Space use of invertebrates in terrestrial habitats: Phylogenetic, functional and environmental drivers of interspecific variations

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Space use of invertebrates in terrestrial habitats: phylogenetic, functional and environmental drivers of interspecific variations

ABSTRACT

Aim: We present the first global database of movement patterns of terrestrial invertebrates, focusing on active dispersal and foraging movements. We depict interspecific variations in movement distances among invertebrates, and assess potential drivers of these variations. We finally contrast our results with those of previous vertebrate studies.

Location: Worldwide.

Methods: We conducted a meta-analysis using 176 studies. They provided 411 movement estimates: 175 foraging movement estimates for 101 species, 51 families and 19 orders, and 236 dispersal estimates for 131 species, 53 families and 16 orders. These estimates were complemented by several organism functional traits: body mass, diet, locomotion mode, and by environmental variables of the study sites: temperature and NDVI. We computed allometric relationships between movement distances and body mass both globally and separately for each taxonomic order with sufficient data. We tested the relative influence of the co-variables on movement distances through model selection.

Results: We reveal a general positive allometric relationship between movement distance and body mass that holds across most taxonomic orders. We evidence a strong phylogenetic signal in movement distances that translates in variable allometries of movement distances with body mass across taxonomic orders. We further find that interspecific variations of movement distances are primarily correlated with functional differences rather than environmental conditions. Locomotion mode is the most important explanatory variable of both dispersal and foraging distances, with larger distances among flying individuals followed by walking and crawling ones for a given body mass. Surprisingly, trophic guild has a low predictive power of invertebrate movement distances as opposed to vertebrates, with unclear differences between invertebrate carnivores, herbivores and decomposers.

Main conclusions: Our study provides general allometric equations for terrestrial movement distances of invertebrates. It further reveals important functional drivers of their interspecific variation in space use with a dominant role of their evolutionary history.

Keywords
Space use, allometry, foraging, dispersal, scaling, movement, invertebrates, functional trait

INTRODUCTION

Animal movements have widespread consequences at population, community, ecosystem and evolutionary levels. They alter local population density and growth rate through emigration and immigration (Law *et al.*, 2003) as well as metapopulation dynamics and evolution (Hanski & Gaggiotti, 2004). At the community level, previous research has mainly focused on the role of dispersal limitation in metacommunity dynamics (Holyoak *et al.*, 2005) and the associated response of biodiversity to climate changes (Lenoir *et al.*, 2020). The key role of other types of movement for community dynamics has also been stressed, in particular the role of foraging movements in the spatial dynamics of foodwebs (Amarasekare, 2008) and more generally community assembly (Schlägel *et al.*, 2020). Animal movements also couple the dynamics of distinct habitats by their associated transfer of matter and energy. A substantial body of theory on such meta-ecosystem dynamics has been developed (Gounand *et al.*, 2018a; Guichard & Marleau, 2021), and available data demonstrate the significance and breadth of such transfers (Gounand *et al.*, 2018b; McInturf *et al.*, 2019).

Animals perform different types of movements at various spatial and temporal scales and for a variety of reasons. Four basic movement types are generally considered (Barton *et al.*, 2015). First, dispersal is generally defined as a unidirectional movement leading to gene flow between distinct populations. This process can either be active, like the mechanical flight of most beetles, or passive with the use of an external vector, like the phoresy of tiny organisms on larger ones (Bartlow & Agosta, 2021). Second, foraging movements are the way animals daily explore their environment for food resources. They are restricted for many animals to a compact area called home range (Burt, 1943). Third, nomadism refers to the movement pattern of an animal that irregularly shifts its home range core location to exploit spatially and temporally fluctuating resources. This type of movement is best described in birds and mammals, but also occurs in a range of diverse taxonomic groups including gastropods (Posso *et al.*, 2012) or even social insects that can occasionally relocate their nests (McGlynn, 2012). Fourth, migration occurs when an animal seasonally undertakes a bi-directional movement. This type of movement connects separated breeding and non-breeding habitats of migratory vertebrates like amphibians and some large mammals, birds or fish. Migratory insects, like some fly, butterfly or moth species (Chowdhury *et al.*, 2021; Hawkes *et al.*, 2022) also migrate over long distances to deal with seasonal variations of resource availability (Dingle, 2014).

Movement ecology has advanced rapidly over the past few decades and a conceptual framework has been proposed to unify research on all movement types within a common context (Nathan *et al.*, 2008). A general understanding of the drivers and spatial extents of animal movements is indeed of particular relevance for diverse research topics, including ecosystem modeling (Earl & Zollner, 2017), biological control (McEvoy, 2018) or niche tracking in a context of global changes (González-Varo *et al.*, 2017). To understand the commonalities in movement patterns across the animal kingdom, data syntheses are needed to document the magnitude and variability of movement rates among and within species, but also to understand their drivers. Several syntheses revealed that interspecific variability in movement distances is mostly driven by functional and life-history traits in vertebrates. Among these traits, body size has been found to be the main factor that correlates positively with migration (Hein *et al.* 2012), foraging (Tamburello *et al.*, 2015) and dispersal distances (Sutherland *et al.*, 2000; Santini *et al.*, 2013). At a global scale, large body sizes and fast life history strategies have been shown to facilitate tetrapod lineage dispersal between biogeographical regions in a majority of clades (Weil *et al.*, 2023). Locomotion mode (flying, walking or swimming) alters the intercept and slope of the allometries between movement and body size because of the varying penetrability of the associated medium (air, land or water). Larger movement distances are observed in more penetrable media (Tamburello *et al.*, 2015; Straus *et al.*, 2022). These studies also evidenced that diet is a significant determinant of space use with carnivores foraging and dispersing over larger distances than herbivores to compensate for lower resource densities (Sutherland *et al.*, 2000; Santini *et al.*, 2013). They have also demonstrated a significant phylogenetic inertia of movement distances with taxon-specific allometric relationships with body size.

