Monitoring animal movement diversity as a component of biodiversity

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Animal movement is increasingly being quantified in novel ways, with high potential for integration into broad-scale efforts to monitor biological diversity. Here, we define movement diversity as a form of biodiversity, measuring variation in animal movement from the level of individual animals to communities. We present a framework to develop a common language for movement diversity metrics, which describes variation in movement patterns, as well as motion and navigation capacities, through both time and geographic space. Developing and using a common language for such metrics will lay the foundation for expanding the application of animal movement data in biodiversity monitoring to address not only the effects of global climate and land-use change on movement diversity but also how movement diversity influences ecosystem functioning.

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Each year, movement ecologists add to an ever-growing list of metrics that quantify the diversity of movement behaviors and strategies exhibited by animals (Strandburg-Peshkin *et al*. 2017; Shaw 2020; Cain *et al*. 2023). These innovations are fueled by data collected from animal tracking devices, which share at least 3 million movement records daily (Kays *et al*. 2022). According to the Group on Earth Observations Biodiversity Observation Network (GEO BON), movement is considered as an Essential Biodiversity Variable for standardized monitoring of global biodiversity, listing a handful of important traits such as dispersal distance and migratory route (Kissling *et al*. 2018). Technology has historically restricted global biodiversity science to these broad measures of animal movement; however, the technology, data, and analytic tools now exist to monitor movement diversity using more refined trait measurements. For example, variation in behavioral states (eg restricted search versus exploration; Spiegel *et al*. 2017) or diversity of foraging movements within a clade of animals (Pigot *et al*. 2020) may be equally important to conservation.

In a nutshell:

- Standardized methods to measure animal movement behavior as a component of biodiversity are limited in scope
- The purpose of this paper is to describe existing metrics of animal movement as components of "movement diversity" and propose a system for incorporating new metrics
- Global change affects movement diversity, although similar disturbances can have opposing effects (positive and negative), with downstream consequences for how animals contribute to ecological processes
- By considering how movement diversity varies in space and time, practitioners can more effectively allocate resources to preserve ecosystem function

We define movement diversity as the variety of movement forms, patterns, and processes displayed by individual animals, groups, populations, species, and communities over a specified spatial extent and time scale (Figure 1). Movement diversity is derived from animal movement metrics, which may include speed and distances displaced (Noonan *et al*. 2019), geometry of home range (Luisa Vissat *et al*. 2023), predictability of routes (Hertel *et al*. 2021; Cain *et al*. 2023), and many others. A shared vocabulary for movement diversity is necessary to compile existing metrics and adopt new ones. The Movement Ecology Framework (MEF) is a guiding principle that can organize animal movement metrics according to the causes and consequences of animal movement: that is, internal state, navigation capacity, motion capacity, and movement path (Panel 1; Figure 2; Nathan *et al*. 2008). The MEF likens animal movement tracks to DNA sequences to show how functional units—analogous to genes—give rise to observed movement patterns (Nathan *et al*. 2008). This analogy can be extended to liken movement diversity to genetic diversity, in which functional units within individual movement tracks and among individuals, groups, populations, and species give rise to variation in movement patterns.

One immediate application of this concept is to describe the role of movement diversity at the nexus of global change and

