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Review

Behavioral diversity knowledge shortfall in biodiversity conservation

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Behavior is a critical but underexplored component of biodiversity, often overlooked in conservation science, ecological restoration, and biodiversity management. We argue that behavioral diversity needs to be formally recognized as a distinct facet of biodiversity, given its critical value as a reservoir of adaptive potential, and that current gaps in knowledge should be acknowledged as what we formally define to be a behavioral diversity knowledge shortfall. Present knowledge shortfalls need to be confronted by establishing standardized behavioral diversity indicators, harnessing recent technological developments and large databases, building capacity, promoting interdisciplinary collaboration, and setting research priorities. Recognizing and reducing the behavioral diversity knowledge shortfall will help better explain existing biodiversity patterns and improve the outcomes of conservation actions.

Highlights

Behavioral diversity represents variability of behavioral traits from the individual level to the ecosystem level, being an essential component of biodiversity that can affect ecological and evolutionary processes.

Behavioral diversity is increasingly recognized for its role as a reservoir of adaptive potential, a driving force of biodiversity dynamics, and a key link between ecological processes and conservation management.

There are considerable knowledge shortfalls about behavioral diversity, especially at larger spatiotemporal scales, at higher levels of organization, and beyond vertebrates.

Recent technological developments offer new opportunities to study behavioral diversity across the tree of life.

The behavioral diversity knowledge gap needs to be recognized as a significant shortfall and extended beyond animals to encompass the behavior of plants, fungi, and microbes.

Behavioral diversity: an underexplored component of biodiversity

A lack of adequate knowledge about the role of multiple facets of diversity across individuals, species, ecosystems, and their interactions can lead to misidentification of evolutionary and ecological processes and to ineffective conservation management and inefficient monitoring [1]. **Behavior** (see Glossary) is a critical but underexplored component of biodiversity [2–4]. While there is increasing recognition of its importance for biodiversity conservation and sustainable use of wildlife stocks (Figure 1) [8–10], it remains largely overlooked in conservation studies and management at ecosystem and regional scales [9,11,12]. Furthermore, behavioral variation across space, time, and taxa is insufficiently quantified, especially at macro scales (**macrobehavior**), for example, spanning many populations, species, generations, and regions [13].

Behavioral diversity (also termed 'ethodiversity' [4]) represents variability of behavioral traits at any level in the biological hierarchy, including the individual level (e.g., personality), the population level (e.g., alternative reproductive strategies), and the ecosystem level (often contrasting behavioral patterns between species) [4]. It encompasses both behavioral richness and its heterogeneity and evenness. Overlooking behavioral diversity is concerning because behavior reflects how an organism responds to its abiotic and biotic environment, mediating selection on an organism's phenotype and moderating adaptive responses over ecological timescales. In many ways, behavior is the first-order gate through which ecological and evolutionary factors affect populations,

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Figure 1. Examples in which knowledge of behavioral diversity can inform conservation and management. (A) A pair of *Bayadera melanopteryx* looking for an oviposition substrate. This species, endemic to South Asia, is behaviorally linked to riparian forest roots for endophytic oviposition, putting it at risk when human activities reduce the availability of these resources (photo by Adolfo Cordero-Rivera) [5]. (B) The globally detected pharmaceutical pollutant clobazam influences shoaling behavior and river-to-sea migration success in Atlantic salmon (*Salmo salar*; inset photo by Jörgen Wiklund), with potentially wide-ranging ecological and evolutionary consequences (photo by Michael G. Bertram) [6]. (C) Cultural transmission of bin-opening innovation in sulfur-crested cockatoos (*Cacatua galerita*) resulted in an 'innovation arms race' with humans trying to implement bin protection measures (photo by Barbara Klump) [7]. (D) The damage made by crop-raiding elephants is mostly caused by 'problem individuals' and mostly males; consequently, management without proper knowledge of individual behavior results in indiscriminate killing and wasted time and effort.

species, and communities [14]. Behavior is highly dynamic, and behavioral changes can provide early indications of human impacts [8,13–15]. As such, shifts in behavioral diversity may be an early-warning signal for conservation planning, monitoring, and management of natural resources and protected areas [9,13,16]. Behavioral diversity is an essential component of biodiversity that allows species to cope with unpredictable environmental changes. Behavioral trait variation can drive strong ecological effects, affecting biotic interactions and whole communities [17]. Intra- and interindividual behavioral variation can only partly be explained by underlying genetic architecture, as behavior can be both genetically and socially transmitted and shaped by early and recent experiences [18]. Therefore, behavioral diversity cannot be preserved by focusing on other components of biodiversity, such as genetic, taxonomic, functional, and ecosystem diversity.

