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Macroecological constraints on species' 'movement profiles': Body mass does not explain it all

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Abstract

Aim: Animals couple habitats by three types of movement: dispersal, migration, and foraging, which dynamically link populations, communities, and ecosystems. Across these types, movement distances tend to correlate with each other, potentially reflecting allometric scaling with body mass, but ecological and evolutionary species' traits may constrain movement distances and weaken these correlations. Here, we investigate multivariate "movement profiles" to better understand patterns in movement across movement types, with the aim of improving predictions in ecology from populations to ecosystems.

Location: Global.

Time period: 1945–2019.

Major taxa studied: Vertebrates.

Methods: We synthesized distances of all three movement types (dispersal, migration, and foraging) across 300+ vertebrate species and investigated how the relationships between movement types and body mass were modified by evolutionary history and trophic guild.

Results: We found that the strength of relationships between movement types and body mass varied among taxa and trophic guilds, for example, strongly positive for mammals but weak for birds, or positive across trophic guilds for foraging and dispersal but not migration. Notably, movement profiles interacted with the effects of shared evolutionary history and trophic guild to diminish covariance between movement types.

Main conclusions: Overall, we find that movement types with distinct ecological consequences (foraging, migration) are often correlated, although some species seem able to overcome biomechanical, evolutionary, and metabolic constraints by reducing correlations among movement types. This integrative assessment of movement can improve ecological prediction by allowing estimation of unobserved movement distances for parameterization of models based on estimation of other movement types.

KEYWORDS
body mass, ecology, metacommunity, movement, spatial use properties

1 | INTRODUCTION

The movement of individual organisms is a key mechanism explaining the persistence of populations (Levins, 1969) and the structure of ecological communities (Leibold et al., 2004; MacArthur & Wilson, 1967) in spatially heterogeneous environments. Constraints on movement affect the flow of energy, matter, and information between 'donating' and 'receiving' ecosystems (Loreau et al., 2003). Movement occurs over at least three different scales, each to meet particular fitness demands: (1) animals move to *forage*, avoid predation, and acquire resources within a seasonal home range; (2) animals *disperse* out of their natal home range to find higher quality mating opportunities and resources; (3) animals *migrate* between seasonal home ranges to reproduce, thermoregulate, and track broad-scale variation in resources and predation. Each of these three movement types occurs at distinct temporal and spatial scales and resolutions (Box 1). Together, dispersal, migration, and foraging combine to create a multivariate 'movement profile' (Figure 1c–e, a subset of 'spatial use properties' summarized by Guzman et al. [2019]). Quantifying movement profiles provides a basis for parameterizing scales of habitat coupling in metacommunity and landscape models that link spatial dynamics to biodiversity observations.

Variation of movement profiles among taxa and body mass is expected from existing movement theories. At the individual level, movement is guided by navigation capacity (termed "spatial information processing" in Guzman et al., 2019), motion capacity, and internal state (Nathan et al., 2008), including breeding status (Beardsell et al., 2021). While internal state, for example, hunger level or illness, will feedback on an animal's propensity to move, biomechanical traits such as body size will have a greater influence on motion capacity. Biomechanical and metabolic constraints may impose covariation among the distances associated with multiple types of movement. Specifically, the total distance an animal moves is the product of their velocity and duration of movement (Peters, 1986). If movement types simply differ in their duration of movement (e.g. migration is just a longer form of dispersal, Box 1), then as a null hypothesis we expect the spatial scales of the three movement types to covary strongly and to scale with body mass (Hein et al., 2012; Peters, 1986, Figure 1a). However, being capable of moving long distances does not necessarily translate to a large spatial displacement, for example, in the case of the tree swallow (*Tachycineta bicolor)* which forages across large home ranges (Stapleton & Robertson, 2006) but disperses short distances (Shutler & Clark, 2003). Different mechanisms may diminish the covariance between movement types and depart from body mass scaling by modifying the velocity or duration of movement separately for each movement type; we propose two hypotheses alternative to our null hypothesis below.

Our first alternative hypothesis, the 'shared evolutionary history hypothesis' (hypothesis 1), is that evolutionary history can explain variation in the covariance between movement types not explained by body size (Figure 1b,Ha 1). Under the null hypothesis, the evolution of traits related to movement should be constrained by the animal's body mass (and thus metabolic rate) and the time it takes to locate the resource of interest, in addition to resource dispersion and renewal rates. Time and distance moved can depend on body mass by, for example, constraining prey size and complexity of sensory organs and thus perceptual range (Mech & Zollner, 2002). However, if there are other unmeasured variables that influence movement profiles, for example, behavioural adaptations to the movement environment or other ecological conditions, or if body mass evolves faster or slower than the morphological traits that influence movement distance, and if these have phylogenetic signals themselves (Uyeda et al., 2017), the scaling relationship between body mass and movement profiles may vary among clades. This could lead to departures from the expected scaling of movement with body mass associated with our null hypothesis.

Our second alternative hypothesis (hypothesis 2), the 'trophic guild hypothesis', is that movement may be constrained by trophic position within food webs (Figure 1b,Ha 2). The duration of movement is linked to resource intake rate, which comprises the ratio of predator and prey body sizes, resource abundance, and the ability to detect prey (Beardsell et al., 2021; Rizzuto et al., 2018). The total duration of movement required to locate resources, and therefore movement distances themselves, should thus differ for foraging, dispersal, and migration. Specifically, intake rates, attack rates, and predator–prey body size ratios vary with trophic guild (i.e., herbivore, insectivore, etc.: Barnes et al., 2010, Tucker & Rogers, 2014), and as a consequence, individuals of certain trophic guilds (e.g., carnivores) may be forced to move across longer distances to meet energy requirements (Harestad & Bunnel, 1979). Theoretical predictions from trophic metacommunity models suggest that predators disperse greater distances than their prey to persist under patch dynamics (Leibold et al., 2004), yet predictions say little about other movement types. Empirical estimates of the relative spatial extents of different movement types are required to extend spatial diversity theories (e.g., metacommunity ecology, spatial coexistence theory) into a multi-trophic context, where interactions (e.g., predation, mutualism) are often realized between species with vastly different body sizes, ecologies, and evolutionary histories (Guzman et al., 2019). Finally, a third alternative is that movement through certain physical media (air, water, and land) diminishes covariances between movement types (or in other words, weakens the signal of allometric scaling); as we will discuss below, we were unable to test this hypothesis formally for reasons that were impossible to know a priori.

We tested our hypotheses using synthesized movement data from databases and published studies for 322 species of animals, including data for their body mass and movement distance while foraging, migrating, and dispersing. We also gathered data on movement media, trophic guild, and taxonomic class. Through our data collection process, it became apparent that available data could not be used to disentangle the effects of medium and taxonomy (i.e., most of the flying animals we found were birds, and most of the land moving animals were mammals), therefore from here onwards we integrated hypotheses 1 and 2, with phylogenetic signal in movement media being one trait that might result in support for shared

BOX 1 Movement types uniquely affect ecological dynamics.

Foraging refers to movement to acquire resources within a species' home range, structuring trophic interactions and competitive interactions. Larger animals and those at higher trophic levels may forage over larger areas to meet resource requirements, and in doing so, connect multiple habitats occupied by the organisms that they consume (McCann et al., 2005; McCauley et al., 2012). Of the movement types considered, foraging generally occurs at the shortest distances (Guzman et al., 2019). Likewise, foraging movements occur most frequently, up to multiple times per day. Resource quality within a habitat patch affects the distance and duration of movement (Charnov, 1976), where organisms foraging within low-quality or high-variability habitats move more often than those in high-quality or low-variability ones. Similarly, generalist species may not need to move as often or far as specialists. Competition within a trophic level may also be influenced by foraging movements. For example, movement into or out of an area may induce or release the negative effects of one population on another's growth rate via competition over shared resources or enemies (Amarasekare, 2008). Here, we use home range size as a proxy metric for foraging movement, because it encompasses foraging movements and is most consistently measured for multiple taxa.

Dispersal refers to individuals' movement when there are consequences for gene flow (Ronce, 2007) and typically occurs once or very few times in an organism's lifespan. Its most common forms are natal dispersal and breeding dispersal (e.g., Paradis et al., 1998, Sutherland et al., 2000). Species vary in the demographic importance of each of these types of dispersal. For example, dispersal may be widespread among individuals within the natal stage followed by a more philopatric adult stage, may be sex biased, or may occur at any life stage as a response to population density or suboptimal conditions (Clutton-Brock & Lukas, 2012; Shutler & Clark, 2003). Interspecific variation in dispersal distance is generally greater than for the other forms of movement (e.g., blue sharks >7500 km vs. common musk turtle <100 m [Jenkins et al., 2007]). Dispersal distances within species often display strongly right-skewed distributions, such that most individuals disperse short distances, and a few disperse very far (Nathan et al., 2003). Dispersing individuals can colonize habitat patches that were previously unoccupied, increasing the geographic range of that species (Holt & Keitt, 2005), or they can move to different areas of an occupied range, thereby demographically and genetically connecting populations. Because of this role in population dynamics, dispersal is the most commonly considered movement type in population and community ecology (Hubbell, 2001; Vellend, 2010). Importantly, "immigration" and "emigration", when used in the context of population genetics and community ecology, usually refer to dispersal into or away from a habitat patch (as opposed to actual "migration").