Similar syntheses on invertebrate taxa are currently lacking. Although invertebrates represent 75% of all described species on Earth and almost 95% of all animal species (Eisenhauer & Hines, 2021), a general picture of the variability of movement distances and their drivers is still lacking for this large group of animals. Hurlbert *et al.* (2008) and Hirt *et al.* (2017) revealed a positive scaling of exploratory speed with body mass across six classes of invertebrates, but they did not study the movement distances of these taxa. We therefore aim at filling this gap and at assessing whether invertebrate movement distances are influenced by the same set of functional traits as vertebrate taxa **(Figure 1a-d)**. We focus on active dispersal and foraging distances, since data about invertebrate nomadism and migration are scarce (Hein *et al.*, 2012). Contrary to the previously cited synthesis on vertebrate movements, we also contend that animal movements depend on the abiotic environmental context and we aim at assessing such abiotic drivers (McManus, 1988). We specifically study the effect of i) temperature because of the ectothermic metabolism of invertebrates (Gibert *et al.*, 2016), and ii) the normalized difference vegetation index (NDVI) used as a proxy for herbivore resource quality and availability (Pettorelli *et al.*, 2011). We expect NDVI to correlate negatively with foraging and dispersal distances, as it does with migration distance in mammals (Teitelbaum *et al.*, 2015) **(Figure 1e)**.

METHODS

Literature search and data selection

We conducted a literature search on the Web of Science and Google Scholar with the title request ((“invertebrate” OR [any known order of terrestrial invertebrate]) AND (“space use” OR “home range” OR “foraging” OR “dispersal” OR “movement pattern” OR “MRR” OR “CMR” OR telemetry OR “harmonic radar”)). Specific words relative to aquatic habitats were specified as unwanted, as well as journal categories like “Toxicology” or “Neurosciences” (see full research strategy in Supporting information). We looked for cited references to similar works within each selected paper and added them to our database when relevant. We found three reviews about movement of specific taxonomic groups, and retrieved the original papers.

Studies were retained if they provided quantitative information about mean active dispersal distance (m) and/or mean foraging distance (m) or home range size (m²) for terrestrial invertebrate individuals. We did not compile data of home range size of social insects' colonies (ants or termites colonies for instance) because they do not correspond to individual traits but to emergent collective patterns (Gordon, 1995). We also excluded genetic and simulation studies that only provided indirect measures of movement distances. Translocation experiments were also excluded, because the ability of an individual to return to its initial territory beyond a certain distance does not only depend on its motion capacities, but also on its memory of visual landmarks and other sorts of cues (Able, 1980). The duration of the studies that we retained varied from a single to a few days or even weeks, because all species do not need the same amount of time to complete a dispersal event. We assumed that the retained dispersal studies tracked individuals' movements during the whole duration of their dispersal event.

Foraging and dispersal distances

We distinguished dispersal from foraging movements based on the claim of each study's authors. When the authors did not precise the nature of the movements that were observed (in 29 cases), we considered random and short movements as foraging behavior, and reported as foraging distance the average maximal distance from the point of release in tracking studies, or from the nest in which individuals were daily observed. Similarly, when the movement type was not clearly defined in a study, we considered oriented or linear movement over great distances as dispersal behavior, and the longest straight line displacement between the first and the last observation was reported as dispersal distance. When studies provided only a home range size in square meters, we used the mean radius of this area as a proxy for foraging distance. Similarly, we performed the reverse operation to transform foraging distances in home range estimates, so that the data on invertebrate home ranges are also available for the scientific community.

Body mass

We reported the mean dry mass of the group of individuals whose movements were studied when available within the publication. Otherwise, we performed a complementary literature search of body mass of the studied taxon. When only fresh mass or body length values could be found, dry mass was calculated thanks to regression coefficients from the literature for distinct taxonomic groups (Petersen, 1975; Sage, 1982; Sabo *et al.*, 2002; James *et al.*, 2012; Newton & Proctor, 2013). When only a mean body length or fresh mass value was available, and when no allometric equation was applicable, we estimated a species' dry mass with an allometric equation of a phylogenetically close species. Calculation details for the dry mass of each species are available in the **Appendix 1**.

Locomotion mode

In terrestrial environments, invertebrates actively move in three different ways: they either fly, walk or run (non-alate or alate species moving on the ground with articulated legs) or crawl (above-ground or below-ground limbless species or larvae). Many invertebrate species undergo a shift in their locomotion mode during their lifetime (e.g. Crawling lepidoptera caterpillars become flying imagos). We therefore associated to each observation in our database the locomotion mode corresponding to the exact life stage of the individuals at the time of the study, and used the corresponding body mass and trophic guild for this life stage.

Trophic guild

We classified species as either carnivores, herbivores or decomposers. We performed this classification in broad trophic groups to avoid a multiplication of specific trophic habits in our database that would have small sample sizes and for which we would not have clear *a priori* predictions. Hence, we classified omnivorous species feeding on both plants and other invertebrates as carnivores. We grouped hematophagous species like ticks or mosquitoes with carnivores. Finally, we pooled granivore and palynivore species with herbivores, and xylophagous, saproxylic, fungivore, detritivore and coprophagous animals as decomposer species.

Habitat

We distinguished *in situ* studies from *ex situ*, laboratory studies. We extracted the location of the study, or used approximate geographic coordinates based on the description of the area for the few studies that did not provide a precise location of their experiment. Two environmental variables were extracted from the location of the *in situ* studies and for the period that matched the time window of each survey: the mean monthly temperature (TerraClimate database, resolution 4km, Abatzoglou *et al.*, 2018) related to the species' ability to get active; and the Normalized Difference Vegetation Index (NDVI, NOAA Climate Data Record of NDVI for years 1982 to 1999, resolution 5km, and satellite MOD13Q1.061 data for years 2000 to 2019, resolution 250m), related to the resource quality of herbivore species (Pettorelli *et al.*, 2011) .

Methodology

Finally, we also reported the methods used to track individuals (capture-mark-recapture, telemetry, harmonic radar, flight mill, visual monitoring or video tracking). The combination between the study condition (*in situ* or *ex situ*) and the tracking method created a new "Method" variable that we used as a random effect in our statistical models (e.g. "*In situ*: CMR" or "*Ex situ*: Flight mill").