The importance of behavioral diversity for conservation lies in its capacity to link ecological processes and human decision-making. Implementation of conservation strategies often hinges on how target species respond behaviorally to management actions, including habitat restoration, protected areas, translocations, harvesting regulations, and human disturbance. Behavioral differences among individuals, populations, or species (Figure 2) can strongly influence the success or failure of these interventions, for example, through variation in habitat use, risk avoidance, dispersal,

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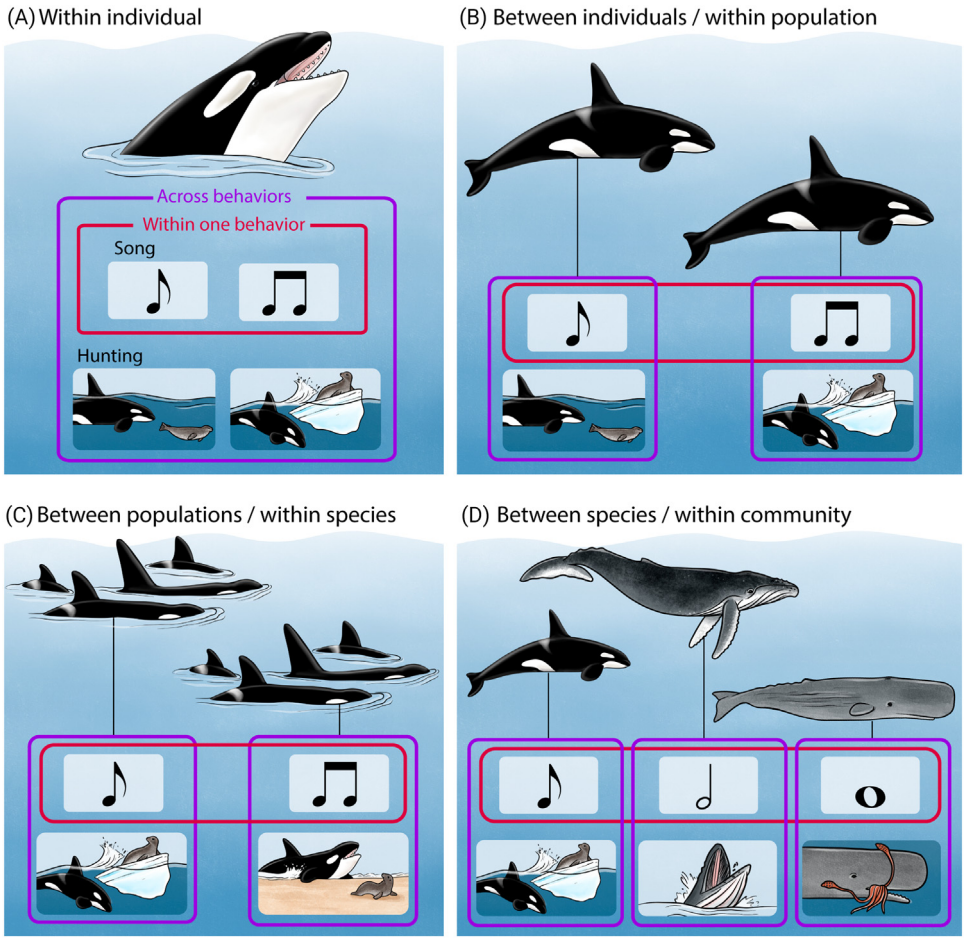


Figure 2. Dimensions of behavioral diversity across different levels of ecological organization, using orcas (*Orcinus orca*) as an example. Musical notes represent different vocal dialects, while icons featuring seals represent different hunting strategies. (A) Within-individual behavioral variation can arise from ontogenetic plasticity, learning, and other mechanisms. (B) Between-individual behavioral variation can arise from differences in ontogeny, personality, social context, and other mechanisms. (C) Between-population behavioral variation can arise from adaptation, differences in culture, systematic developmental differences, and other mechanisms. (D) Between-species behavioral variation can arise from adaptation, phylogenetic history, and other mechanisms. Behavioral diversity may influence conservation outcomes, since behavior is often adaptively plastic and is the first step in responding to novel environmental threats. For example, hunting strategies and vocal dialects of orcas are known to be highly diverse but stable within their kin groups, maintained across generations through vocal learning and culturally acquired dietary preferences [19]. The success of the translocation or reintroduction of an individual orca may depend on the compatibility of its vocalizations and hunting behavior with the host population, as orca pods use vocalizations to coordinate learned hunting strategies (artwork by Julie Johnson, Life Science Studios).

or tolerance of human presence. For instance, serial translocations in North Island saddlebacks (tīeke; *Philesturnus rufusater*) generated cultural bottlenecks, drift, divergence, and reduced song variability [20], affecting behavioral evolution and management success. Analogous to genetic bottlenecks, the implementation of conservation measures preserved population size while still resulting in the loss of a socially inherited component of biodiversity.

Beyond its application to conservation, behavioral diversity has important value as a reservoir of adaptive potential that helps minimize declines in the adaptive capacity of populations,

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species, and communities. For example, behavioral diversity in the chimpanzee (*Pan troglodytes*) functions as an important reservoir of adaptive options in variable environments [21] but can be eroded by anthropogenic impacts [22]. This mirrors the importance of genetic diversity for evolution, through the concept of evolutionary rescue, where heritable variation allows adaptive responses and the potential reversal of population declines [23]. Behaviorally driven evolutionary rescue may occur in cases where behavioral traits are associated with different genotypes. However, behavior can also be transmitted and maintained without genetic processes, via socially inherited knowledge. For example, in the migratory whooping crane (*Grus americana*), social learning from older birds in a reintroduced population significantly improved migratory performance and route accuracy, with no effects of genetic relatedness on these patterns [24].

