Title: Monitoring animal movement diversity as a component of biodiversity

Running head: Monitoring biodiversity with animal movements

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Key words: biodiversity, climate change, conservation, land use change, movement ecology

Open Research Statement: No new data were collected or analyzed in this paper.

Abstract

Animal movement is increasingly being quantified in novel ways, with high potential for integration in 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 movement diversity metrics will expand the use of animal movement data in biodiversity monitoring to address the effects of global climate and land use change on movement diversity, and how movement diversity influences ecosystem functioning.

In a nutshell

- Organized ways 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 framework for incorporating new metrics.
- Global change affects movement diversity, although similar disturbances can have opposing effects (positive and negative, respectively), 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.

Introduction

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 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, movement is considered 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 analysis tools now exist to monitor movement diversity using more refined trait measurements. For example, variation in behavioral states (eg, restricted search vs. 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.

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, ie, 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 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 providing prey for other animals (Lundberg and Moberg 2003; Jeltsch *et al.* 2013). A unified framework and 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 a shared vocabulary for measuring the diversity of animal movements in both marine and terrestrial ecosystems and a road map for using movement diversity to inform biodiversity conservation.

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 example, at the landscape level, species characterized according to movement syndromes (eg, migratory, nomadic, central-place forager) can be described according 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). Movement diversity can also be quantified using methods to assess other forms of behavioral diversity, such as hierarchical N-mixture models that describe the relationship between an environment and the probability of observing a behavior (Ke *et al.* 2022). While movement paths can be quantified in ways that indicate biodiversity, the underlying processes producing these patterns can reveal how biodiversity is generated and maintained (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 (**Figure 1**). Multi-year tracks of individuals can lend insight into how movement behavior varies through time and across life stages. 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), and another showed that site fidelity and movement predictability of griffon vultures (*Gyps fulvus*) increases with age (Acácio *et al.* 2024). Although theories related to animal migration have been developed largely around animals of the Northern Hemisphere that undertake relatively predictable migrations in space and time, seasonal animal movements do not always constitute migrations in a strict sense. Nomadic species, for example, track resources with less spatiotemporal predictability (Abrahms *et al.* 2017). Similarly, aggregations of individuals can change in size and shape through time, with consequences for collective sensing of resources and risk (Strandburg-Peshkin *et al.* 2017; Hughey *et al.* 2018).

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 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 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 human footprint reduces mammal displacements worldwide (Tucker *et al.* 2018) and human presence increases nocturnality of many species (Gaynor *et al.* 2018). In homogeneous landscapes, such as 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. Whether movement diversity is a favorable or unfavorable conservation outcome depends on how it relates to environmental stressors and resulting impacts on ecosystems.

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 influences herbivore movements in turn. Animals move nutrients within and among ecosystems by distributing 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). An important area of future research is to understand how movement diversity has cascading effects on ecological communities and resultant ecosystem functioning.

Considering movement diversity in conservation

Animal movement data has 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 USA protects migratory birds from human threats such as capture, killing, and destruction of nests (U.S. Government 2019). 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. Further exploration of movement diversity as a critical component of biodiversity, using the common language proposed here (**Figures 1-2; Panel 1**), can better inform habitat conservation while preserving ecosystem function in response to global change.

Future directions

Because animal movements exert a strong impact on spatiotemporal patterns of biodiversity, and 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 towards understanding its role in global ecosystem dynamics, including cases where heightened movement diversity is a conservation priority, and cases where it 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 among tropical latitudes (Kays *et al.* 2022). Typical home range size is a baseline species trait that can vary among individuals and populations, yet this information is missing for many species (Jaap *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, Animal Telemetry Network, and EuroDeer, are critical sources of information for efforts to monitor movement diversity (Kays *et al.* 2022). Facilitating the use of these databases towards 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 easily be integrated into the proposed Global Biodiversity Observing System (GBiOS) 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 towards preserving global biodiversity and ecosystem functioning.

Acknowledgments: This paper is the product of weekly discussions among members of the UCLA Movement Ecology Group from 2020-24; we thank additional members who contributed to these discussions, including Chloe Nouzille, David Daversa, Adam Pingatore, Elizabeth Young, Ellen Bolas, Janine Fischer, Amandine Gamble, Megan Edic, Nitika Sharma, and Samantha Snowden. NJR acknowledges funding from the NSF Graduate Research Fellowship Program.