Statistical analysis

<u>*Taxon-specific allometry of space use.*</u> Prior to all analyses, we log-transformed (Log_{10}) body mass and movement distances to linearize movement responses. We first performed ordinary least square (OLS) regressions to assess the allometry of space use for each taxonomic order that presented more than seven observations in our database. Since we found that movement distances estimated by *ex situ* studies are significantly larger than those estimated *in situ* (dispersal: *ANCOVA*: F = 76.232, p = 5.15; foraging: *ANCOVA*: F = 42.925, p = 6.50e-10), we performed our analyses on *in situ* studies only, except for the *Haplotaxida* order for which we only found foraging data from laboratory studies. For each taxonomic order, we performed mixed models with a species random intercept to deal with multiple data

per species, and with tracking method also incorporated as a crossed random effect on the intercept value when several types of tracking methods were used.

Functional and environmental drivers of interspecific variations in space use. Because of the significant differences found between the *in situ* and *ex situ* movement estimates, we continued to perform our next analyses on the subset of the *in situ* studies only. We first tested the influence of functional drivers on movement distances, by assessing whether the locomotion mode and trophic guild influenced the coefficients of our initial allometric models: "(Dispersal or foraging) Distance ~ Dry Mass". We built mixed models to test each predictor separately for both dispersal and foraging data sets, with tracking method included as a random effect, and taxonomic order and species identity incorporated as a nested random effect, all on the intercept value. These random effects allowed us to deal with multiple tracking methods and multiple points per species while accounting for phylogenetic interdependence. We tested interaction effects between body mass and locomotion mode, and between body mass and trophic guild. We finally combined these two hypothesized functional drivers into a "full" model. The relative support of each model was assessed with the Akaike Information Criterion corrected for small samples (AICc). The marginal and conditional R^2 of the models were calculated to assess the proportion of variance explained respectively by the fixed effects alone, and by both fixed and random effects, with the "r.squaredGLMM" function from the 'MuMIn' R package (Bartoń, 2023).

The second analysis aimed at assessing the relative influences of functional and environmental drivers using the dataset of *in situ* studies only. We built a mixed model with the following potential drivers of space use: body mass, trophic guild, locomotion mode, temperature and NDVI. We computed the partial eta-squared of these different predictors to assess their relative influence on movement distances in our dataset, with random effects on the intercept values associated with tracking method and species identity nested within taxonomic order.

Comparison with previous vertebrate studies. Finally, we extracted dispersal and foraging regression parameters for terrestrial vertebrates from previous syntheses of the literature to contrast with our own regression parameters. Dispersal distance regression estimates for terrestrial mammals were obtained from Santini *et al.* (2013) and transformed to express movement distance from kilometers to meters. Home range allometric relationships were obtained from Tamburello *et al.* (2015) for mammals, birds and reptiles, and recomputed from the original database with the radius of the home range area (m^2) used as a proxy for foraging distance. For consistency with our invertebrate analysis, we used the following k factors to convert vertebrate fresh body mass to dry body mass: mammals: k=0.2845 (Schlesinger & Potter, 1974); birds: k=0.344 (Sturges *et al.*, 1974); reptiles: k=0.24 (Barron, 1997) where dry mass = k x fresh mass. We then compared the foraging allometry of invertebrates with those of the different vertebrate groups (birds, mammals and reptiles) using a Chow test implemented in the 'gap' package (Zhao *et al.*, 2023). The Chow test could not be used for the comparison of the dispersal behavior of invertebrates and mammals, for which we only had regression parameters and no raw data.

Phylogenetic signal

We also performed a phylogenetic analysis of the interspecific variation in movement distances. We constructed phylogenetic trees with dated branches thanks to the OneTwoTree pipeline (Drori *et al.*, 2018) for a subset of the species in our database (174 out of 2176). We calculated the phylogenetic signal in movement distance using Pagel's lambda metric that is adapted to continuous response variables. Pagel's λ ranges from 0 if there is no link between the response variable and phylogeny, to 1 if closely related species respond exactly the same way to the predictor variables (Pagel 1997; Pagel 1999). Because phylogenetic relatedness between species is likely to cause an inter-dependency of the observations of movement distances, we computed phylogenetic generalized least squares regressions (PGLS) using the 'nlme' package in R (Pinheiro *et al.*, 2023) to account for interspecific autocorrelation and we compared the PGLS regression results with the fit of non-phylogenetic, ordinary least square regressions (OLS). All analyses were performed on R 4.2.1 (2022.06.23).

RESULTS

Datasets

We assembled a database of 176 scientific articles that met our selection criteria. They provided 411 movement observations of individuals from 217 species, 82 families and 22 orders. These data correspond to 236 observations of dispersal (57%) and 175 observations of foraging (43%) distances, with a heterogeneous distribution between trophic and locomotion groups **(Table S1 in Appendix 2)**. The dispersal database contains 158 *in situ* and 76 *ex situ* movement observations, and the foraging database contains 147 *in situ* and 26 *ex situ* movement observations. Biogeographical realms are unequally represented, with 80% of the total observations coming from the Nearctic and Palearctic world regions, while only 14% is from the Southern hemisphere of the globe **(Figure S1 in Appendix 2)**. However, the two environmental variables (temperature and NDVI) still cover a large and continuous spectrum of values, from 5 to 30°C (about 40% of the total range within the critical thermal limits of -6 and +57°C for terrestrial ectotherms, Hoffmann *et al.*, 2013) and from 0.0 to 0.9 values of NDVI **(Figure S2 in Appendix 2)**. Our data compilation encompasses wide ranges of movement distances (from 10^{-2} to 10^{5} m) and of body masses (from 10^{-4} to 10^{4} mg) **(Figure S3 in Appendix 2)**. Data sources are provided online on Zenodo: https://zenodo.org/records/10230297.

Allometry of space use

Body mass significantly explains both dispersal and foraging distances (OLS regressions: $R^2 = 0.26$ for both movement types), but with a far lower predictive power than previous synthesis studies conducted on vertebrates. The Pagel's λ-statistic shows strong and highly significant phylogenetic signals for both dispersal and foraging movement distances (Dispersal: $\lambda = 0.99$, p = 1e-22, n = 108; foraging: $\lambda = 0.90$, p = 6e-12, n = 76). However, the fit of the models does not improve when performing phylogenetic regressions (PGLS: dispersal: $R^2 = 0.26$; foraging: $R^2 = 0.21$). For a given body mass, dispersal distance is significantly larger than foraging distance (*ANCOVA*: F = 162.41, p < 2.2e-16, dispersal intercept: 1.37, foraging intercept: 0.13).