The importance of behavioral diversity is seen across all levels of ecological organization, from individuals to populations, communities, and whole ecosystems. Behavioral diversity in a population or community is shaped by the fitness of individual behavioral traits, with trade-offs across different life stages, environments, and contexts, ensuring that no single behavior maximizes fitness and that multiple behavioral types are maintained among individuals over time [25]. Behavioral differences are among the main drivers of individual specialization, in which individuals consistently use different resources and subsets of the population's niche [26]. Individuals can differ in foraging patterns, resource use, habitats, and phenology, affecting the species' niche, biotic interactions, evolutionary patterns, and ecosystem processes [17]. Individuals are not behaviorally interchangeable, so average trait values can fail to capture the important ecological effects of behavioral variation [17]. Behavioral diversity can affect the functioning of social groups and populations through collective decision-making, resilience to environmental change, and the ability to adapt to novel conditions. For instance, while learning and cultural transmission are the primary mechanisms for the evolution of ungulate migrations, such as those in bighorn sheep (*Ovis canadensis*) [27], restored populations have a narrower behavioral repertoire than long-established populations and are largely nonmigratory, affecting their resilience and recovery potential [28]. Behavioral diversity can also affect trophic interactions through diversification of foraging tactics and contribute to ecosystem resilience by buffering disturbance [17,25]. Behavioral diversity research thus should be considered relevant both for its practical applications in conservation science and as a fundamental scientific endeavor.

Hortal *et al*.'s [1] unified biodiversity knowledge shortfall framework is a valuable approach for identifying gaps in broad dimensions of biodiversity knowledge and to understand how the processes behind these gaps interact. The aim of their framework is to (i) evaluate how well each dimension is known for a given group of organisms or geographic domain, (ii) address the impacts of a lack of data on understanding different biodiversity patterns, and (iii) identify the scientific, sociopolitical, and economic constraints on advancing knowledge due to these data gaps. There have also been subsequent calls to describe and tackle other shortfalls that bias or hinder conservation efforts [29].

We suggest that current gaps in behavioral diversity knowledge must be recognized as an additional shortfall, the behavioral diversity knowledge shortfall (hereafter, 'behavioral shortfall'), also termed the 'Tinbergenian shortfall' after Nikolaas Tinbergen [16]. We identify the factors that drive or exacerbate gaps in behavioral knowledge, key methodological challenges to obtaining behavioral diversity data, and recent technological developments that are opening new research opportunities, and we discuss potential solutions and ways forward. We also extend the concept of behavioral diversity and associated knowledge shortfalls beyond animals to include plants, fungi, and microbes (Boxes 1–3).

Glossary

Animal culture: information or behavior shared within a community that is acquired from conspecifics through some form of social learning.
Behavior: internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses that are more easily understood as developmental changes.
Behavioral diversity: the variability of behavioral traits at any level of the biological hierarchy, including the individual level (e.g., personality), the population level (e.g., alternative reproductive strategies), and the ecosystem level (which may involve contrasting behavioral patterns between species).
Behavioral inertia, or the Bogert effect: the restraining role that homeostatic behaviors (such as thermoregulation or hydroregulation) exert on evolution.
Behavioral syndromes: a correlated suite of behaviors expressed either within a given behavioral context or across contexts.
Evolutionary trap: a situation in which an evolved trait of an animal becomes maladaptive as a result of a change in local environmental conditions.
iEcology: the study of ecological patterns and processes using online data generated for other purposes and stored digitally.
Macrobehavior: the investigation of variation in behavior over large geographic, taxonomic, and temporal scales and of the ecological and evolutionary implications of this variation.
Personality: consistent individual differences in behavior across time and context.
Social learning: the individual use of socially acquired information.
Umwelt: the 'perceptual world' of any individual, meaning the sum of the information received and processed by its nervous system.

About behavior, behavioral diversity, and impacts on biodiversity patterns

Behavioral diversity is an essential component of population and species persistence and is critical for biodiversity dynamics by driving the processes of speciation, extinction, and diversification [67]. A population or species with greater behavioral diversity will increase the chances that a variant can rapidly adapt to altered conditions, preventing local extinctions [2,68]. Just as high genetic diversity can enable adaptation to environmental change, behavioral diversity can often facilitate rapid responses, including on subgenerational to generational timescales [69]. Furthermore, through 'cultural' transmission, behavior and information can be transmitted among individuals, allowing relatively rapid population-wide responses to external stimuli [9]. Conversely, behavioral diversity can also reduce selection pressure on nonbehavioral traits, such as morphology and physiology, ultimately suppressing a key pathway for adaptation to environmental impacts, such as climate change, and dooming some species to extinction (i.e., **behavioral inertia**, or **the Bogert effect**) [70].

Behavioral changes can have far-reaching consequences for populations, communities, or ecosystems, even when they occur within single species [71]. For example, in reef fishes, behaviorally different individuals contribute differently to nutrient cycling. Selective harvesting of more active individuals changed the behavioral composition of assemblages, strongly reducing nutrient supply and potentially altering ecosystem functioning [72]. Behavior is an important response mechanism to human-induced rapid environmental change [14], such as climate change [73], harvesting [10], urbanization [74], and deforestation and habitat fragmentation [15]. In contrast, behavioral adaptations can also lead to ecological or **evolutionary traps**, where a mismatch between cues and optimal responses results in population declines [75].

Box 1. Behavioral diversity and knowledge shortfall in plants

Plant behavior can be broadly defined as a rapid and reversible response to environmental stimuli [30,31]. However, relatively little is known about the different responses (both intra- and interspecific) or the internal and external factors that affect them.