Migration refers to cyclical (e.g., seasonal) movements to track resources or mates and thus has a regular and unique temporal structure. Migration ranges from hundreds of metres (for amphibians accessing breeding ponds) to hundreds of kilometres (ungulates tracking food). Migration occurs one or more times in an organism's lifetime, depending on a species' life history. Rather than connecting different populations, it connects different habitats used by the same population, as well as places along a migratory route. Migration is a necessary strategy for persistence (Sinclair, 2003) but remains understudied in metapopulation and metacommunity ecology, despite its trophic and competitive effects on donor, recipient, and en-route communities through which animals move (Cohen & Satterfield, 2020). Instead, migration is of particular interest to ecosystem and meta-ecosystem ecology, as migratory species can transport nutrients over vast distances, affecting the functioning of far-flung ecosystems (Bauer & Hoye, 2014; Gounand et al., 2018). In addition, migratory movements are often undertaken by entire populations or aggregations of animals, which can engineer the timing and magnitude of ecosystem dynamics such as primary production (Geremia et al., 2019) or create large, temporally discrete pulses of nutrients (Subalusky et al., 2017).
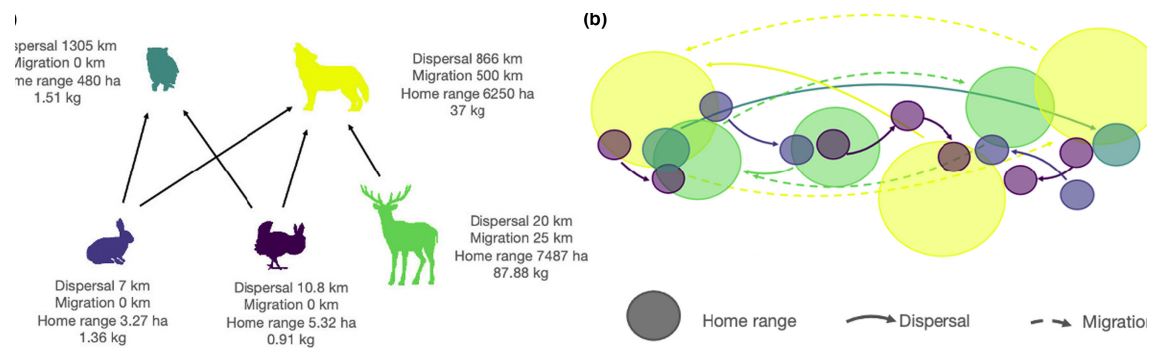
BOX FIGURE 1. Understanding the consequences of differences in forms of movement is an open area of research in ecology. Doing so requires identifying how forms of movement vary across ecological communities such as food webs. For example, a hypothetical food web with three herbivores and two carnivores shows potential variation in each of the forms of movement and therefore spatial scales. In this study, we take the first step towards this synthesis and present the variation of movement distances across trophic guilds. (a) Each species has its own mean dispersal, migration, foraging (home range) distance, and body size. (b) Each of the three types of movements influences when and where members of the food web interact.
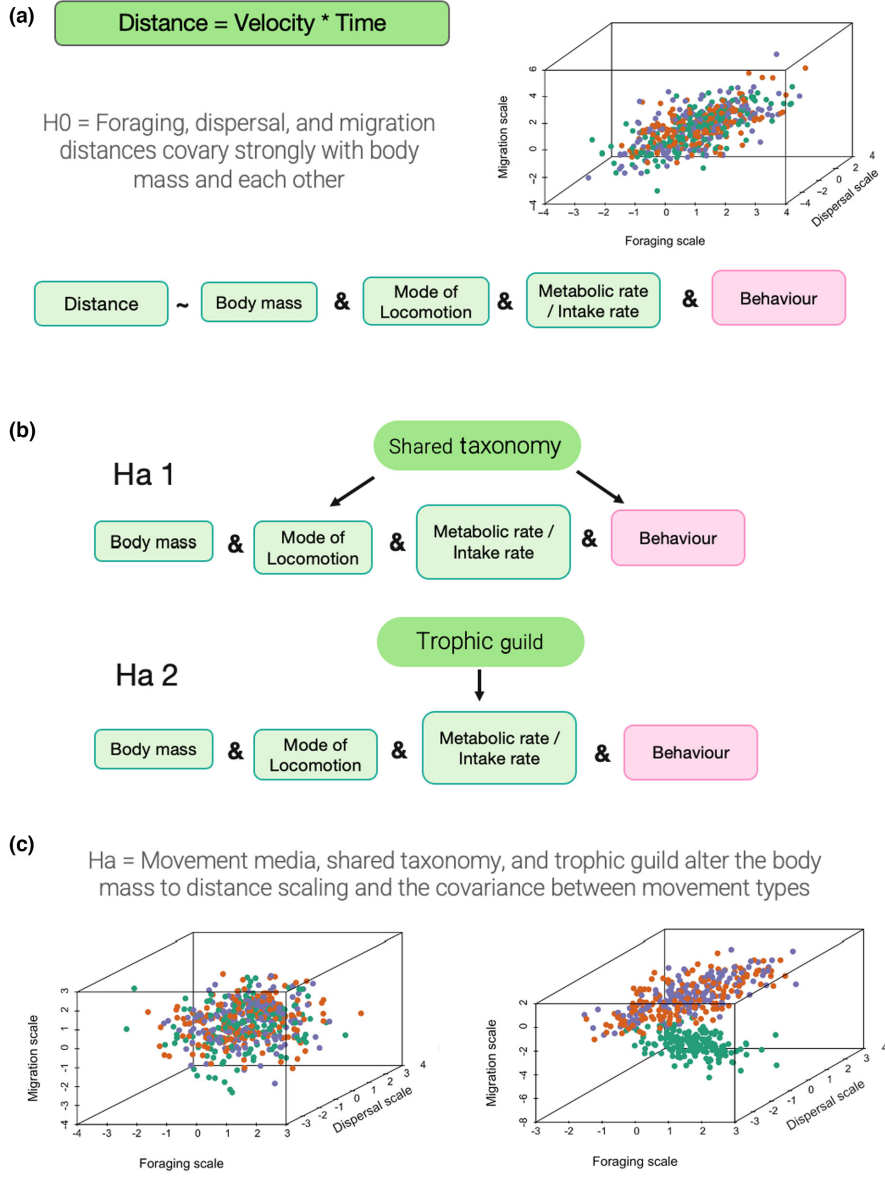
(a)

Distance = Velocity * Time

H0 = Foraging, dispersal, and migration distances covary strongly with body mass and each other

Distance ~ Body mass & Mode of Locomotion & Metabolic rate / Intake rate & Behaviour

(b)

Ha 1

Shared taxonomy

Body mass & Mode of Locomotion & Metabolic rate / Intake rate & Behaviour

Ha 2

Trophic guild

Body mass & Mode of Locomotion & Metabolic rate / Intake rate & Behaviour

(c)

Ha = Movement media, shared taxonomy, and trophic guild alter the body mass to distance scaling and the covariance between movement types

FIGURE 1 If all movement types are constrained by body mass, then we expect covariance across all three movement types, with each point representing a species (a). (b) Hypothesized constraints on movement distance (shared evolutionary history and trophic guild) may diminish the covariance between movement types. (c) Hypothetical 3D scatterplots demonstrate that this departure from covariance can occur in different ways. See also Table 1. Each of these three movements may be influenced by behaviour (pink boxes). We did not explicitly test the role of behaviour, even though it may interact with other hypotheses.

evolutionary history. If our null hypothesis that movement distance scales with body mass is supported, the covariance between movement types should disappear when we account for body mass with a quarter-power scaling exponent. Deviations from this expectation can be explained by accounting for movement medium, evolutionary history, or trophic guild (Figure 1). Many ecological models rely on organism movement to connect ecological dynamics occurring at different spatial and temporal scales (e.g., McCann et al., 2005). To further improve predictions in ecology from populations to ecosystems, we need a better understanding of how to estimate distance of the three movement types when data on each movement type for each species of interest are not available, as is the case for most species. Our approach is intended to synthesize estimates of movement distance for a variety of species and to help ecologists better understand whether an observed distance for one movement type can be used to estimate distance for another type in the absence of empirical observations.