When looking at the different taxonomic orders separately, we confirm a strong phylogenetic signal in movement distances with a wide variation of regression estimates among taxonomic orders for both foraging **(Figure 2)** and dispersal **(Figure 3)** movements. We recover a positive relationship between body mass and movement distances for most taxonomic orders, but with variable slopes **(Table 1)**. Only *Odonata* show a non-significant negative correlation between body mass and both dispersal and foraging distances **(Table 1)**. We also note a strong dispersion of data points of Coleoptera and Hemiptera dispersal distances around the regression line, whose slope coefficients are almost null ($b = 0.03$ and 0.00, respectively, **Table 1**).

Effects of functional traits and environmental factors on movement distances

We found that locomotion mode is the most influential driver of interspecific variations in movement distances. The effect size of locomotion on foraging movement is particularly strong, about 3.6 times larger than its effect size on dispersal (**Figure 4).** The other drivers have comparatively low effects with partial-η^2 values below 0.1. Body mass is the second most influential driver of foraging distance (partial-$\eta^2 = 0.10$), followed by trophic guild, while temperature and NDVI have almost null effects. For dispersal distance, body mass, temperature and NDVI have low but comparable effect sizes (partial-$\eta^2 = 0.076$, 0.071 and 0.078, respectively) and trophic guild ranks last among the tested dispersal predictors. For consistency with the other analyses, **Figure 4** includes taxonomic order, species identity and tracking method as random effects. However, phylogeny predominates all other factors of dispersal distance, and ranks second for foraging movements when tested as a fixed effect **(Figure S4 in Appendix 2)**.

Consistently with our a priori predictions, we found that flying individuals in our database move further than walkers, themselves moving further than crawlers when controlling for body mass variations (**Figure 5a, Figure 5b**). However, while the relationship between foraging distance and body mass did not significantly differ between locomotion modes (*ANOVA:* $F = 0.406$, $p = 0.67$), we found a significant interaction effect between locomotion mode and body mass for dispersal movements (*ANOVA*: $F = 8.95$, $p = 2.11e\text{-}04$). We found that, the bigger the species, the smaller the difference in dispersal distances between locomotion strategies. We even observe a small inversion between flyers and walkers movement distances for the largest organisms due to the smaller slope coefficient for flying individuals in the dispersal full model **(Figure 5b**, **Table 2)**.

Our a priori prediction that carnivores should forage further than the other two trophic guilds was not supported by our analysis (**Figure 5c**). Plus, we did not find a significant interaction between trophic guild and body mass for foraging movements (*ANOVA*: $F = 0.20$, $p = 0.82$). Regarding dispersal, we found a significant interaction effect between trophic guild and body mass (*ANOVA*: $F = 5.05$, $p = 7.55e\text{-}03$). This led to a positive relationship between body mass and dispersal for carnivores and herbivores, but not for decomposers (**Figure 5d**).

Comparison with terrestrial vertebrates

Invertebrate body mass in our study spans eight orders of magnitude, exceeding vertebrate body mass range in Tamburello *et al.* (2015) and Santini *et al.* (2013) by two and three orders of magnitude, respectively **(Figure 6)**. The observed overlap of body weights between vertebrates and invertebrates comes from the 25 vertebrate species, mostly passerines and rodents, that have lighter dry masses than the heaviest invertebrate in our database, which is the Giant African land snail (*Lissachatina fulica*, Férussac 1821). We find clearly different dispersal allometries between invertebrates and mammals, the latter having an intercept value two orders of magnitude above that of invertebrates ($\log_{10}(a) = 3.40$ versus 1.62) and a regression slope 3.6 times steeper ($b = 0.68$ versus 0.19). We also find that the allometry of foraging of invertebrates is significantly different from that of birds and mammals (Chow-test invertebrates-birds: $F = 4.77$, $p = 9.07\text{e-}03$; invertebrates-mammals: $F = 8.40$, $p = 2.66\text{e-}04$), but not significantly different from the foraging allometry of reptiles (Chow-test: $F = 0.14$, $p = 0.87$) (**see Figure S5 in Supplementary information**).

DISCUSSION

We assembled the first global database of movement patterns of terrestrial invertebrates, focusing on active dispersal and foraging movements. Using this database, we documented allometric relationships between body mass and foraging and dispersal movement distances across major terrestrial invertebrate taxonomic orders. We then assessed whether invertebrate movements were driven by the same functional traits as those evidenced for vertebrate taxa. The relatively low contribution of body mass to the variability of invertebrate movement distance strongly contrasts with previous results on vertebrates. While 24% and 20% of variability is explained by invertebrates' body mass for dispersal and foraging movements respectively in simple linear models, these values fall down to 7% and 10% (marginal R-squared values) when considering taxonomy and tracking method as random effects. In a similar analysis conducted on vertebrate species, Tamburello *et al.* (2015) evidenced that body mass alone explained up to 44% of home range variability when controlling for taxonomy and tracking method. Regarding the dispersal distance of mammals, Santini *et al.* (2013) evidenced that body mass alone explained up to 64% of variance using a simple linear regression model.

A possible explanation for this discrepancy is that other morphological traits that do not necessarily correlate with body mass may be better predictors of movement capacities in many invertebrate taxa. In flying invertebrates for example, wing morphology (length, area, elongation) or wing loading (*i.e* ratio body mass:wing area) may be more determinant for movement distance than body mass alone (Flockhart *et al.*, 2017). A second and linked explanation for the lower explanatory power of body mass on invertebrate movements compared to vertebrates might lie in the larger morphological variability of these organisms. Tamburello *et al.* (2015) evidenced differences in home range allometries between birds, mammals and reptiles (Figure 6). We similarly evidenced differences in movement allometries between different invertebrate orders, but with a much stronger variability between these groups (Figures 2 and 3, Figure S4). This may explain the lower predictive ability of body mass alone across taxonomic orders of invertebrates.