Plants exhibit diverse responses, including foraging for water and nutrients, adjusting reproductive investments, fine-tuning defenses against herbivores and pathogens, and engaging in conditional mutualisms [32]. Research on light-related behaviors indicates that many species exhibit a shade avoidance behavioral syndrome (Figure I), characterized by delayed germination, increased shoot elongation, reduced root and storage organ growth, and accelerated flowering [35]. Other species tolerate shade, responding to low ratios of the red-to-far-red spectrum by producing broader, thinner leaves and initiating physiological mechanisms for more efficient light use.

Behavioral cues are often conserved among species; for example, jasmonates consistently function as indicators of tissue damage [36]. Other cues are diverse and specialized; for example, those linked to damage in sagebrush exhibit intraspecific variation that constrains their recognition and activity [37].

There is also considerable variation in responses to environmental heterogeneity across tissues and within and among individuals, populations, and species [38], with some more responsive than others. However, the phenotypes produced across different environments (termed reaction norms) are jointly determined by genes, internal conditions, and the environment [39].

Another key question focuses on the fitness consequences of specific plant behaviors. For example, shade avoidance responses have clear fitness benefits for some plants [40]. Broader insights could emerge from applying game theory and other modeling frameworks, which remain underutilized in plant studies.

Likewise, it is important to understand how plants prioritize responses to multiple stimuli and integrate localized responses. Trade-offs between different plant behaviors have been documented, such as between improved anti-herbivore defense and reduced resistance to pathogens and abiotic stress [41].

Behavioral diversity knowledge offers potential for the applied sciences, as variation in plant behavior could inform agricultural production. For example, breeders could select for greater yields at the expense of behaviors that have been favored by natural selection but are counter-productive in agriculture (e.g., shade avoidance) [42].

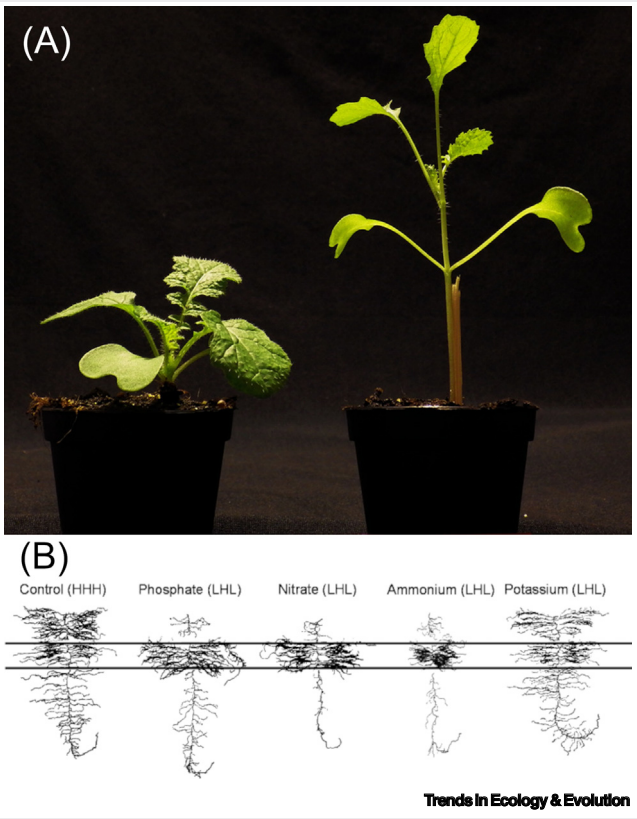


Figure I. Examples of plant behavior. (A) Shade avoidance in black mustard (*Brassica nigra*), characterized by shoot elongation but inhibited leaf lamina expansion under low light quality (plant on the right; photo by Ronald Pierik) [33]. (B) Proliferation of primary and secondary lateral roots under different nutrient concentrations [34].

A lack of appropriate behavioral mechanisms and naïveté toward non-native predators, competitors, or toxic prey are key factors that increase extinction risks, particularly in isolated localities [76]. For example, populations of Australian marsupial and reptile predators have declined due to ingestion of toxic, invasive cane toads (*Rhinella marina*) [77].

Behavioral diversity has been less studied at the community level than other facets of biodiversity [2,4]. Importantly, few studies predict the response of behavioral diversity to environmental changes across different scales, but those that do reveal the scaling-up of behavioral differentiation from individual to collective behavior. For example, individual differences in sociability and boldness shaped leadership, spatial position, movement, foraging success, and fitness in schooling sticklebacks (*Gasterosteus aculeatus*) [78], while experimentally assembled guppy (*Poecilia reticulata*) shoals showed that bold-biased, shy-biased, and mixed groups differed in social-learning pathways [79]. It is often assumed that different levels of biodiversity will be nested in a hierarchical fashion (i.e., that behavioral and genetic diversity are both nested within species diversity) [4]; thus, areas of high species diversity will have high behavioral diversity, but this relationship remains poorly studied. However, due to the complexity of processes and phenomena that generate and maintain behavioral diversity, such as **social learning, behavioral syndromes**, and **animal culture** [4,9], other diversity facets may not adequately explain or reflect behavioral diversity. Indeed, knowledge shortfalls related to animal movement [80], animal culture [9], and natural history [81] can be considered as subsets of the wider behavioral shortfall.

Box 2. Behavioral diversity and knowledge shortfall in fungi

Fungi comprise the second-largest group of eukaryotic species after invertebrates [43] and support crucial ecosystem processes such as carbon storage and nutrient cycling. Yet, the inclusion of fungi in biodiversity goals and conservation efforts lags behind other taxonomic groups [44].