2 | METHODS

2.1 | Data sources

We synthesized observations of movement distance for each movement type for species comprising major vertebrate taxonomic groups, a wide range of body masses, and representing aquatic and terrestrial life histories. While organisms can also differ in the velocity or duration of their movement to forage, migrate, and disperse (Figure 1), this type of data is less readily available, and therefore, we focus on the movement distance only. We drew upon existing databases and individual empirical studies (see Supplementary References). We drew upon home range databases for mammals and birds (Armstrong, 1965; Tamburello et al., 2015) and amphibians, migration databases for all taxa (Hein et al., 2012; Trochet et al., 2014), and dispersal databases for reptiles and amphibians (Jenkins et al., 2007; Trochet et al., 2014) and mammals (Santini et al., 2013).

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TABLE 1 Table with listed hypotheses.

Hypothesis	Description	Prediction	Model
H0: Body size, Figure 1a	Covariance between movement types results from allometric scaling	Positive covariance between movement types and body size	M0
H1: Shared evolutionary history hypothesis, Figure 1b,Ha 1	Covariance results from shared taxonomic history	Expect taxonomy to decouple covariance between movement types, e.g., phylogenetic inertia	M1
H2: Trophic guild hypothesis, Figure 1b,Ha 2	Foraging movement should be linked with trophic guild, as carnivores may forage over larger distances. Other movement types may not be affected by trophic guild	Expect diet to decouple covariance between foraging and other movement types, e.g., higher trophic levels moving farther	M2

For species to be included in our dataset, an estimate for each of the three movement types and body mass had to be available.

We also conducted a systematic search using Web of Science Core Collection (licensed to the University of British Columbia) that filtered by English language, article document types, and citation indices from 1900 to 2019. We used the following search terms: (Set 1: Topic = (migration OR dispersal OR home range); Set 2: Topic = (meta-analysis OR database); Set 3: Set 1 AND Set 2). Our search included the following categories: behavioural sciences, biodiversity conservation, biology, ecology, entomology, evolutionary biology, fisheries, limnology, marine freshwater biology, ornithology, and zoology. If individual values were found from both existing published databases and from our Web of Science search, we chose the former. Finally, to fill in individual missing values (e.g., the dispersal range of a species for which we had already found values for home range size and migration distance) after Web of Science results were exhausted, we used Google Scholar, IUCN, Encyclopedia of Life (EOL), Animal Diversity Web (ADW), and included government reports and theses alongside peer-reviewed articles. Each Google Scholar search was confined to the top 50 returned items to standardize search effort.

2.2 | Data standardization

Decisions were made during data collection to ensure high data standards and comparability across species, for each movement type. Dispersal distance was collected from experimental studies, observational studies, and meta-analyses. We only included species for which we could find adult median or mean dispersal distances (units: kilometres), excluding juvenile, propagule, and natal distances. When mean, median, or mode distances were not provided, maximum dispersal distance was used (Nathan et al., 2003; see Supplemental Tables S1 and S3 for a breakdown of data availability). Our largest dispersal database, published by Jenkins et al. (2007), included only maximum dispersal distances, and several databases reported maximum for some species and mean for others. Although it is unclear how close reported maximums are to means, because they are typically based on relatively few observations, values are unlikely to represent extremes of a species' dispersal kernel. When multiple means were provided within any one study, we calculated an average distance weighted by sample size. Active dispersal distances were chosen over passive dispersal, for example, in the case of larval fish or amphibians. In rare cases ($n=9$), movement was estimated from maps (i.e., map of distance between two populations with gene flow to estimate dispersal). Migration distances (units: kilometres) were collected from experimental and observational studies. We assumed a migration distance of 0 km for non-migratory species. When more than one migration distance was provided by the same source, the largest distance was used. The weighted average was also used when migration distances were different between multiple individuals, or between males and females. Likewise, foraging distance, estimated as the diameter of the home range area (assuming a circular home range, units: kilometres), was also collected from experimental and observational studies. Similar to migration, the largest foraging distance listed was used if more than one was given for a species, as well as the average between males and females.

We collected data on four predictors of movement that aligned with our hypotheses: body mass, movement media, taxonomic classification, and trophic guild. Adult body weight measured in mass (kg) was collected for all species (Armstrong, 1965; Harestad & Bunnel, 1979; Tamburello et al., 2015; Trochet et al., 2014). The average was used when multiple body weights were available. Similarly, the average was taken for male and female measurements. We characterized each movement type as occurring on land, water (aquatic or marine), air, or a combination of these media. Movement media were inferred for species with unambiguous locomotion. For example, the medium a hummingbird uses to locomote is air, and for a shark it is water (marine). For most species, locomotion medium was confirmed with a literature search. A combination of media was recorded if more than one medium significantly contributes to the movement of an animal. For example, an amphibian that reproduces in the water but lives on land might have land as a medium of dispersal and migration and "land_aquatic" as a foraging medium. If a species engages in a form of locomotion only over extremely short distances compared to another form of movement, that movement medium was not considered. For example, a grouse that forages on the ground and only flies in short bursts to avoid predators would have land as its medium. The trophic guild for each species was classified as herbivore, omnivore, invertivore, or carnivore. Data were gathered from the data papers and meta-analyses the movement data had been extracted from, where possible, and otherwise

from the Encyclopedia of Life (https://eol.org), Animal Diversity Web (https://animaldiversity.org), or primary literature searches. Following Hein et al. (2012) and Tamburello et al. (2015), we grouped species by taxonomic class and order. We obtained class and order for each species using the R-package *taxize* using NCBI and ITIS databases (Chamberlain & Szöcs, 2013). We created a phylogeny using the R-package *datelife* (O'Meara et al., 2023). As mentioned previously in relation to our third hypothesis, most of these predictors are not completely independent, such that the species that move through air in our assembled dataset are largely the same species that are birds. We tested for potentially confounding associations among predictor variables using contingency tests (Table S5). After the data gathering process, our contingency tests showed that we did not obtain data on sufficient species to successfully disentangle the movement media and taxonomic hypothesis at the level of class; therefore, we only present results from the Bayesian regressions models containing taxonomy but note that movement media could explain the same patterns.

2.3 | Statistical analyses

2.3.1 | Descriptions of data

First, we calculated the pairwise covariance between log10-transformed movement distance and log10-transformed body mass for each movement type. We log10-transformed our data to satisfy the assumption of normality.

2.3.2 | Covariance between movement types

Then, we explored correlations among movement distances among different movement types, and whether these correlations were related to shared evolutionary history or trophic guild. We did so with principal component analyses (PCAs) for the tri-dimensional movement profiles of species using the *vegan* (2.5.7) (Oksanen et al., 2022) and *stats* (4.0.5) packages in R (4.0.5) (R Core Team, 2023). For each hypothesized mechanism, we conducted PCAs on (i) movement distances (standardized and log10-transformed) and (ii) standardized residuals from a regression of movement distance as a function of log10-transformed body mass. This second PCA was included to test our null hypothesis that movement types will be correlated due to underlying body mass scaling relationships.

2.3.3 | Macroecological constraints on movement profiles

Next, we estimated how each movement type was associated with body mass and whether the relationship between the distance of each movement type and body mass was better explained by including other variables in the models. We used Bayesian-generalized linear

regressions using Stan through the *brms* package (Bürkner, 2018). We used a lognormal response distribution for movement distances to satisfy assumptions of normality. We used an identity function for dispersal and foraging distance because these variables were continuously distributed and bounded at zero. We used a hurdle lognormal response distribution for migration because it allowed us to model non-migratory species (value of 0), as well as the distribution of the migratory species (values above 0). A gamma link function provided the same results (not shown), but the lognormal distribution was a better fit. For each hypothesis, we tested a univariate model for distances associated with each movement type as a function of body mass (Model 0 – null hypothesis).

We modelled the relationship between body mass and movement using random effects to vary predictor variables and test hypotheses (see Table 1). The null model (Model 0) was compared to models including shared evolutionary history (Model 1 using taxonomic class for Model 1.1, phylogeny for Model 1.2 and taxonomic order for 1.3) and trophic guild (Model 2) with intercept and slope random effects. We also included a fixed effect term for the year the study reporting the movement data was published to account for changes in methodologies used as technologies for quantifying movement through time (e.g., technologies that allow for long-distance tracking). We used a fixed effect to directly test for the effect of study year, rather than using a random effect to simply account for variation caused by study year. Unfortunately, not all databases reported the year of the original study, and therefore all we could use was the year the database was published. Two of our dispersal databases (158 entries, 49% of dispersal data) did not report the year of the original study. One of these studies, published by Jenkins et al. (2007), contained 143 entries alone and spanned terrestrial vertebrates. The second, published by Tittler et al. (2009), contained 19 entries and focused on songbirds. Two migration databases likewise did not report the year of the original study (24 entries, 7.5% of migration data). Both studies reported migration distances of birds and contained 6 and 18 of our entries (La Sorte et al., 2013; Møller, 1987, respectively).