We further reported different allometries between invertebrates and vertebrates, except regarding the foraging of reptiles (Figure 6) which share ectothermic metabolism with invertebrates. Taken together, vertebrates have larger movement distances for a given body mass and steeper allometric curves. A possible explanation for this discrepancy between vertebrates and invertebrates may lie in differences between these groups in their mode of thermoregulation, terrestrial vertebrates being in majority endothermic while invertebrates are ectothermic. The energetic cost of endothermy may explain larger foraging distances of endotherms to cope with this energy expenditure.

Consistently with our predictions, longer dispersal and foraging distances are observed in flying organisms when controlling for body mass, while walking and crawling organisms travel distances that are about one to three orders of magnitude shorter, respectively. We conclude that, as in vertebrate species, invertebrate movement distances correlate with the cost of transport associated with the movement media (Shepard *et al.*, 2013). Our prediction that carnivores would move further than herbivores and decomposers to compensate for lower resource densities is not supported by our data. In the present dataset however, we lack information on potential interaction effects between locomotion mode and trophic guild, due to a strong lack of balance between these two variables in our databases. We dealt with an over-representation of flying individuals in the dispersal database, and of walking individuals in the foraging one, with trophic guilds not being equally represented in both databases either (see **Table S1 in Supporting information**). Still, results of several complementary analyses are globally consistent, reinforcing the robustness of our results.

Neither temperature nor NDVI significantly explained interspecific variations in foraging distances, although both environmental variables had the same predictive power of dispersal distances as body mass. These results contrast with the fact that environmental conditions are known to modify the movement behavior and plasticity of individuals in several ways (Johnson *et al.*, 1992). An explanation for this discrepancy is the temporal grain used to estimate these two environmental variables. We tested the influence of monthly mean climatic and environmental factors, while individual movement behavior is also driven by weather conditions at finer temporal and spatial scales (*e.g.* daily temperature, wind velocity, Knight *et al.*, 2019). Since most studies did not report weather conditions, we were not able to incorporate these environmental variables in our model selection framework.

Some other potentially influential co-variables could not be assembled for our dataset. Habitat and vegetation structure have been found to significantly affect mean displacement range in some invertebrate taxa (Crist *et al.*, 1992) as for vertebrates (Bowers *et al.*, 1996). However, the limited resolution of spatial products available at the global scale and for ancient dates did not allow capturing relevant habitat and vegetation structure metrics for most invertebrate species of our database that have movement distances below 250 meters (foraging distance: median - 3rd quartile = 6 - 21m; dispersal distance: median - 3rd quartile = 107 - 592m). We were neither able to collect enough diet and habitat specialization data to explore the links between specialization level and movement distances that have been evidenced in some taxa. For instance, carabid beetles that are strict specialists of woodlands move much more slowly than habitat generalist species (Brouwers & Newton, 2008). Differences in dispersal distance have also been evidenced between habitat specialists and generalists, the latter ones being more explorative and dispersing further than specialists in gastropods (Dahirel *et al.*, 2015).

Our synthesis reveals an over-representation of arthropods in invertebrate movement studies (themselves being dominated by Coleopterans), while extensive data on the space use of annelids, molluscs, nematodes and more generally of the tiniest species are still needed. Tracking methods initially designed for vertebrates, like telemetry or harmonic-radar, have only recently become suitable for studying the movement of the largest invertebrate species (Chapman *et al.*, 2004; Kissling *et al.*, 2014). The development of innovative tracking methods should improve the spectrum of animals whose movements might be studied in future years (see for example Cointe *et al.*, 2023). For the tiniest invertebrates however, the contribution of active movements to overall displacements is likely to strongly decrease compared to the contribution of passive phoretic movements, especially for dispersal. The exact mechanisms and the spatial extent of phoresy processes remain unclear (Bartlow & Agosta, 2021). It would thus be inaccurate and misleading to extrapolate our dispersal data to phoretic animals following our allometric equations.

Our synthesis offers ready-to-use allometric equations to predict terrestrial invertebrate active movements from the sole knowledge of their body mass and a small set of additional functional traits (locomotion mode, diet and body mass). This new information is pivotal for a number of applications, such as the prediction of future species ranges under climate change (Mammola *et al.*, 2021), the design of agroecological landscapes favoring biological control (Haan *et al.*, 2020) or the analysis of connectivity issues for conservation planning (Keeley *et al.*, 2021). More fundamentally, our study also highlights the similarities and differences between vertebrate and invertebrate movements. While we recovered that similar functional traits were driving both vertebrate and invertebrate movements, such as body mass, locomotion mode and phylogeny, the relative influences of these different drivers strongly differ between vertebrate and invertebrate taxa. Although body mass significantly positively correlates with dispersal and foraging distances among the majority of invertebrate orders, its predictive power is clearly lower for invertebrate taxa compared to vertebrate ones. More subtle and taxon-specific approaches might therefore be needed to refine movement inferences from invertebrate traits.