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Figures

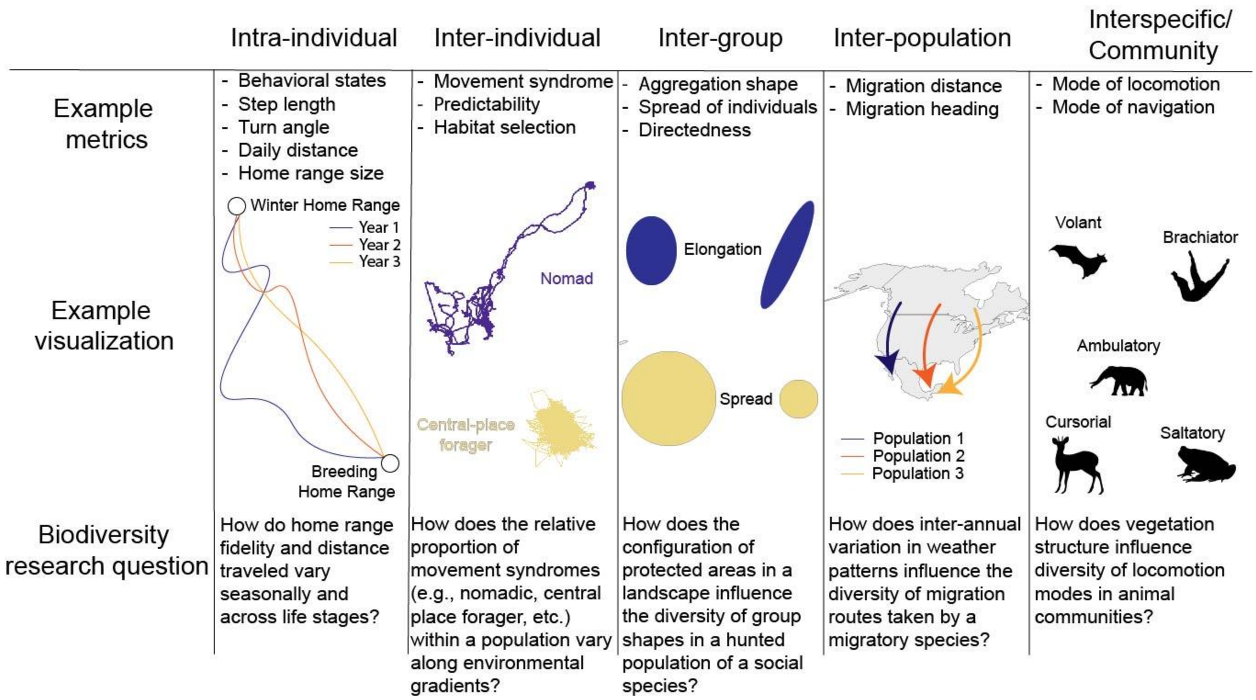

Figure 1: A framework for metrics that can be used to quantify animal movement diversity, from the level of an individual animal to a community, with example visualizations and research questions. Animal silhouettes from phylopic.org. Example “Inter-individual” illustration from movebank.org (“Hornbill e-obs Cameroon”, study ID 2016993973).