Models 1.1, 1.2, and 1.3 test the effects of shared evolutionary history through class (1.1), phylogeny (1.2), or order (1.3). Results of Model 1.1 (class) and Model 1.2 (phylogeny) are presented in the main figures, and results for model 1.3 (order) are in the Supplementary Materials. We used the natural logarithm of body mass for all models. We fit the following models:

The null model, Models 0 (M0), tests the effects of body mass, where β represents fixed effect coefficients, εd_i and εf_i represent lognormally distributed error terms for the dispersal and foraging models, respectively, and εm_i represents the hurdle lognormally distributed error term for the migration model:

$$dispersal_i = \beta_0 + \beta_{bodymass[i]} + \beta_{studyyear[i]} + \varepsilon d_i$$

$$\varepsilon d_i \sim LogNormal(\mu, \sigma^2)$$

$$foraging_i = \beta_0 + \beta_{bodymass[i]} + \beta_{studyyear[i]} + \varepsilon f_i$$

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$$\varepsilon h_i \sim LogNormal\left(\mu, \sigma^2\right)$$

$$migration_i = \beta_0 + \beta_{bodymass[i]} + \beta_{studyyear[i]} + \varepsilon m_i$$

$$\varepsilon m_i \sim HurdleLogNormal\left(\mu, \sigma^2, \eta\right)$$

Models 1–2 followed a similar formulation, with random slope and intercept terms ($\alpha_{0constraint}$ and $\alpha_{bodymassconstraint}$ for intercept and slope, respectively, in model formulation below) added for each constraint and the same error structure as model 0. By using random effects, each category (i.e., taxonomic category or trophic guild) within a hypothesis received a slope and intercept estimate, but all the slopes or intercepts across a model were drawn from the same distribution. Models M1 and M2 (shared evolutionary history and trophic guild, respectively) followed the formulation:

$$movementtype_i = \beta_0 + \beta_{bodymass} + \beta_{studyyear[i]} + \alpha_{0constraint} + \alpha_{bodymassconstraint}$$

The phylogenetic model has the same formulation, where the species-level observations are correlated as specified by the covariance matrix calculated from the phylogeny. Full-model formulations can be found in the supplemental materials. All models used weakly informative priors (See Appendix S1) with four chains, using defaults for warm-up with no thinning. In order to improve model convergence, the acceptance rate (adapt delta) was increased to 0.995 and the maximum tree depth of the NUTS sampler to 15. Model convergence

was assessed through visual inspection and where $\hat{R} = 1$. M0 used 3000 iterations for each submodel; M1 used 3000 iterations for each submodel l; M2 used 5000 iterations for the foraging and dispersal submodels and 4000 iterations for the migration submodel. To assess the performance of Models 1 and 2 compared to the null model, we compared the leave-one-out information criterion (LOOIC) across each model set defined by movement type. Finally, as a test of robustness of the hurdle model, we performed a second set of analyses on migratory and non-migratory animals separately. Figures were generated using *ggplot2* and *PNWColors* packages (Lawlor, 2020; Wickham, 2016). All data and code are deposited in Zenodo.

3 | RESULTS

3.1 | Descriptions of data distributions

We found data for all three movement types for 320 taxa. Birds and mammals were over-represented in the final dataset relative to other taxa, with 159 and 116 species, respectively, and the remaining 47 species were amphibians, reptiles, and sharks. Migration distances were strongly bimodal within groups, with 138 species being entirely non-migratory (i.e., migration distance of zero, Figure 2), while dispersal and foraging distances were only slightly bimodal (i.e., low and high modes). The movement distances within guilds were
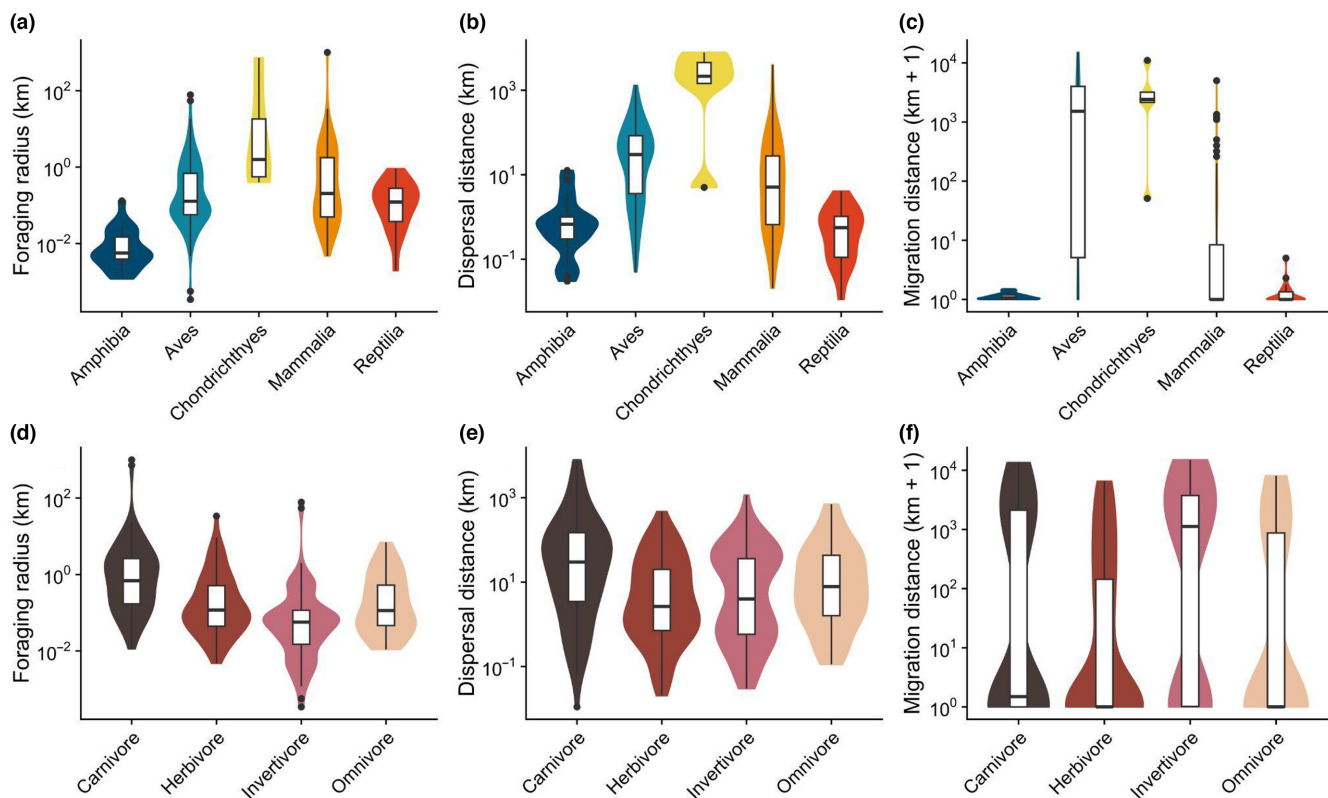

FIGURE 2 Distribution of movement types by taxonomic class (a–c) and trophic guild (d–f). *y*-axes were log10-transformed, except for migration which was log10+1-transformed. See Supplemental Figure S1 for data distributions for different movement media.

primarily unimodal, with bimodality emerging when considering all groups together. Of the 320 dispersal distances, 185 were maximum dispersal and 135 were mean, median, or mode (hereafter for brevity: mean) of dispersal. There was a fairly even split between the two categories for birds. However, despite efforts to prioritize mean dispersal distances, amphibians, reptiles, and sharks are skewed heavily towards maximum values for taxonomic class (Table S1). Similarly, for trophic guild, between 45% and 65% of entries were maximum dispersal distances within each group (Table S2). We estimated a post hoc modification of our null model that included type of dispersal measurement as a random effect with random slope and intercept. We found that slope and intercept values overlapped with the original null model that did not include dispersal type (Table S3). Thus, we present the results that do not include dispersal type as a random effect.

Initial examination of evidence for each potential constraint in the absence of the others indicated that different taxonomic groups had different scales of movement (Figure 2a–c); and that unlike for taxonomy, species belonging to different trophic guilds had substantial overlap in their distribution of movement distances (Figure 2d–f). Our contingency test found a positive association between predictor variables. In particular, birds and reptiles skew towards the carnivore trophic guild and amphibians skew towards invertivores (Table S5). While we did not formally test this hypothesis, we also examined the data distributions of movement distances by movement medium and found that species dispersed and foraged over greater distances in water than on land but migrated further through air than in the other two media (Figure S1).