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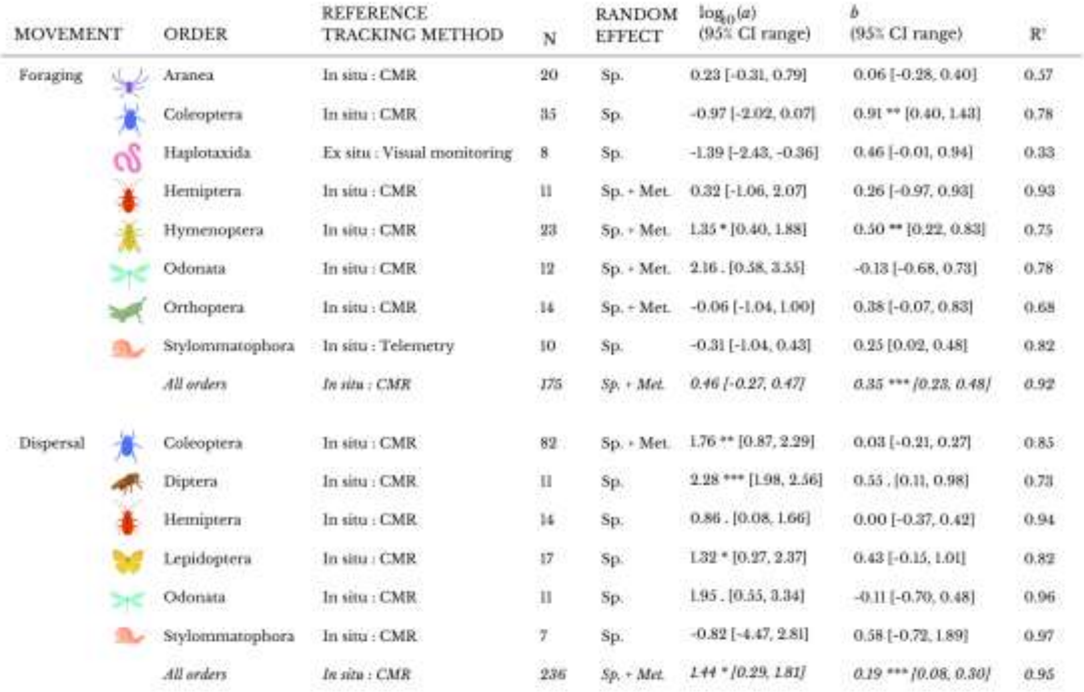
DATA ACCESSIBILITY STATEMENT

The compiled database and accompanying R script are available on Zenodo: https://zenodo.org/records/10230297

