *Biol. Conserv.* **2018**, *221*, 78–85. doi:10.1016/j.biocon.2017.12.024.
 61. Ronquillo C, Alves-Martins F, Mazimpaka V, Sobral-Souza T, Vilela-Silva B, G. Medina N, et al. Assessing Spatial and Temporal Biases and Gaps in the Publicly Available Distributional Information of Iberian Mosses. *Biodivers. Data J.* **2020**, *8*, e53474. doi:10.3897/BDJ.8.e53474.
 62. Ensing DJ, Moffat CE, Pither J. Taxonomic Identification Errors Generate Misleading Ecological Niche Model Predictions of an Invasive Hawkweed. *Botany* **2013**, *91*, 137–147. doi:10.1139/cjb-2012-0205.
 63. Tessarolo G, Ladle RJ, Lobo JM, Rangel TF, Hortal J. Using Maps of Biogeographical Ignorance to Reveal the Uncertainty in Distributional Data Hidden in Species Distribution Models. *Ecography* **2021**, *44*, 1743–1755. doi:10.1111/ecog.05793.
 64. Geldmann J, Heilmann-Clausen J, Holm TE, Levinsky I, Markussen B, Olsen K, et al. What Determines Spatial Bias in Citizen Science? Exploring Four Recording Schemes with Different Proficiency Requirements. *Diversity Distrib.* **2016**, *22*, 1139–

1149. doi:10.1111/ddi.12477.
65. Ladle R, Hortal J. Mapping Species Distributions: Living with Uncertainty. *Front. Biogeogr.* **2013**, *5*. doi:10.21425/F5FBG12942.
66. Sigler K, Warren D, Tracy B, Forrestel E, Hogue G, Dornburg A. Assessing Temporal Biases across Aggregated Historical Spatial Data: A Case Study of North Carolina's Freshwater Fishes. *Ecosphere* **2021**, *12*, e03878. doi:10.1002/ecs2.3878.
67. Schmidt BR, Cruickshank SS, Bühler C, Bergamini A. Observers Are a Key Source of Detection Heterogeneity and Biased Occupancy Estimates in Species Monitoring. *Biol. Conserv.* **2023**, *283*, 110102. doi:10.1016/j.biocon.2023.110102.
68. Łopucki R, Kiersztyn A, Pitucha G, Kitowski I. Handling Missing Data in Ecological Studies: Ignoring Gaps in the Dataset Can Distort the Inference. *Ecol. Model.* **2022**, *468*, 109964. doi:10.1016/j.ecolmodel.2022.109964.
69. Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M. Remote Sensing for Biodiversity Science and Conservation. *Trends Ecol. Evol.* **2003**, *18*, 306–314. doi:10.1016/S0169-5347(03)00070-3.
70. Zhang K, Zhang F, Wan W, Yu H, Sun J, Del Ser J, et al. Panchromatic and Multispectral Image Fusion for Remote Sensing and Earth Observation: Concepts, Taxonomy, Literature Review, Evaluation Methodologies and Challenges Ahead. *Inf. Fusion* **2023**, *93*, 227–242. doi:10.1016/j.inffus.2022.12.026.
71. Bacaro G, Fonda F. Towards the Full Operationalization of the Dark Diversity Concept in Environmental Impact Assessments: A Call to Revise International EIA Standards. *Conserv. Lett.* **2025**, *under review*.