3.2 | Covariance between movement types

We found partial support for our null hypothesis that body mass is responsible for covariation between movement types (Figure 3); however, body mass was not the only source of this covariation. We drew upon two pieces of evidence to test this null hypothesis. The first line of evidence is the pairwise covariance values between movement types and body mass. We found high pairwise covariance (c) between body mass and foraging distance ($c = 0.80$). Covariances were weaker between dispersal distance and mass ($c = 0.51$), dispersal and foraging distances ($c = 0.61$), migration and dispersal distances ($c = 0.60$), and migration and foraging distances (0.25), with almost no covariance found between mass and migration distance ($c = -0.20$, Figure 3). Second, we might expect that controlling for body mass would cause foraging and dispersal distances to become decoupled if body mass were the main cause of their covariance. Indeed, our PCA found this to be the case to an extent: dispersal and foraging distances covary (i.e., similar loadings on PCA axes 1 and 2; Figure 4; Supplemental Table S6) but less so when controlling for body mass (i.e., dissimilar loadings on PCA axes 1 and 2 in our analysis using the residuals of linear models of movement distance as a function of body mass). This difference occurred despite the inclusion of body mass having no effect on the total amount of variance

in the dataset summarized by the first two PCA axes (85% with body mass, 82% without body mass).

We found the strongest support for the 'shared evolutionary history' hypotheses, and less support for the 'trophic guild' hypothesis, as explanations of covariance among movement types (Figure 4). In all cases, separation happened primarily along PCA axis 1, as different groups generally represented species that moved more or moved less overall, as opposed to moving more or less for specific movement types. Nonetheless, one of our most striking observations is that controlling for body mass either reduces (e.g., taxonomy) or completely collapses (e.g., trophic guild) differences among groups that were otherwise pronounced on both PCA axes (Figure 4).

3.3 | Movement profile in three-dimensional trait space

Visualization of all three dimensions of species' movement profiles at once reveals not only covariance structures but also features that may reflect biological or physical constraints on movement. First, two major areas of the volume were unfilled by any species in our dataset: areas characterized by long foraging distances and short dispersal distances, and the converse, short foraging distances with long dispersal distances. Second, we observed that movement profiles for several species had extreme values relative to the rest of the dataset, most notably, four species: two with extreme distances for all movement types (i.e., *Physeter catodon* (Sperm whales; Mammalia), *Prionace glauca* (Blue shark; Chondrichthyes)) and two with exceptionally long (i.e., *Rangifer tarandus* (Reindeer; Mammalia) and short (i.e., *Asio flammeus* (Short-eared owl; Aves)) foraging distance for a given dispersal distance. Third, foraging radius had the widest range of values, spanning approximately 12 orders of magnitude, greater than dispersal (6 orders) and migration (5 orders), owing equally to extremely high (10^6 km) and extremely low (10^{-6} km) foraging distances. Importantly, movement distances in Figure 3 are shown in log space, highlighting differences in the orders of magnitude of movement differences. When considering the boundaries of our three-dimensional trait space, we found that foraging and dispersal distances had uneven boundaries, particularly for migrating species. In contrast, boundaries on migration distances were more defined, both at the lower bound (for obvious reasons, as several species do not migrate) and also at the upper bound.

3.4 | Macroecological constraints on movement profiles

Finally, we used hierarchical models with random slopes and intercepts to test how much variation was contained in the slopes within each group. We found that variation in foraging and dispersal distances was partially explained by body mass (M0: slopes: 0.52 ± 0.07 and 0.33 ± 0.09, respectively), while migration movement was not (slope: 0.06 ± 0.17, Figure 5, Table 2, Table S4). Model M1, testing
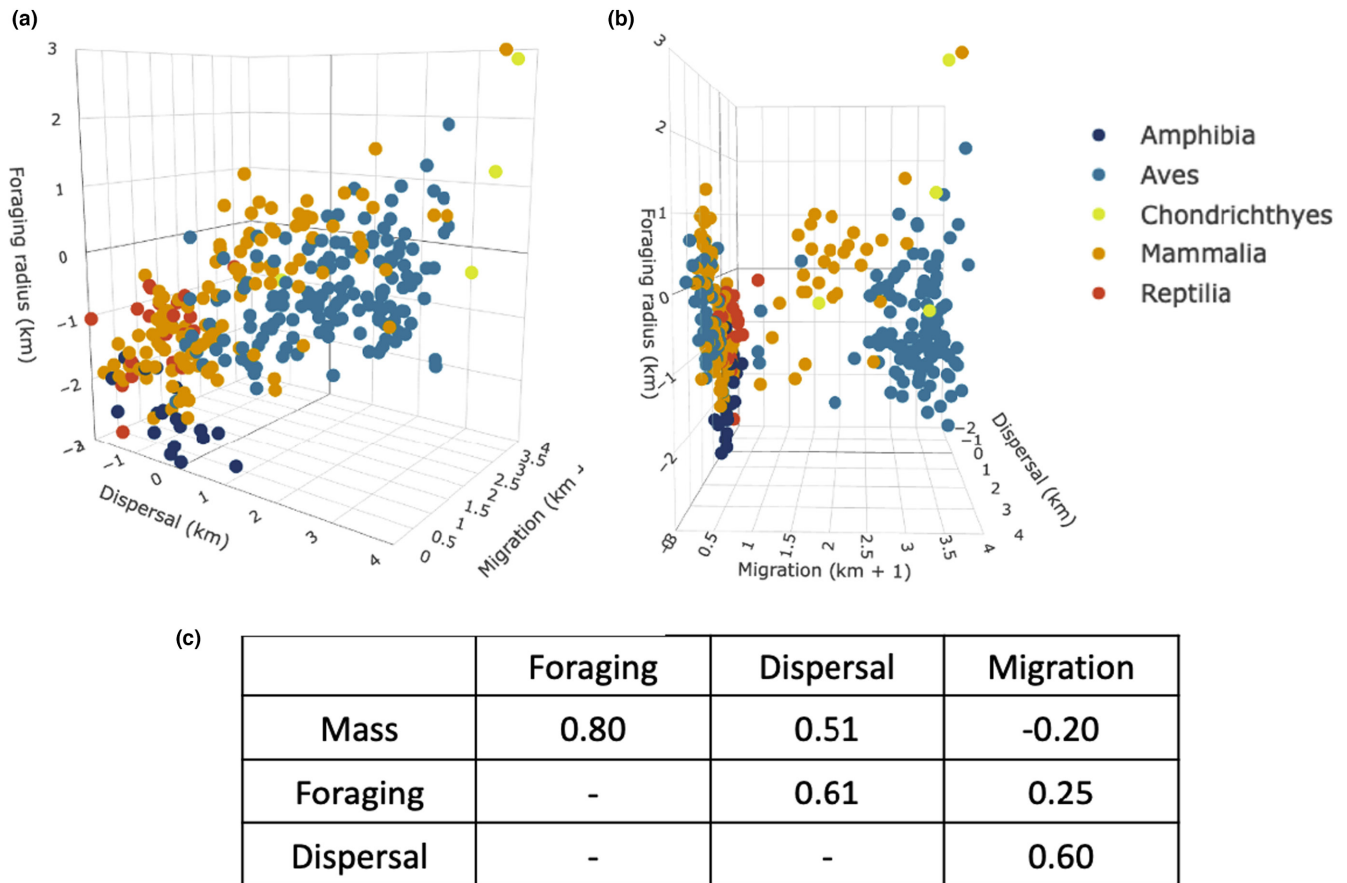
FIGURE 3 Panels (a) and (b) depict log10-transformed movement types (foraging, migration, and dispersal) on 3-axes for 320 species, shown from different angles. See https://sdstraus.shinyapps.io/3dplot/ for interactive plot. Panel (c) is the covariance matrix for each movement type and body mass. Migration values log10+1-transformed to account for non-migratory vertebrates.

the shared evolutionary history hypothesis, was the best performing model, with strong evidence of taxonomic constraints on movement distance (Figure 5a–c, Table 2). We found that movement distance increased with body mass for most taxonomic classes when considering foraging and dispersal movements, with dispersing amphibians as the only exception (Figure 5, Table S4). However, different classes varied in their relationships between body size and migration distance. We found positive slopes between body size and migration distance for mammals (0.51±0.15) and sharks (0.87±0.70), no relationship for amphibians (−0.01±0.59) or reptiles (0.39±0.57), and a negative relationship for birds (−0.15±0.14). Organisms belonging to different taxonomic orders within the same class tended to move similar distances with similar body-size scaling relationships (Supplemental Material, Figure S2). The order Galliformes (i.e., landfowl) was, however, one major exception to this observation (Figure S2, top right). We found positive relationships between body mass and foraging and dispersal distances for all trophic guilds except dispersing omnivores (Figure 5d–f, Table S4). However, there was no relationship between body mass and migration distance for any trophic guild (Table S4).