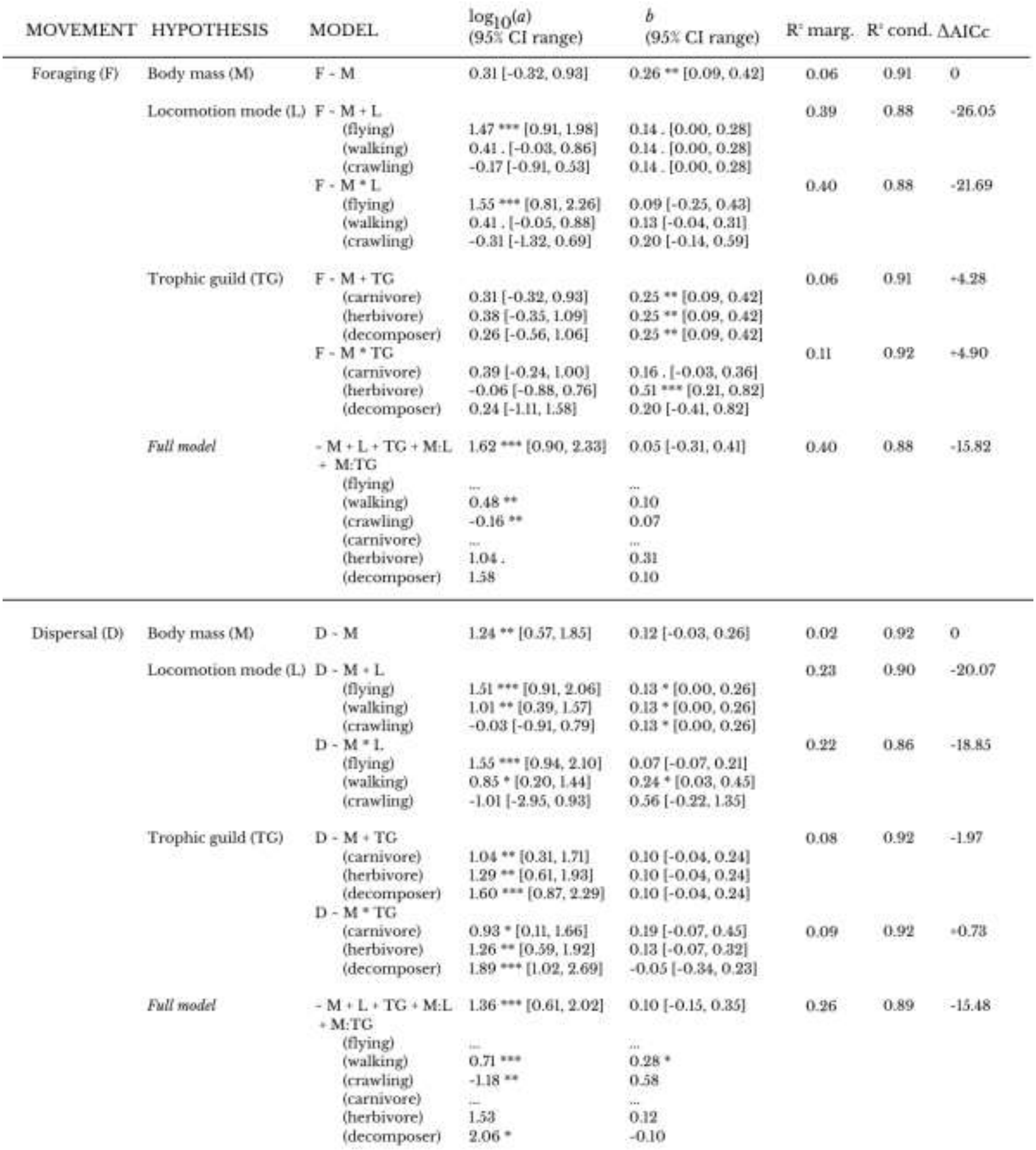
TA



MOVEMENT	ORDER	REFERENCE TRACKING METHOD	N	RANDOM EFFECT	$\log_{10}(a)$ (95% CI range)	b (95% CI range)	R^2
Foraging	Aranea	In situ : CMR	20	Sp.	0.23 [-0.31, 0.79]	0.06 [-0.28, 0.40]	0.57
	Coleoptera	In situ : CMR	35	Sp.	-0.97 [-2.02, 0.07]	0.91 ** [0.40, 1.43]	0.78
	Haplotaxida	Ex situ : Visual monitoring	8	Sp.	-1.39 [-2.43, -0.36]	0.46 [-0.01, 0.94]	0.33
	Hemiptera	In situ : CMR	11	Sp. + Met.	0.32 [-1.06, 2.07]	0.26 [-0.97, 0.93]	0.93
	Hymenoptera	In situ : CMR	23	Sp. + Met.	1.35 * [0.40, 1.88]	0.50 ** [0.22, 0.83]	0.75
	Odonata	In situ : CMR	12	Sp. + Met.	2.16 . [0.58, 3.55]	-0.13 [-0.68, 0.73]	0.78
	Orthoptera	In situ : CMR	14	Sp. + Met.	-0.06 [-1.04, 1.00]	0.38 [-0.07, 0.83]	0.68
	Stylommatophora	In situ : Telemetry	10	Sp.	-0.31 [-1.04, 0.43]	0.25 [0.02, 0.48]	0.82
	All orders	*In situ : CMR*	*175*	*Sp. + Met.*	*0.46 [-0.27, 0.47]*	*0.35 *** [0.23, 0.48]*	*0.92*
Dispersal	Coleoptera	In situ : CMR	82	Sp. + Met.	1.76 ** [0.87, 2.29]	0.03 [-0.21, 0.27]	0.85
	Diptera	In situ : CMR	11	Sp.	2.28 *** [1.98, 2.56]	0.55 . [0.11, 0.98]	0.73
	Hemiptera	In situ : CMR	14	Sp.	0.86 . [0.08, 1.66]	0.00 [-0.37, 0.42]	0.94
	Lepidoptera	In situ : CMR	17	Sp.	1.32 * [0.27, 2.37]	0.43 [-0.15, 1.01]	0.82
	Odonata	In situ : CMR	11	Sp.	1.95 . [0.55, 3.34]	-0.11 [-0.70, 0.48]	0.96
	Stylommatophora	In situ : CMR	7	Sp.	-0.82 [-4.47, 2.81]	0.58 [-0.72, 1.89]	0.97
	All orders	*In situ : CMR*	*236*	*Sp. + Met.*	*1.44 * [0.29, 1.81]*	*0.19 *** [0.08, 0.30]*	*0.95*

Table 1. Regr

ession parameter estimates for body mass across separate taxonomic orders with $n \geq 7$ observations. Global regressions (*'All orders'*) include all taxonomic orders in our databases without constraint on minimal number of data. Mixed linear models are of the form $\log_{10}(D) \sim \log_{10}(a) + b \times \log_{10}(M)$ where D: movement distance and M: dry mass. Mixed linear models include the tracking method as a random effect. Mixed linear models include the species ('Sp.') and the tracking method ('Met.') when needed as a random effect. We used the most frequently used tracking method as the reference for each taxonomic order. $\log_{10}(a)$: intercept; b: slope; 95% CI: 95% confidence interval. R^2 corresponds to the conditional R^2 for mixed models. Significance (p-values) codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '.



MOVEMENT	HYPOTHESIS	MODEL	$\log_{10}(a)$ (95% CI range)	b (95% CI range)	R^2 marg.	R^2 cond.	ΔAICc
Foraging (F)	Body mass (M)	F - M	0.31 [-0.32, 0.93]	0.26 ** [0.09, 0.42]	0.06	0.91	0
	Locomotion mode (L)	F - M + L			0.39	0.88	-26.05
		(flying)	1.47 *** [0.91, 1.98]	0.14 . [0.00, 0.28]			
		(walking)	0.41 . [-0.03, 0.86]	0.14 . [0.00, 0.28]			
		(crawling)	-0.17 [-0.91, 0.53]	0.14 . [0.00, 0.28]			
		F - M * L			0.40	0.88	-21.69
		(flying)	1.55 *** [0.81, 2.26]	0.09 [-0.25, 0.43]			
		(walking)	0.41 . [-0.05, 0.88]	0.13 [-0.04, 0.31]			
		(crawling)	-0.31 [-1.32, 0.69]	0.20 [-0.14, 0.59]			
	Trophic guild (TG)	F - M + TG			0.06	0.91	+4.28
		(carnivore)	0.31 [-0.32, 0.93]	0.25 ** [0.09, 0.42]			
		(herbivore)	0.38 [-0.35, 1.09]	0.25 ** [0.09, 0.42]			
		(decomposer)	0.26 [-0.56, 1.06]	0.25 ** [0.09, 0.42]			
		F - M * TG			0.11	0.92	+4.90
		(carnivore)	0.39 [-0.24, 1.00]	0.16 . [-0.03, 0.36]			
		(herbivore)	-0.06 [-0.88, 0.76]	0.51 *** [0.21, 0.82]			
		(decomposer)	0.24 [-1.11, 1.58]	0.20 [-0.41, 0.82]			
	Full model	- M + L + TG + M:L + M:TG	1.62 *** [0.90, 2.33]	0.05 [-0.31, 0.41]	0.40	0.88	-15.82
		(flying)	...	...			
		(walking)	0.48 **	0.10			
		(crawling)	-0.16 **	0.07			
		(carnivore)	...	...			
		(herbivore)	1.04 .	0.31			
		(decomposer)	1.58	0.10			
Dispersal (D)	Body mass (M)	D - M	1.24 ** [0.57, 1.85]	0.12 [-0.03, 0.26]	0.02	0.92	0
	Locomotion mode (L)	D - M + L			0.23	0.90	-20.07
		(flying)	1.51 *** [0.91, 2.06]	0.13 * [0.00, 0.26]			
		(walking)	1.01 ** [0.39, 1.57]	0.13 * [0.00, 0.26]			
		(crawling)	-0.03 [-0.91, 0.79]	0.13 * [0.00, 0.26]			
		D - M * L			0.22	0.86	-18.85
		(flying)	1.55 *** [0.94, 2.10]	0.07 [-0.07, 0.21]			
		(walking)	0.85 * [0.20, 1.44]	0.24 * [0.03, 0.45]			
		(crawling)	-1.01 [-2.95, 0.93]	0.56 [-0.22, 1.35]			
	Trophic guild (TG)	D - M + TG			0.08	0.92	-1.97
		(carnivore)	1.04 ** [0.31, 1.71]	0.10 [-0.04, 0.24]			
		(herbivore)	1.29 ** [0.61, 1.93]	0.10 [-0.04, 0.24]			
		(decomposer)	1.60 *** [0.87, 2.29]	0.10 [-0.04, 0.24]			
		D - M * TG					
		(carnivore)	0.93 * [0.11, 1.66]	0.19 [-0.07, 0.45]	0.09	0.92	+0.73
		(herbivore)	1.26 ** [0.59, 1.92]	0.13 [-0.07, 0.32]			
		(decomposer)	1.89 *** [1.02, 2.69]	-0.05 [-0.34, 0.23]			
	Full model	- M + L + TG + M:L + M:TG	1.36 *** [0.61, 2.02]	0.10 [-0.15, 0.35]	0.26	0.89	-15.48
		(flying)	...	...			
		(walking)	0.71 ***	0.28 *			
		(crawling)	-1.18 **	0.58			
		(carnivore)	...	...			
		(herbivore)	1.53	0.12			
		(decomposer)	2.06 *	-0.10			