Recent discussions of knowledge shortfalls in fungal biology [45] have focused primarily on species diversity, distributions, conservation assessments, and persistence. In contrast, fungal behavioral diversity remains poorly defined and quantified across the fungal tree of life (Figure II) [46]. Because some fungi are extremely long-lived, we also know little about how behaviors relate to fungal life histories and are triggered at particular life stages.

Fungal trait databases are rapidly evolving, complementing sequencing data and allowing assessments of distribution and prevalence across communities and ecosystems worldwide [47]. Indeed, sequencing studies now frequently classify fungi into trophic guilds [47,48], providing indirect insights into behavior related to nutrient acquisition. Some fungi form mycorrhizal associations with plants, where the fungi recognize, communicate, and exchange nutrients such as phosphorus and nitrogen with plant roots for photosynthates. Establishing and maintaining this interaction requires a repertoire of unique traits and behaviors [49]. Global maps of mycorrhizal fungal diversity hotspots have revealed that these species are not well protected [50], yet the extent of behavioral diversity within this guild remains unknown.

Observing fungal behavior in nature is challenging because fungi are often embedded in soil or wood. However, emerging approaches, including microfluidic chip systems and long-term robotic monitoring of fungal cultures, may allow fungal behavioral repertoires and phenotypic plasticity to be more easily studied [51,52]. Safeguarding fungal behavioral diversity will thus depend on mapping specific behaviors and broadening knowledge across species and contexts.

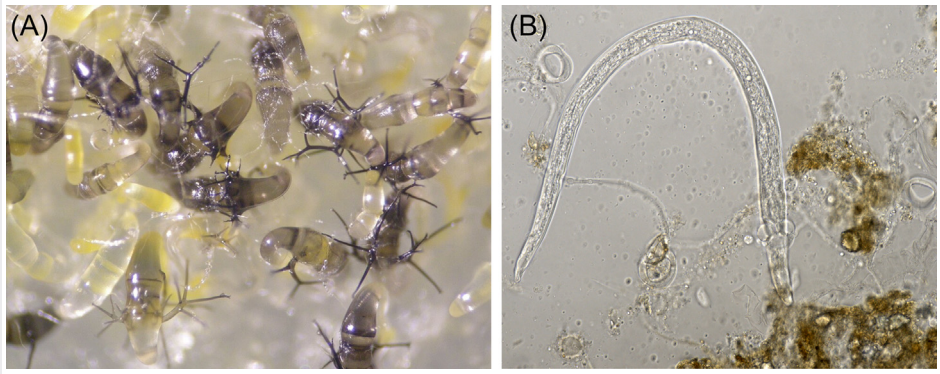


Figure II. Examples of fungal behavior. (A) The fungus *Phycomyces blakesleeanus* reacts to different environmental signals and exhibits various behaviors, including phototropism and an avoidance response (photo by Nhu Nguyen, CC BY-SA 3.0). (B) *Arthrobotrys* spp. exhibiting predatory behavior by producing hyphal rings that constrict and entrap nematodes, which they then colonize and break down from within (photo by Fredrik Klinghammar, documented in a Soil Chip inoculated with field soil).

Key drivers of the behavioral diversity knowledge shortfall

Research biases

Knowledge about behavioral diversity is affected by many common biases, such as a disproportionate focus on the Northern Hemisphere and temperate regions [16], larger organisms and those attracting higher societal interest, and better coverage of easily accessible habitats [82]. It is also highly biased toward model taxa (e.g., *Drosophila*) and specific behaviors (e.g., social behavior in mammals, especially primates, vocalizations in birds and frogs, and, overall, on species with more novel or unique behavior). Behavioral diversity in groups such as plants, fungi, microbes (i.e., protists, bacteria, and archaea), and most insects is heavily underexplored and is often more challenging to study due to different temporal and allometric scales at which

Box 3. Microbial diversity and behavior: the black box of conservation biology

Most biodiversity on Earth is microbial. Microbes comprise the two prokaryotic domains, bacteria and archaea [53], and most of the eukaryotic domain (protists and some fungi) [54]. They drive global biogeochemical cycles and perform most photosynthetic primary production in aquatic systems. Despite being vital to ecosystems [55], microbes are largely overlooked in conservation.

Unlike most larger organisms, microbial species are difficult to define. The phylogenetic similarity criteria typically used to delimit prokaryotic operational taxonomic units would place almost all mammals within a single species. Microbial species boundaries are also blurred by horizontal gene transfer. This contributes to pangenomes (the collective genomes of a species), which are far larger than individual genomes [56]. This genetic flexibility, along with large population sizes and short generation times, allows microbes to evolve rapidly, creating further challenges for researchers.

Microbes display remarkable individual and collective behavior [57,58] that goes beyond simple plasticity, including environmental sensing, directed motility, aggregative behavior, kin recognition, predatory strategies, and even learning. Individual bacteria sense and modulate their movement during chemotaxis, while diverse photosynthetic prokaryotes and eukaryotes steer toward or away from light, with some protists integrating excitable electrical signaling to guide locomotion [59]. At the population level, collective behavior is biochemically coordinated during quorum sensing in bacteria or cAMP-dependent aggregation in social amoebae [60], or emerges from local physical interactions, for example, swarming motility in myxobacteria [61]. Predatory prokaryotes (Figure III) and protists can recognize kin and select prey, actively controlling bloom formation and dynamically structuring ecosystems and communities beyond abundance [63]. Some protists have specialized foraging systems, including dinoflagellates with sophisticated eye-like and harpoon-like structures to sense and catch prey [64]. Increasing evidence suggests that some microbes can learn, changing their behavior on the basis of past experience [65].