As a check of robustness of our hierarchical models, we generated plots of the posterior predictive distributions and posterior means (Supplemental Figure S5), which demonstrate that our models fit the

data well, and we provide distributions of the posterior mean slopes from our hierarchical models (Supplemental Figures S6 and S7). We also ran each set of models separately for migratory and non-migratory species. We found that, overall, migratory species were driving the majority of our observations (Supplemental Figures S3 and –S4). Additionally, the covariance between body mass and foraging, body mass and dispersal, and foraging and dispersal is slightly higher for migratory species than for non-migratory species (Supplemental Tables S7 and –S8).

4 | DISCUSSION

Animal movement plays an important role in structuring ecological communities, but allometric constraints on covariances between different types of movement distances are unknown. Here, we collated a large database to address three possible constraints on animal movement, in addition to body mass, focusing on three types of movement (foraging, dispersal, and migration). Knowing the constraints on animal movement can help us to parameterize ecological models and better understand the role of movement at local, regional, and landscape scales.

Our results provide a more nuanced view of body size as a key trait that is positively correlated with all movement types, as is
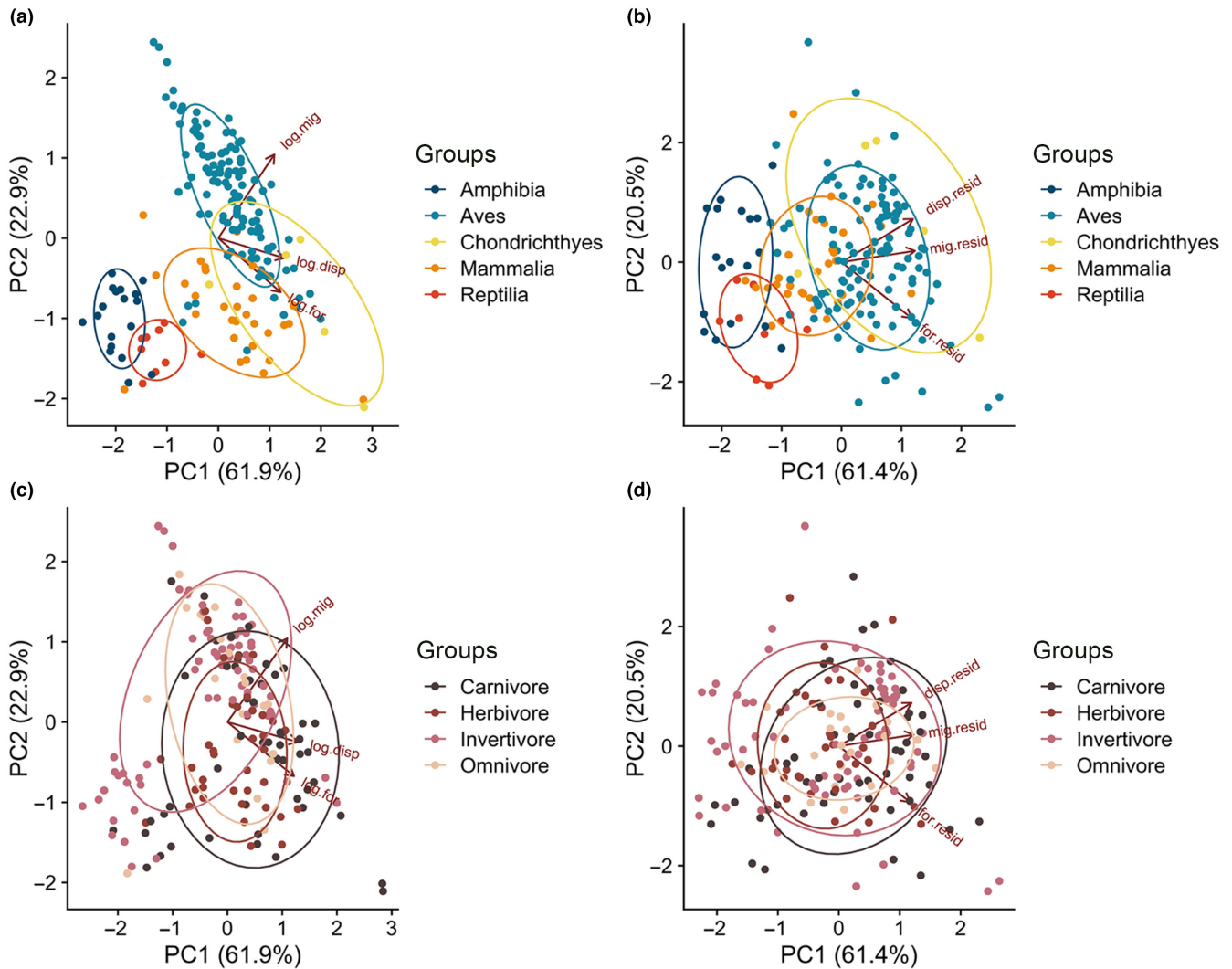
FIGURE 4 The left column (a, c) depicts PCA plots of standardized log10-transformed movement ("log.for" for foraging distance, "log.disp" for dispersal distance, and "log.mig" for migration distance in km, respectively). The right column (b, d) depicts PCA plots of the residuals of linear models of movement distance as a function of body mass. When accounting for body mass, groups still separate to some extent by taxonomic class, but not for trophic guild.

commonly assumed in other studies (e.g., Hein et al., 2012). Here, instead, body size was a strong predictor of dispersal and foraging distances, but not migration distance, and these covariances could be decoupled by shared evolutionary history and trophic guilds. Even though movement distance scaled positively with body mass for all three types of movement, the strength, slope, and even direction of that relationship depended on the taxonomic group or trophic guild. Notably, covariances between body mass and migration were much weaker for birds than for other groups, where long migrations can be undertaken by small-bodied animals with smaller foraging and dispersal distances.

4.1 | Shared evolutionary history hypothesis

Our analysis provides strong support for the hypothesis that movement distance is constrained by evolutionary history. Our shared