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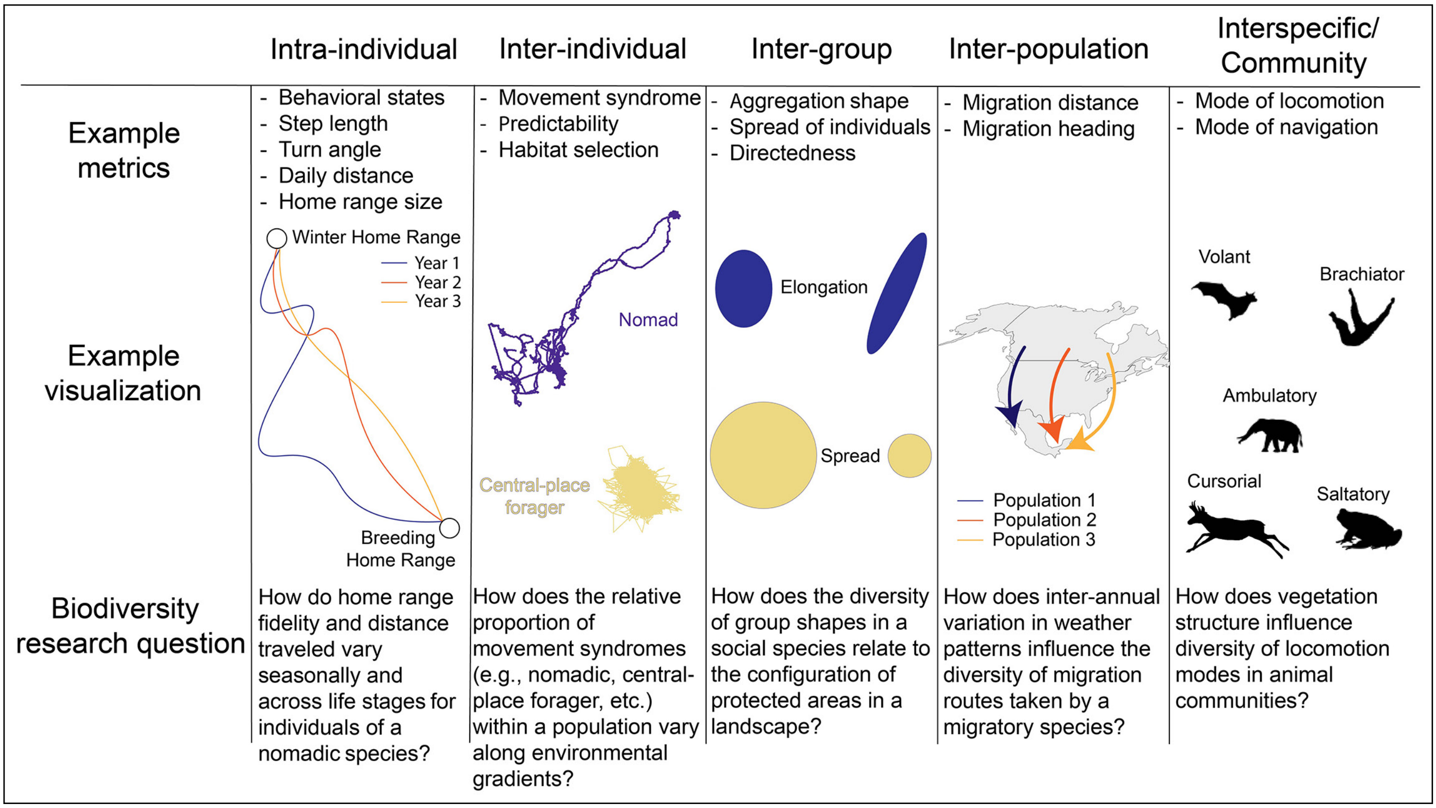

Figure 1. A framework for metrics that can be used to quantify animal movement diversity, from the level of an individual animal to a community, with example visualizations and research questions. Animal silhouettes from phylopic.org. Image credits, clockwise from top left: ©Melissa Ingala, ©Margot Michaud, ©Dennis Murphy, ©Margot Michaud, ©T Michael Keesey. Example "Inter-individual" illustration from movebank.org ("Hornbill e-obs Cameroon", study ID 2016993973).

Panel 1. The Movement Ecology Framework as an organizing principle for movement diversity

The Movement Ecology Framework (MEF) provides a paradigm for movement ecology research, demonstrating how variation in environmental factors, internal state (motivation to move), motion capacity (how to move), and navigation capacity (where to move) influences animal movement patterns, which can feed back to influence the internal state (Nathan *et al.* 2008) and, in some cases, environmental factors (Russo *et al.* 2023). Movement diversity metrics can be organized according to this framework from the individual to community level, although some components of the framework (eg motion capacity and navigation capacity) may not pertain to each level of organization. For instance, modes of locomotion and navigation are normally ascribed to species but not individuals. In addition, environmental factors and the internal state are drivers but not components of movement diversity. Several metrics exist to describe movement diversity according to multiple components of the MEF, and across levels of organization (Figure 2), but many metrics have yet to be applied to biodiversity monitoring.