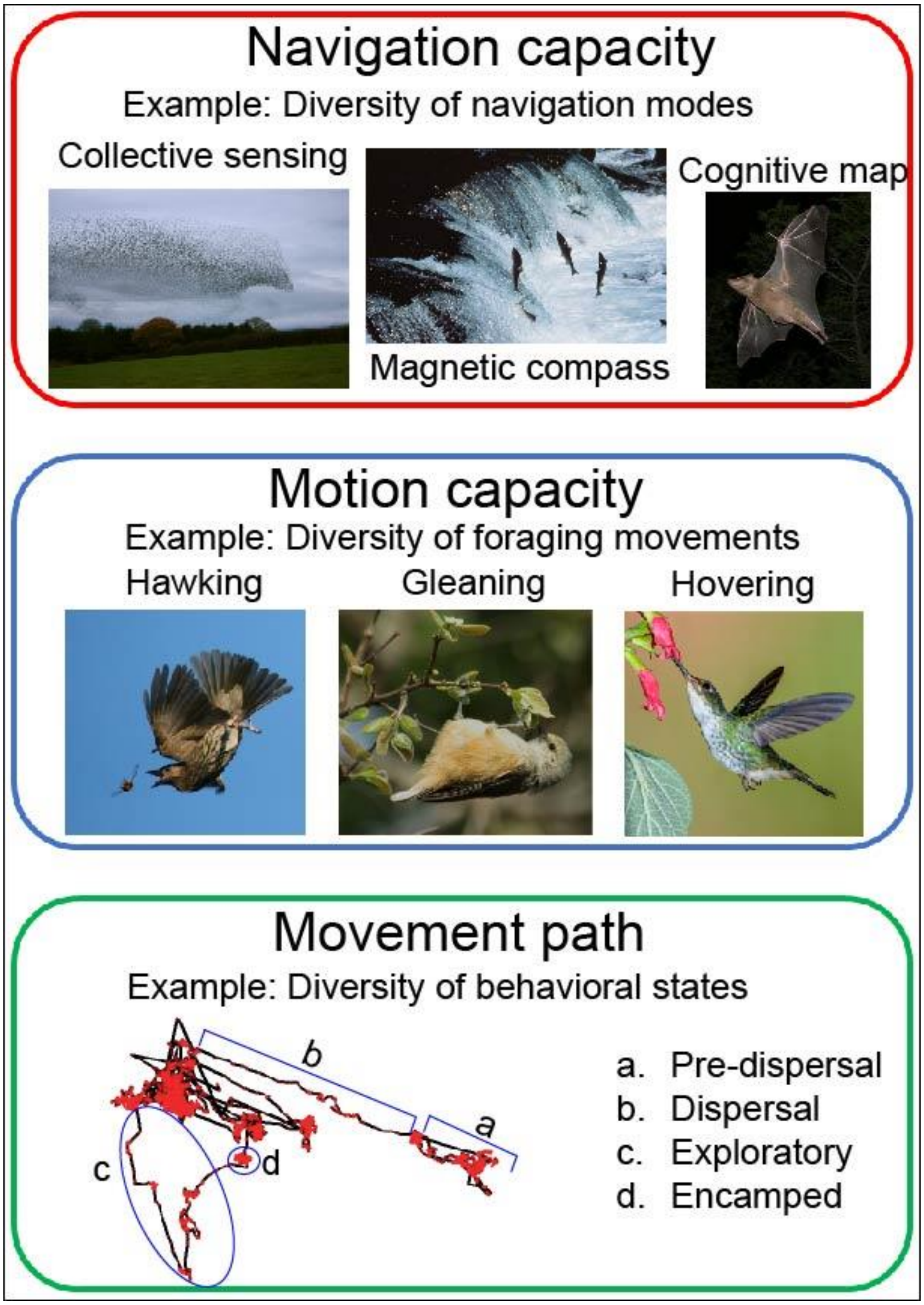

Figure 2: Examples of movement traits and metrics that can be used to characterize movement diversity according to the Movement Ecology Framework (Nathan *et al.* 2008). Image credits (clockwise from top left): © ad551; © USFWS Pacific; © Zoharby; © Andy Moffrew; © Alan Manson; © Mdk572. Example "Movement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

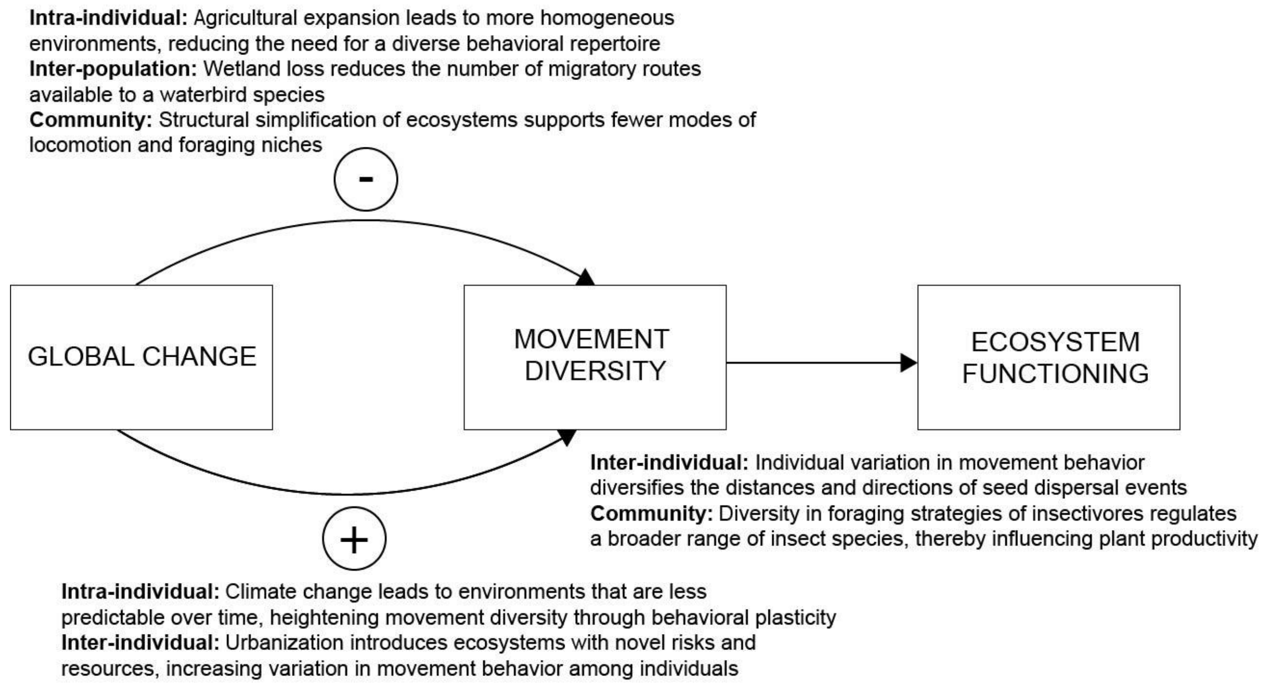

Figure 3: Movement diversity at the nexus of global change and ecosystem functioning, including hypothesized relationships among the three components.

Panels

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) influence 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 and navigation capacity) may not pertain to each level of organization. For example, modes of locomotion and navigation are normally ascribed to species but not individuals. In addition, environmental factors and the internal state are causes 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 have not yet been applied to biodiversity monitoring.