Microbial behavior may be important for conservation in several ways. Resting stages, such as spores or cysts, and dormancy may allow microbes to survive adverse conditions and facilitate dispersal [66]. Studying behavior in the field, rather than in monospecific cultures, is critical. Ultimately, preserving microbial diversity, as communities of evolving species, with their full behavioral repertoires will require protecting diverse microbial ecosystems.

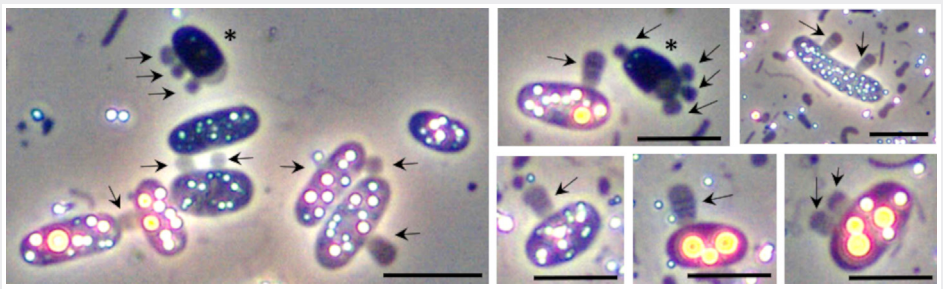


Figure III. Members of predatory Patescibacteria feeding on other bacterial cells [62]. Members of *Vampirococcus lugosii* (Absconditabacteria; arrows) are attached to their preferred anoxygenic photosynthetic hosts (*Halochromatium* sp.; note the refractile sulfur granules accumulated in their cytoplasm, resulting from the use of H_2S as an electron donor for carbon fixation). They are observed in natural samples (Chiprana Saline Lake, Spain). The host cells labeled with an asterisk are dead due to predation (note the absence of sulfur granules and their dark appearance). Scale bar: 5 μm (photos by Ana I. Lopez-Archilla).

behavior manifests in these groups (supplementary information online). Knowledge of behavioral diversity is also highly biased across behaviors within species (e.g., toward particular life stages, such as adults). Social and antipredatory behavior and behavioral processes such as learning and animal **personality** have been much-less studied within a biodiversity conservation context and in the wild than under laboratory conditions [11]. Knowledge biases are also driven by the limited ability to perceive, study, and understand the **Umwelt** (including species-specific sensory capacities) of most animals, and even more so in taxa that are more phylogenetically distant from mammals.

Challenges related to the inherent characteristics of behavioral diversity

Behavior is highly dynamic and context-dependent, influenced by the interplay of local environmental factors with macroecological processes [13]. The field of macrobehavior explores behavioral variation across large spatial, temporal, and taxonomic scales (i.e., dozens of populations, generations, or species) to identify general principles that underlie these patterns and enable prediction of their consequences [13]. Yet studying macrobehavior is currently limited by available data and research biases.

Behavioral diversity is more objectively addressable for some questions and more readily quantifiable at lower scales, but it becomes more challenging to standardize at larger scales and across species. Addressing this major challenge requires developing adequate standardization techniques. To use behavioral knowledge effectively for conservation science, we must select appropriate indicators or proxies based on behavior for specific conservation questions, taxa, and spatiotemporal scales. Thus, behavioral diversity should not be understood as a single, fully standardized metric analogous to species richness. Instead, it represents a set of measurable attributes, some of which are more tractable and policy-relevant than others.

Another challenge is studying cryptic behavior, including behaviors that are difficult to distinguish from other behaviors but are driven by different internal mechanisms [83]. For example, the extinction of the large blue butterfly (*Maculinea arion*) across the United Kingdom, despite intensive conservation efforts, was reversed only after improved knowledge of its complex behavior, involving species-specific ant brood parasitism [84]. The crypticity of behavior is analogous to the concept of shadow diversity [85], which includes ignored, obscured, undiscovered, and unimagined diversity. Shadow behavioral diversity means that estimates of behavioral diversity systematically underrepresent some behaviors or their variability.

Local or regional erosion of behavioral diversity may be difficult to observe and study, given the timescales required to measure changes. This challenge is also impacted by shifting baselines in the perception of behavioral diversity [86] and a lack of historical data and reference points for past behavioral diversity. Historical behavioral data are poorly preserved because the technologies and capacity required to measure and store data on a large scale are relatively new.

Methodological and technological challenges

Behavioral research in the field is often hindered by logistical, financial, ethical, and welfare constraints that are also experienced in other ecological studies [9,87]. Given difficulties in measuring behavior *in situ*, controlled or semi-controlled laboratory studies can offer valuable causal insights into processes driving behavioral diversity, but *in situ* studies are still critical for a comprehensive view of existing diversity [88]. It is challenging to ensure animals behave naturally in experimental settings [89], particularly when documenting interspecific differences or studying large or symbiotic organisms. Experimental setups are limited in capturing the full range and variability of natural behavior and its ecological significance, and rarely focus on behavior that demands specific conditions, such as migration [89,90]. This issue is further compounded when experimental studies focus on only a limited number of model species [90], focus on domesticated or captive-bred individuals, or involve rearing conditions that do not reflect those found in the wild (e.g., unnaturally high densities, readily available food, and absence of predation), leading to behavioral shifts, reduced behavioral variation, and reduced reactivity [91].