ecosystem functioning. Animal movements are threatened by agents of global change such as human activity, human footprint, and climate change, which can limit displacement (Tucker *et al.* 2018) and cause phenological mismatches along migration routes (Szesciorka *et al.* 2020). Consequently, ecosystem functions and services that depend on animal movements are also threatened (Tucker *et al.* 2021). As animals move, they serve as "mobile links" among ecosystems by distributing nutrients, seeds, and diseases; engineering ecosystems; and depredating or acting as prey for other animals (Lundberg and Moberg 2003; Jeltsch *et al.* 2013). A unified language for movement diversity will be useful in understanding the diverse repertoire of animal behaviors on Earth, how predictable they are, and how anomalies in animal movement may impact ecosystem functioning. As global biodiversity plummets (Dirzo *et al.* 2014), it is important to know whether movement diversity is also decreasing, or whether animals are adapting to changing environments by diversifying their movement strategies. In this paper, we introduce not only a shared vocabulary for measuring the diversity of animal movements in both marine and terrestrial ecosystems but also a road map for using movement diversity to inform biodiversity conservation.

Defining movement diversity

Several metrics can be used to quantify animal movement diversity, and still others remain to be developed. At the level of an individual animal, diversity in movement step lengths (straight-line distance between consecutive GPS locations) and turn angles (angle of movement step relative to previous step) can indicate different behavioral states, such as resting or commuting between foraging locations. Coupled with detailed field observations, it is possible to link environmental stressors to behavioral diversity and, consequently, survival and reproduction. Movement patterns of animal groups (two or more individuals) are often described based on the centroid of the group or in terms of emergent properties, such as the shape and spread of the group (Strandburg-Peshkin *et al*. 2017; Hughey *et al*. 2018), and rarely by the same metrics used to characterize the movement of individuals. Collective movement of social species is a fast-growing field, and advances in machine learning with drone imagery have enabled continuous tracking of group movements and 3D body position (Koger *et al*. 2023). At broader levels of biological organization (eg population, community), fewer movement diversity metrics have been developed and explored. For example, animal species differ in navigation modes and capabilities, but the consequences of this variation for emergent community composition is unclear. It might be expected that animals that use "piloting" as a navigation strategy would be more threatened by land-use change than animals with cognitive map-based navigation (Toledo *et al*. 2020), due to the former's reliance on permanent landscape features. Organizing movement metrics based on the level of biological organization and according to components of the MEF (Panel 1; Figure 2) will help identify gaps in movement diversity metrics and lay the foundation for incorporating them into biodiversity monitoring frameworks (Figure 1).

Monitoring movement diversity

Biodiversity monitoring addresses changes in both the composition and functional diversity of ecosystems through time and across space (Pollock *et al*. 2020). Movement diversity can be readily integrated into existing methods to monitor biodiversity by treating movement characteristics as functional traits of individuals, populations, or species. Using a movement metric as a unit of movement diversity, it is possible to estimate alpha, beta, and gamma diversity across landscapes. For instance, at the landscape level, species characterized according to movement syndromes (eg migratory, nomadic, central-place forager) can be described according