evolutionary history models had the best fit of our hierarchical models (Table 2). Shared evolutionary history modified the relationship between movement distances and body mass, and it accounted for more variation than trophic guild. This strong effect of taxonomy can also be driven by the media animals are moving in (i.e., land, water, and air). Despite collecting data on movement media, we were unable to disentangle the taxonomy and media hypotheses because most of the flying animals were birds (we were unable to obtain all forms of movement for bats and insects). Evidence of the decoupling of movement types was the strongest within migration where birds tended to migrate the greatest distances. Most mammals and reptiles do not migrate, but the distribution of their movement distances was highly right-skewed, such that a small handful of mammalian species (primarily ungulates) migrated extremely long distances. Dispersal distance followed a similar but less extreme pattern for each group, where sharks and birds disperse the farthest, followed by mammals, reptiles, and amphibians. We found that foraging distance did not separate
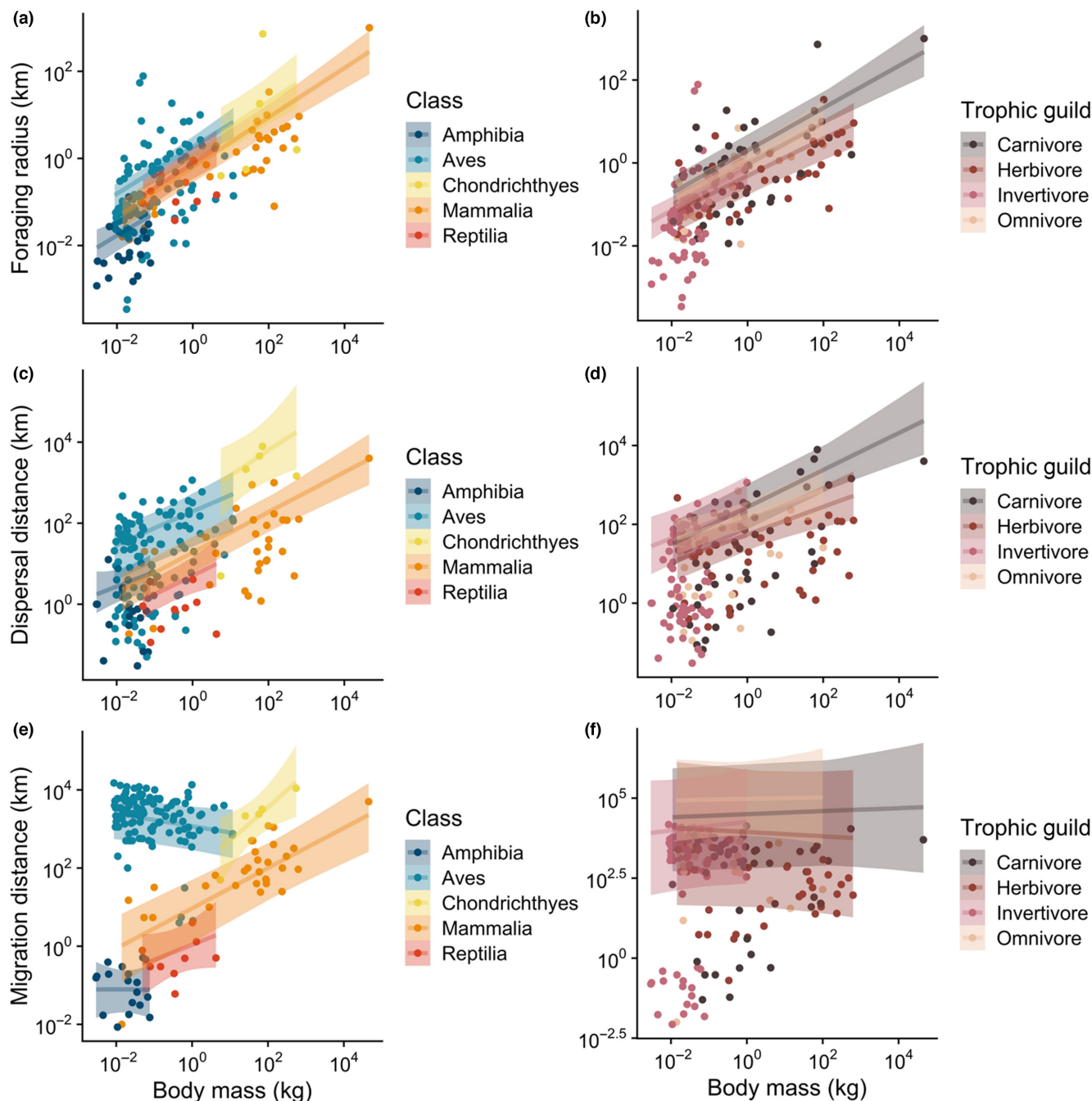
FIGURE 5 The relationships between mass and (a) foraging, (c) dispersal, and (e) migration for each taxonomic class. Relationships are generally positive, except for Aves. The relationships between mass and (b) foraging, (d) dispersal, and (f) migration for different diet categories. Relationships are positive for all diet types for foraging and dispersal, but weakly negative for migration. Shaded bands represent the expectation of predicted draws (95%).

strongly by class. This may suggest that migration is more reflective of upper physiological limits that are evolutionarily constrained, while dispersal and foraging are more labile. Dispersal and foraging could instead be constrained by, for example, population dynamics or selection on other traits (Burgess et al., 2016) and ecologically determined optimal foraging (Pulliam, 1974), respectively, and so do not display as strong of taxonomic signals. Supporting this idea is the total distance moved in each category, which is an order of magnitude larger

for migration (Figures 2 and 3). Also supporting this assertion is the plethora of specialized adaptations in the longest-distance migrators (Weber, 2009), though these adaptations are fairly labile within clades of birds (Pulido, 2007). For example, in our dataset, the bird Order Galliformes had a significantly lower migration intercept than other groups (Figure S2). This group, containing pheasants, prairie chickens, and other land fowl, is characterized by high wing-loading and low wing aspect ratios (Rayner, 1988), making them relatively weak flyers.

Movement type	Hypothesis	Model	LOOIC (SE)	Bayes R^2
Foraging	Null	M0	123.1 (87.4)	0.24
	Taxonomy	M1.1	85.9 (89.1)	0.18
	Phylogeny	M1.2	**55.1 (89.4)**	0.18
	Trophic Guild	M2	100.6 (88.4)	0.42
Dispersal	Null	M0	2725.2 (93.5)	0.38
	Taxonomy	M1.1	2594.2 (91.9)	0.53
	Phylogeny	M1.2	**2554.2 (92.3)**	0.56
	Trophic Guild	M2	2702.3 (92.7)	0.53
Migration	Null	M0	3361.1 (147.3)	0.5
	Taxonomy	M1.1	3016.3 (142.3)	0.47
	Phylogeny	M1.2	**2996.2 (141.4)**	0.57
	Trophic Guild	M2	3362.5 (147.5)	0.5

TABLE 2 Model comparisons for Bayesian Regression Models including Leave-one-out AIC (LOOIC) with standard error and Bayes R-squared for each model set within movement type.

Note: **Bolded LOOIC** indicates lowest LOOIC score within the model set. See Table S1 for model coefficients.

4.2 | Trophic guild hypothesis

We found that the model including trophic guild was a better fit than the null models but to a lesser extent than for shared evolutionary history (Table 2). Our analysis found that both dispersal and foraging distances increased with body mass within all guilds (Table S4, Figure 5d–f). However, body masses are not evenly distributed across the trophic guilds. In our dataset, invertivores had the smallest body masses, omnivores and herbivores slightly larger, and carnivores representing the largest body masses. This is in contrast somewhat with the findings of Potapov et al. (2019) who found a relationship between trophic guild and body mass across groups for marine organisms, but not terrestrial or freshwater. However, the Potapov et al. (2019)'s study also considers invertebrates, including zooplankton and phytoplanktons, while our study only considers vertebrates. We found statistically similar slopes between trophic guilds when considering both foraging and dispersal (Figure 5b,d, Table S4). Conversely, all slopes were not significantly different than zero for migration (Figure 5f, Table S4), such that smaller organisms migrate the same distances as larger ones within different trophic guilds. Unlike the other two analyses described above, where aerial movement occurs primarily by birds (Aves), groupings in this analysis are influenced by shared evolutionary history. Trophic guild, while not entirely independent of shared evolutionary history, is less influenced by it (Table S5). As such, there are no distinct groupings of points for trophic guild as for taxonomy (Figure 3 interactive plot, Figure 4c). In our PCA, our finding of near complete overlap in trophic guilds when accounting for body mass suggests that movement distances are more strongly influenced by body mass than trophic guild (Figure 4d). This is in contrast to shared evolutionary history, in which groups are still separated along the principal components even after accounting for body mass.

A third a priori hypothesis that we were unable to formally test due to data limitations is that movement medium influences the covariance between movement types. Different media cause different energetic costs of movement, reflecting physical factors such as viscosity, drag, and gravity ("substrate penetrability", Shepard et al., 2013). Movement of a body requires that thrust (including lift) must overcome drag from medium viscosity, and the relative forces required for this differ for water and air (Vogel, 1996). Movement velocity can vary due to the mode of locomotion (i.e., flying, walking, swimming, etc.) and body mass, where velocity increases with body mass. Organisms that fly can reach higher maximum velocities than organisms that swim or run (Peters, 1986), and thus this mode is associated with longer distances (Hein et al., 2012). This may be in part due to the Reynold's number of the organism, a measure of inertia relative to viscous forces based on size and shape (Vogel, 1996). Larger animals tend to have larger Reynold's numbers, but these values can change depending on medium viscosity. Further, medium influences the energetic costs associated with the air, land, or water landscape, where inclines, drafts, and currents can all relieve or exacerbate the energetic cost of locomotion as well as its velocity (Gallagher et al., 2017; Shepard et al., 2013). Importantly, some species may use different media for different movement types, which may further erode the covariance between movement types.

4.3 | Constraint envelope

Beyond individual movement types, the distribution of movement profiles that we observed could be hinting at constraints on movement distance (i.e., unfilled traitspace in Figure 3). To consider this, we apply the concept of a 'constraint envelope' (e.g., Diniz-Filho, 2004). A constraint envelope is the boundary in phenotypic space between phenotypes with values that are evolutionarily accessible or inaccessible, with 'inaccessibilities' arising via trade-offs among functional trait dimensions and biophysical limits on any one dimension. Boundaries are difficult to ascertain with available data, such as when

sampling of taxa is inexhaustive, but constraint envelopes can be interpreted in the realm of probability rather than in the realm of possibility (e.g., some phenotypes are more represented than others). Exceptional taxa (i.e., outliers that move extremely long distances compared to similarly sized species) demonstrate that it is possible to break beyond those constraints, for example, in the case of blue sharks (*Prionace glauca*) which have the second largest foraging diameter in our dataset (723 km) but weigh only 70 kg. Importantly, the constraint envelopes we observe appear to differ among taxonomic groups, leading to uneven distributions when data are aggregated across taxa. Within taxonomic groups represented in our dataset, either biophysical limits or a lack of ecological necessity has prevented these groups from expanding their current range of movement distances, despite these expanded ranges being present in other taxa. We have made important observations for vertebrates, which should serve as a basis for a further examination encompassing a wider range of animals; including different taxonomic groups could increase the coverage of data in this trivariate volume. We have compiled the most comprehensive dataset that includes multiple movement types to date (e.g., other papers that comprehensively evaluate within a single movement type: Hein et al., 2012, Tamburello et al., 2015).