Studying behavioral diversity is also challenging because of technological, measurement, observation, and sampling limitations. First, the lack of standardized data and harmonized protocols impedes comparisons across studies due to the different behavioral and response variables

measured (e.g., one study may measure activity in a home-range using direct visual observation over a short period, while another may use long-term GPS tracking). Second, unlike standardized repositories for spatial occurrence, genomic, or plant trait data, we lack archives and repositories for behavioral data across taxa [92]. While there have been initiatives to establish behavioral databases, such as MammalNet, a database of annotated behavioral videos of mammals [93], and BEBE, a benchmark database for behavioral estimation from bio-logger data [94], as well as those on animal movement (MoveBank; https://www.movebank.org) and social behavior (ASNR; https://bansallab.github.io/asnr/), the next step will be to develop their interoperability. New infrastructure to create and maintain these databases and the practical capacity to share data efficiently may be costly, since raw data may include large files such as videos and high-resolution images. Third, given the cost, time, and expertise required to study behavior, it is rarely documented across large spatial, temporal, and taxonomic scales [13]. Finally, behavioral ecology researchers are often disconnected from those in the fields of macroecology, biogeography, and macroevolution, who have the skills to place behavior into a macroecological context, as well as from conservation scientists and practitioners, who could help bridge the present gap between behavioral and conservation science [18].

Impacts of other biodiversity knowledge shortfalls

The behavioral shortfall is exacerbated by other shortfalls, including undocumented behaviors exhibited by species that are not yet described or from unknown areas of species' distributions; a lack of understanding of the evolutionary dynamics of behavioral traits or ecophysiological responses; and many kinds of sampling biases (as addressed by the STRANGE framework) [90]. In turn, the behavioral shortfall negatively affects the understanding of ecological functions and interactions, which can be strongly modified by behavior. For example, dung beetles (Scarabaeoidea) exhibit a wide range of nesting behaviors across species (from 'dweller' species that nest within the dung pat and dung–soil interface, 'tunnelers' that bury dung in tunnels under the dung pat, and 'rollers' that roll a dung ball for burial far from the dung pat, to species that parasitize other dung beetles' brood balls or nest elsewhere), which, in turn, affect many ecological processes, such as soil aeration, nutrient cycling, and secondary seed dispersal [95]. Insufficient behavioral knowledge regarding this key function could lead to inadequate understanding of the many ecosystem functions performed by this highly diverse group of insects.

New research opportunities

Recent technological developments create new opportunities to address the behavioral shortfall more effectively [96–99]. Automated behavioral diversity monitoring and data collection can be achieved using high-throughput systems, such as networks of automatic environmental recorders [97], drones [98], biomimetic robots [100], camera systems [101], and high-resolution animal tracking and biologging [96]. Studying behavioral diversity at large spatial scales could also be supported by satellite tracking and initiatives such as the International Cooperation for Animal Research Using Space [102,103]. All of these advances can help to reduce behavioral data gaps for less-studied kingdoms and taxa. Notably, novel data sources and technologies can be especially valuable for studying cryptic species and cryptic or rare behavior [103–105].

Digital images and video data, including those from citizen/community science platforms [106] and **iEcology** data sources [105], can provide vast amounts of behavioral observations across broad spatial, temporal, and taxonomic scales. However, these datasets present their own challenges, which have been discussed elsewhere [107].

Extracting useful information from existing behavioral datasets will require time to develop relevant tools and algorithms [99], as well as interdisciplinary collaboration, especially with data scientists.

Some challenges may be overcome by recent developments in artificial intelligence technologies [103], including computer vision [99]. Automated behavioral classification methods, which have so far been used primarily for domestic animals in agriculture and aquaculture, and for experimental animals in veterinary and human health [108], could be applied to large unlabeled digital datasets from camera traps, smartphones, and online social media platforms, thereby underpinning the implementation of large-scale behavioral monitoring programs [93]. Large benchmark datasets [93] and behavioral classification protocols [109] are already available for the study of mammal behavior in the wild, but few ecological studies have taken advantage of these tools. This could reflect the need for significant computer science expertise and expensive computational resources to apply computer vision technology [99]. Bioacoustic databases, such as the BioAcoustica online repository (https://bio.acousti.ca) and FishSounds (https://fishsounds.net), are additional promising sources of large-scale behavioral data that require relatively inexpensive recording equipment.

Concluding remarks

Addressing the behavioral shortfall requires developing a broad, unifying, and operational classification of behavior, behavioral repertoires, and variability across species. Attempts to study behavior beyond individuals within single populations and species must also be encouraged. These across-taxa comparative studies provide critical insights into the origins and evolutionary relevance of behavioral diversity for focused research questions [110], while fostering greater unification of data-collection protocols and behavioral classification for the entire research community [92]. Moreover, the behavioral shortfall must be recognized as extending beyond the behavior of animals, stimulating increased efforts to characterize the behavior of other groups, such as plants (Box 1) [30], fungi (Box 2) [46], and microbes (Box 3) [57].