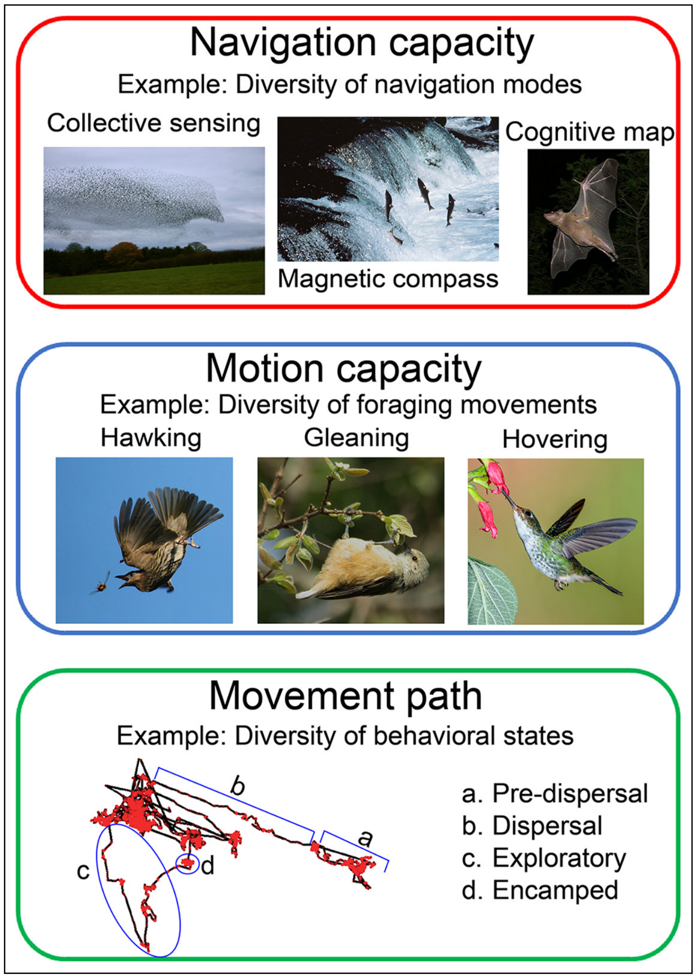

Figure 2. Examples of movement traits and metrics that can be used to characterize movement diversity according to the Movement Ecology Framework (Nathan *et al*. 2008). Image credits, clockwise from top left: ©ad551; ©USFWS Pacific; ©Zoharby; ©Andy Morffew; ©Alan Manson; ©Mdk572. Example "Movement path" illustration from movebank.org ("Hornbill e-obs Cameroon", study ID 2016993973).

to alpha diversity (the number, or richness, of movement syndromes in a community), beta diversity (the turnover in movement syndromes across adjacent communities), or gamma diversity (the pooled richness of movement syndromes across the landscape) (Abrahms *et al*. 2017; Pollock *et al*. 2020). While movement paths can be quantified in ways that indicate biodiversity, the underlying processes producing these patterns, such as physiological state and navigation process, are also important to understand for explaining movement diversity patterns (Joo *et al*. 2022).

Spatiotemporal scales of movement diversity

Organismal movement describes displacement in space over a specified extent of time; consequently, spatiotemporal scales should be considered when quantifying movement diversity. Within a population, individuals can differ in the predictability of their movements, often due to intrinsic traits such as life

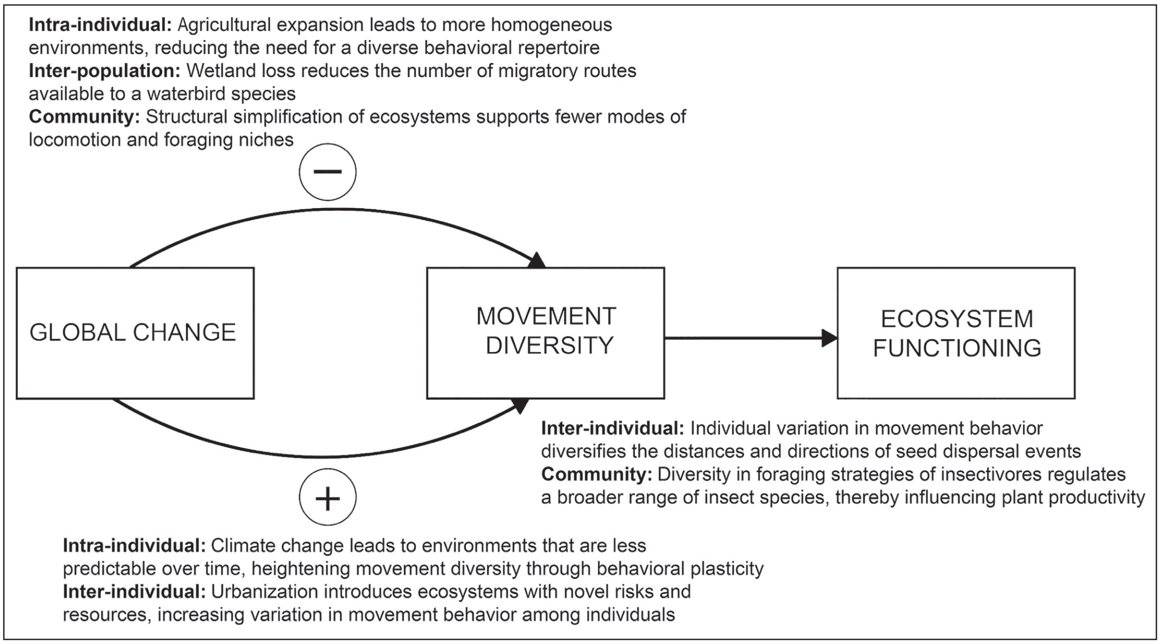

Figure 3. Movement diversity at the nexus of global change and ecosystem functioning, including hypothesized relationships among the three components.