4.4 | Exceptions, caveats, and implications

We can further understand constraints on movement by examining exceptional species in our dataset, which reveal the potential importance of factors we did not consider or measure in our analysis. For some species, behaviour can constrain movement, for example, in the case of colonial birds like tree swallows, which cover large foraging ranges while exhibiting more philopatric dispersal. We did not explicitly include behaviour in our analyses, and behaviour likely interacts with shared evolutionary history and foraging guild to determine movement at different scales. For other species, exceptions to general observations may be bounded by physical limits. For example, sperm whales (*Physeter catodon*) have enormous foraging ranges, spanning 2000 kilometres, whereas other, smaller species (e.g., migratory birds) migrate on average over five orders of magnitude times farther than the diameter of their foraging range (a staggering ratio). If a sperm whale migrated at distances this many times greater than its foraging range, migration would exceed the circumference of the Earth. While sperm whales appear to be outliers in their order (Artiodactyla) in both body size and foraging range, they are also only one of two toothed whales included in the dataset, the rest of the order being land mammals. The other toothed whale, the common bottlenose dolphin (*Tursiops truncatus*), is two orders of magnitude smaller. We might expect that, if future work could fill in gaps in the available movement data, toothed whales have less constrained movement profiles than the rest of their order. Another potential confounding factor that we did not consider in our study is vertical movements undertaken by organisms that move in three dimensions. Returning to the sperm whale example, individuals regularly dive as deep as 1 km below the surface (Watkins et al., 2002)

and many birds migrate at high altitudes. Pressure gradients in these different media may alter constraints on movements, and organisms moving in these extreme environments may thus present as outliers. Differences in dimensionality of movement (e.g., 2d for movement on land, 3d for movement through air or water), especially when considering three-dimensional energy landscapes, may influence how and when organisms acquire resources (Pawar et al., 2012; Shepard et al., 2013). Lastly, some deviations from general relationships may also result from underlying environmental conditions (e.g., productivity, Pettorelli et al., 2011). Two animals of the same body mass may need larger or smaller foraging ranges depending on the productivity of their environments. However, this environmental constraint on food availability in their foraging ranges may not affect the distance they disperse or migrate.

While our study represents the largest assembled database on animal movement to date, our results are still limited by the fact that not all taxa could be included. We were able to find dispersal, migration, or foraging distances for many more species, but the number of species that had all three forms of movement characterized was limited. Notably, the data set we compiled does not contain any invertebrates or passive dispersers. These two types of organisms would likely drastically change the covariance relationships we observed here. For example, passive dispersal in marine invertebrates or zooplankton typically occurs in early life stages, where smaller body mass may translate to the ability to passively disperse long distances (Fontaneto, 2019). As such, we predict that passive dispersal could diminish the covariance structure that we observe in active dispersers. Using mean values of movement may also hide interesting variation within species, for example, facultative versus obligate migration (Newton, 2012), or even within individuals (e.g., Beardsell et al., 2023). Indeed, there is a growing research effort towards evaluating the causes and consequences of individual variation in movement, however, existing data covering a wide diversity of species cannot yet examine variation with this level of detail.

There are also challenges in disentangling the effects of shared evolutionary history and trophic guild. Our contingency analysis found that some taxonomic groups strongly skewed towards certain trophic guilds, for example, amphibians in our dataset were overwhelmingly invertivorous, while all of the sharks were carnivorous (Table S5). Some of this pattern is likely due to the influence of shared evolutionary history, while some of it is due to a lack of data availability. As such, our findings relating to the most represented classes, birds, and mammals are the most robust. Our evaluation of trophic guild is quite broad, missing key details such as differentiating scavengers from other carnivores, or differentiating frugivores and granivores. Finally, synthesis studies of this nature are typically spatially biased, with most records coming from North America, Europe, and Australia (Dornelas et al., 2018; Gonzalez et al., 2016; Poisot et al., 2021). Because our study used existing databases, some of which did not list their primary sources, we were unable to explicitly examine spatial bias in this study; however, we suspect that the species for which we could find complete data are not evenly distributed across the globe.

Our main analysis, which combined migratory and non-migratory animals, may obscure some of the nuances of animals with different life history strategies. For example, many non-migratory animals go through torpor to escape extreme environmental conditions (Auteri, 2022). However, we feel that combining these groups is justified, as changes to the covariance structure between movement types and body mass were small. Our supplemental analyses that include only migratory or non-migratory animals show similar patterns in the scaling of foraging and dispersal distances, supporting the results of our main analysis that combines the two migration modes (Figures S3 and S4). Additionally, we excluded nomadic animals from this dataset because nomadism is a movement strategy that is understudied while also combining characteristics of the other modes of movement. Nomadism, where animals make seemingly random, long-distance movements, typically occurs in resource-variable environments and should also influence ecological dynamics (Teitelbaum & Mueller, 2019).

Movement may also be constrained by traits that we did not consider in this study. For example, pack hunting animals, for example, wolves, may benefit from reduced searching and handling times for prey. This could lead to a greater intake rate and reduce the amount of time, and thus movement distance, needed to forage (Figure 1b). Reproductive status may also modify movement distances (Beardsell et al., 2022), where higher status individuals may inhabit higher quality home ranges, potentially reducing foraging time. Finally, because in our study we relied on already published dispersal, foraging, and migrating distances, we are relying on these estimates being measured accurately. As such, these types of correlative studies require validation, especially in the cases of data-poor species, to improve our predictive ability of animal movement. We hope the present study will encourage researchers to measure these forms of movement for other types of organisms, and to expand on the types of movement and potential constraints considered.

We contend that quantifying movement profiles and comparing these among taxa and trophic guilds can help advance and simplify an ecological understanding of the inherent constraints to which animal movements are subject. Additionally, quantifying movement profiles can focus a macroecological lens on how and why movement types are distributed as they are among groups (analogous to the plant trait spectrum in Díaz et al. (2016)). Because movement types differ in how they manifest through both space and time, each is expected to have unique contributions to ecological dynamics (Box 1). An exploration of the dynamics that might emerge depending on movement profiles of interacting species in communities is a fruitful avenue of future research, and modelling efforts could benefit from a rough baseline to parameterize movement rates and distances in models, as we provide here. We show that there are no universal scaling relationships between movement types—for individual taxa, movement distances depend on movement type, in ways that reflect body mass, taxonomy, and trophic level. However, we do find boundaries on movement distance, helping to narrow in estimates, as well as differences in overall order of magnitude between movement types. We expect empirical estimates to be particularly useful in extending spatial diversity theories (e.g., metacommunity ecology, spatial coexistence theory) into a multi-trophic context, where interactions (e.g., predation, mutualism) are often realized between species with vastly different body masses, ecologies, and evolutionary histories. These theories have made monumental contributions to our understanding of spatial processes and local-regional coupled dynamics, but until recently have left aside information about foraging and migration (Guzman et al., 2019).

5 | CONCLUSION

In sum, we explored how dispersal combines with migration and foraging movements and body mass to create species' movement profiles. We provide five key insights from our study:

1. Dispersal distances, foraging distances, and body mass all strongly covary, but covariance with migration distance is much weaker.
2. Shared evolutionary history and trophic guild modify the relationships between body mass and movement, but shared evolutionary history explains more variation in movement than trophic guild.
3. Overall distribution of movement profiles provides insight into constraints placed on organisms, either through biophysical limits or a lack of ecological necessity; however, some taxa may be able to break beyond this constraint envelope.
4. This dataset represents the most comprehensive movement dataset to date, as it is rare for datasets to contain information on multiple types of movement, yet important gaps remain that must be filled by empirical research, namely information on other taxonomic groups.
5. Our study provides a holistic view of movement that is overlooked when considering each movement type in isolation, and these types of syntheses are crucial for improving ecological understanding that integrates across scales.

As movement ecologists seek greater integration with conservation (Fraser et al., 2018), understanding how the myriad types of movement can better inform management and restoration efforts will be key. The generalized patterns we describe here can thus augment movement information on data-poor species. This information is needed for the design of protected areas (Noonan et al., 2020), wildlife corridors (Ford et al., 2020), the spread of pathogens (Nobert et al., 2016), and new formulations of critical habitat designations (Davy et al., 2017).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code are available on GitHub and mirrored in Zenodo at https://zenodo.org/record/7940849.

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