Key steps in tackling the behavioral shortfall ought to include efforts to establish standardized protocols for creating indicators or measures of behavioral diversity, and the creation of better database infrastructure to harness new technological developments and enable unification across disciplines. Generating large datasets and databases will revolutionize our ability to ask new questions: for example, the DISPERSE database on aquatic macroinvertebrate dispersal has opened new research avenues on the ecology of aquatic insects [111]. Some of the present behavioral diversity knowledge gaps could be bridged through advanced predictive and extrapolative modeling approaches [112] or by identifying suitable behavioral traits at the individual level, or proxies that could be measured at broad scales, across populations, species, and ecosystems [5,13]. The large literature on flight-initiation distances provides one example [113].

Existing methods from information theory adopted by geneticists and ecologists [114] can also be tailored to quantify behavioral diversity across disparate forms of behavior within and across species (see the tutorial and worked example by Nelson *et al*. [115]). Furthermore, experimental protocols must be improved to more closely reflect natural biotic and abiotic conditions [89], while novel technologies can be employed to improve studies in natural settings [116]. We must also identify, digitize, and share existing but highly fragmented data [92], following FAIR principles, to develop approaches that can combine complex and disparate data types [115] and to integrate them within centralized information repositories. This can be facilitated by AI tools [103,112]. Such efforts require expertise from diverse fields, including behavioral ecology, biogeography, macroecology, conservation science, agricultural practices, management, and data science [13,112]. International research networks can facilitate expertise and data sharing, as well as globally distributed experiments [13,117]. Building capacities and strengthening international collaboration in underrepresented regions are also essential [81], as is improving inclusivity more broadly across behavioral ecology, to ensure diverse, innovative teams.

Outstanding questions

What constitutes behavioral diversity?

How can behavioral diversity be measured from individuals to ecosystems?

What practical proxies and surrogacy approaches might be used to quantify behavioral diversity and associated knowledge shortfalls on a macro scale?

What unifying behavioral classification permits standardized inventories and the quantification and comparison of behavioral diversity across taxonomic groups and contexts?

What are the most effective methods and measures to address the present behavioral diversity knowledge shortfall?

What types of behavior should be recognized as future research priorities for reducing the knowledge shortfall?

How does reducing the behavioral diversity knowledge shortfall affect other knowledge shortfalls?

How can behavioral diversity knowledge be effectively mobilized in conservation planning, management, and policy?

How will the behavioral diversity knowledge shortfall impact the effectiveness of biodiversity conservation efforts in the presence of global change?

Are taxonomically isolated species also unique in their behavioral repertoires?

How much does human behavioral diversity shape animal behavioral diversity in human-dominated habitats, and how does this interplay affect conservation management?

How does behavior that plays out between individuals at small spatial and temporal scales interact with large-scale macroecological processes?

How do we quantify behavioral diversity at different scales in modular organisms (e.g., fungi, clonal plants, and corals), where defining an individual becomes challenging?

Developing future research priorities (see Outstanding questions) will be required to reduce the behavioral shortfall. For example, each behavior can have specific conservation relevance; as with differences between species, the more dissimilar a behavior is to others, or the rarer a behavior is, the more valuable it might be to conserve [118]. Conservation and management programs must consider the need for priority setting regarding behaviors that (i) should be studied to reduce the present knowledge shortfall; (ii) have disproportionate importance for conservation and ecosystem functioning, such as 'keystone behaviors' (e.g., learning, behaviors important for community resilience, intraspecific or population-level dynamics, or ecosystem engineering, such as dam-building in beavers); (iii) represent fitness-relevant behavior (i.e., behaviors that help explain why a population is either declining or thriving to the point of becoming a pest); (iv) have special conservation or management concern (e.g., behaviors that disproportionately affect conservation effectiveness or drive the impacts of invasive species); (v) are of particular sociocultural or economic value for humans (e.g., behaviors that lead to higher visibility, risk, or harvest/catchability); and especially (vi) are rare, threatened, and undiscovered. Such prioritization could be supported by classification frameworks based on the uniqueness, rarity, threat level, and ecosystem and social-ecological relevance of behavior, similar to frameworks for other facets of biodiversity (e.g., EDGE) [119]. Conservation priority frameworks need to apply the precautionary principle when confronted with substantial knowledge shortfalls [9].

Another frontier is to address the interface between non-human and human behavior studies. First, exploring this interface may reveal not only common principles underlying behavior across species but also actionable pathways for integrating human behavioral diversity (especially in contexts where human activities have a relevant impact on organismal behavior) into biodiversity conservation strategies. Second, including human psychology, shared patterns, and evolutionary drivers could help refine our understanding of cognition, decision-making, and social dynamics in other species, as well as conservation-relevant behavioral change in humans [120].

Adopting a Big Science approach will integrate technological solutions to ensure efficiency and scalability, engage with local communities and citizen scientists, and link biodiversity information (e.g., behavioral diversity indices) to ecosystem functions, benefits to people, and socioeconomic outcomes, while recognizing the uncertainty derived from the lack of comprehensive data on behavior. In doing so, behavioral diversity can be integrated in a fair and robust way into international biodiversity conservation and restoration strategies.

How far are we from an exhaustive list of behavior? What is the proportion of the total behavioral diversity that we have sampled so far?

How can we study odor-based and other behavioral cues that are outside the range of human or remote-recording detection, in natural settings?

How can emerging big databases alongside new technologies be harnessed to accelerate the discovery and documentation of behavioral diversity across taxa?

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Declaration of interests

The authors declare no competing interests.

Supplemental information

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