stage. For example, a recent study showed that white storks (*Ciconia ciconia*) develop migratory behavior by exploring routes and then refining them until they exhibit more directed movements later in life (Aikens *et al.* 2024), while another study showed that site fidelity and movement predictability of griffon vultures (*Gyps fulvus*) increase with age (Acácio *et al.* 2024). These examples show how age distributions can be a driver of movement diversity within populations, and how movement diversity at the level of an individual can vary across time scales. Animals of the same species can also differ in long-distance movement strategies. Nomadic individuals, for instance, track resources with less spatiotemporal predictability than migrants (Abrahms *et al.* 2017; Teitelbaum and Mueller 2019). Similarly, aggregations of individuals can change in size and shape through time and across geographic space, with consequences for collective sensing of resources and risk (Strandburg-Peshkin *et al.* 2017; Hughey *et al.* 2018). Quantifying movement diversity at the population or species level will inherently occur at a broader spatial scale than quantifying movement diversity at the level of an individual animal or group. Consequently, empirical studies that carefully consider spatial and temporal scale are needed to advance mathematical models that can reveal both the causes and consequences of movement diversity.

Effects of global change on movement diversity

Climate change influences animal movements by shifting resource availability and driving thermoregulatory behaviors. For example, droughts can increase variability in animal movement distances due to physiological stress and the difficulties of finding resources (West *et al.* 2024). Consequences of climate-driven effects on animal movement diversity include increased probability of species interactions and shifting predator–prey dynamics (West *et al.* 2024). Temperature can also drive year-to-year variation in the timing of animal movements—in marine ecosystems, blue whales (*Balaenoptera musculus*) arrive earlier to feeding locations if sea-surface temperatures were cooler the year before (Szesciorka *et al.* 2020). As climate change increases the frequency of temperature- and precipitation-associated anomalies, animals of both terrestrial and marine environments may adapt their movements to survive and reproduce.

Animals also shift their movements in response to human impacts, but it is unclear whether anthropogenic factors reduce movement diversity or lead animals to employ a greater variety of movement strategies to meet new challenges (Figure 3). Large-scale analyses have shown that the human footprint reduces mammal displacements worldwide (Tucker *et al.* 2018). However, in homogeneous landscapes, such as areas under intensive agriculture, animals may travel farther to procure all the resources they need for survival and reproduction (Tucker *et al.* 2019). Human impacts also influence the predictability of resources in time and space, which can lead populations to become more sedentary if they discover a reliable food source (Gilbert *et al.* 2016). Moreover, habitat fragmentation can increase landscape heterogeneity and therefore movement diversity when both bold and risk-avoiding individuals are present in a population (Rohwäder and Jeltsch 2022). That said, efforts to conserve movement diversity may not always align with those that conserve other forms of biodiversity (eg species diversity) because movement diversity may reflect adaptations of animals to environmental stressors (Teitelbaum and Mueller 2019; Hertel *et al.* 2021).

Whether movement diversity is a favorable or unfavorable conservation outcome depends on how it relates to environmental stressors and resulting impacts on ecosystems. One potential solution is to couple movement data with demographic data to determine whether animals can travel through landscapes in ways that enable them to meet requirements for survival and reproduction.

Effects of movement diversity on ecosystem functioning

Because animals serve as mobile links among ecosystems (Lundberg and Moberg 2003), they modify landscapes in ways that feed back to affect their own movement behavior (Russo *et al.* 2023). For example, variation in the intensity of herbivory through space and time can influence spatiotemporal patterns of plant productivity (Geremia *et al.* 2019), an ecosystem function that in turn influences herbivore movements. Animals move nutrients within and among ecosystems through the distribution of their dung and carcasses, which directly alters nutrient cycles across spatial scales (Ellis-Soto *et al.* 2021), and individual variation in movement behavior of seed dispersers influences plant community composition by diversifying seed dispersal distances (Graf *et al.* 2024). Scaling from individuals to population- and species-level patterns is necessary to understand the impacts of movement diversity on ecosystem functioning. For instance, what are the ecological effects when many individual herbivores move along the same migratory route versus along a staggered and more diffuse series of routes? Considering the ecosystem effects of movement diversity will therefore be important for designing effective conservation strategies.

Considering movement diversity in conservation

Animal movement data have typically informed conservation policies such as the creation and expansion of protected areas and regulations on human activities, such as fishing practices (Hays *et al.* 2019). Recognizing that animal movements traverse sociopolitical boundaries, the Migratory Bird Treaty Act of 1918 between Canada, Mexico, Japan, Russia, and the US protects migratory birds from human threats, such as the capture and killing of individuals as well as the destruction of nests. Similarly, the Convention on the Conservation of Migratory Species of Wild Animals provides a platform for international policy that safeguards the movements of hundreds of marine and terrestrial species (CMS 2024). Policy targets to preserve biodiversity should address the diversity of movement behaviors needed to sustain a population, in addition to protecting migration corridors and animal home ranges. The Kunming-Montreal Global Biodiversity Framework advocates for the conservation of at least 30% of land, inland waters, and seas by 2030; conservation decisions can therefore consider the size and connectivity of habitats needed for animals to employ a diverse suite of movement strategies (CBD 2022). Further exploration of movement diversity as a critical component of biodiversity, using the common language proposed here (Figures 1 and 2; Panel 1), can better inform habitat conservation while preserving ecosystem function in response to global change.

Future directions

Because the movement of animals exerts a strong impact on spatiotemporal patterns of biodiversity, and animals are themselves affected by changing landscapes, movement diversity is at the nexus of global change and ecosystem functioning. Our shared vocabulary for movement diversity is the first step toward understanding its role in global ecosystem dynamics, including cases where (i) heightened movement diversity is a conservation priority and (ii) movement diversity reflects animal responses to environmental stressors. Factors that will enable the widespread integration of movement diversity in biodiversity research include technological innovations and advanced coordination of monitoring methods and networks.

Animal movements are inadequately known in many parts of the world, and especially in the Global South (Kays *et al.* 2022; Ellis-Soto *et al.* 2025). Typical home range size is a baseline species trait that can vary among individuals and populations, yet this information is lacking for many species (Broekman *et al.* 2023). Targeting data-deficient geographic regions and taxa for animal tracking research will be important for deriving large-scale characterizations of animal movement diversity. In addition, most tracking data reflect 2D space use, but most animals move through 3D space, including vegetation, airspace, and water (Gámez and Harris 2022). Methods to characterize 3D space use are better developed in marine ecosystems (Gámez and Harris 2022), although devices exist to obtain reliable estimates of 3D position in terrestrial environments using pressure and temperature sensors (Shipley *et al.* 2017).

Coordinated monitoring of movement diversity will involve building connections between data science and practice. Repositories for animal movement data, including Movebank (https://www.movebank.org), Animal Telemetry Network (https://ioos.noaa.gov/project/atn), and Euromammals (https://euromammals.org), are critical sources of information for efforts to monitor movement diversity (Kays *et al.* 2022). Facilitating the use of these databases toward calculating movement diversity metrics is a high priority; the MoveApps collection of web applications for visualizing and summarizing animal movement data can help address this priority because it was designed for widespread use by a diverse range of scientists and practitioners (Kölzsch *et al.* 2022). In this way, animal movement diversity could readily be integrated into the proposed Global Biodiversity Observing System (GBiOS) and recently created Animal Movement Biodiversity Observation Network (Move BON; https://geobon.org/move-bon) to inform efforts to mitigate rapid and widespread biodiversity loss (Gonzalez *et al.* 2023).

Conclusions

Movement diversity is a largely underexplored dimension of biodiversity that influences genetic diversity, species interactions, and ecosystem function. Animals adapt to global climate and land-use change by shifting their movement patterns, although the direction of change can vary depending on the intensity and predictability of the stressor, with consequences for broader biodiversity patterns. Individual animals, as well as groups, populations, species, and communities, exhibit variation in movement behaviors across spatial and temporal scales. Dozens of metrics already exist to characterize movement diversity at each level of biological organization, as well as the drivers and patterns of animal movement. Organizing these metrics according to their utility in biodiversity monitoring is a critical step toward preserving global biodiversity and ecosystem functioning.

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No new data were collected or analyzed for this article.

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