Table 2. Allometric regression results for linear mixed-effect models. Taxonomic order and species were included in all models as nested random effects, and tracking method was included as a simple random effect. *$\log_{10}(a)$*: intercept; *b*: slope; R^2 marg.: marginal R^2; R^2 cond.: conditional R^2; AICc: Akaike information criterion corrected for small sample sizes. Slope and intercept estimates are reported for each factor as absolute values. Significance (p-values) codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '.

FIGURES

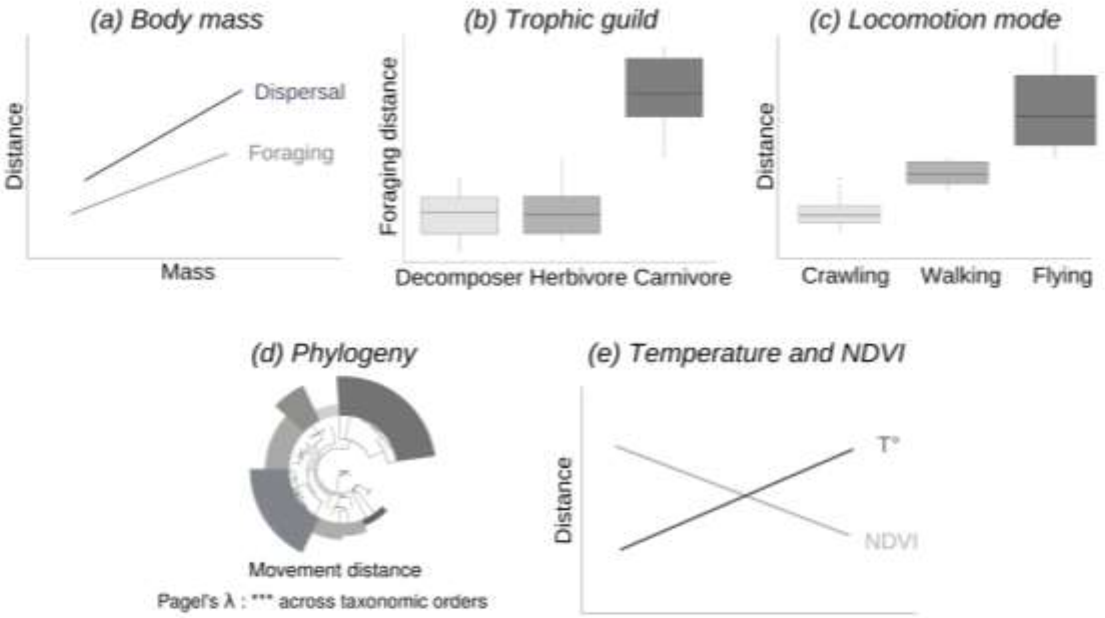
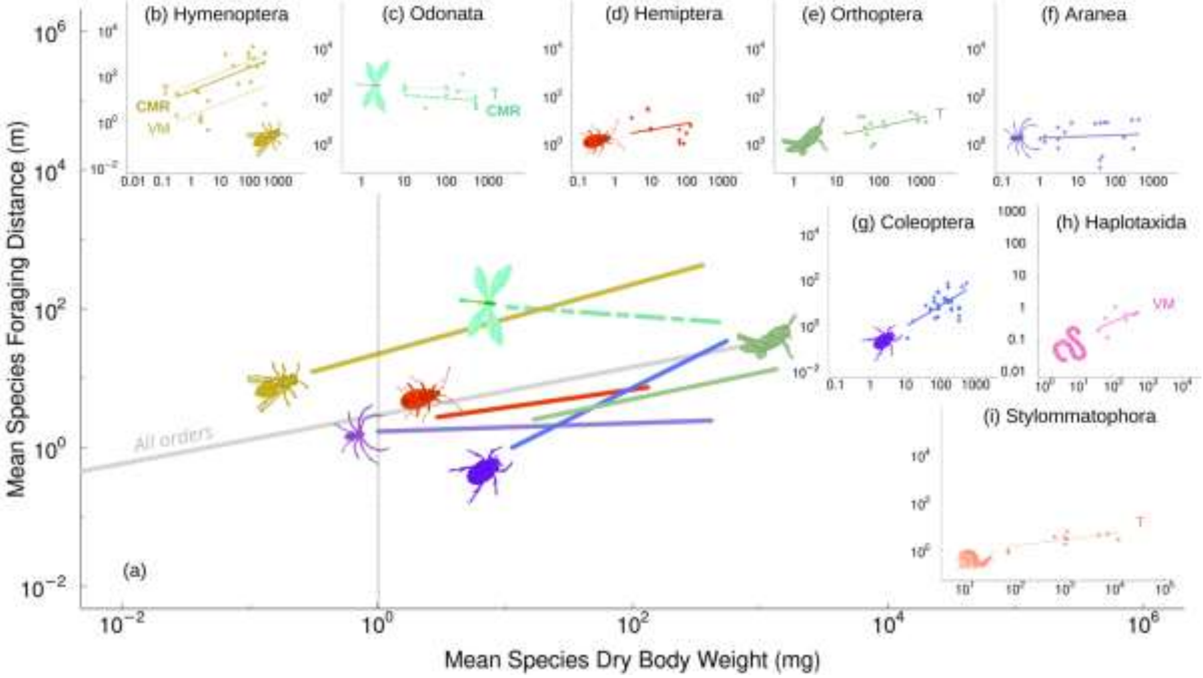
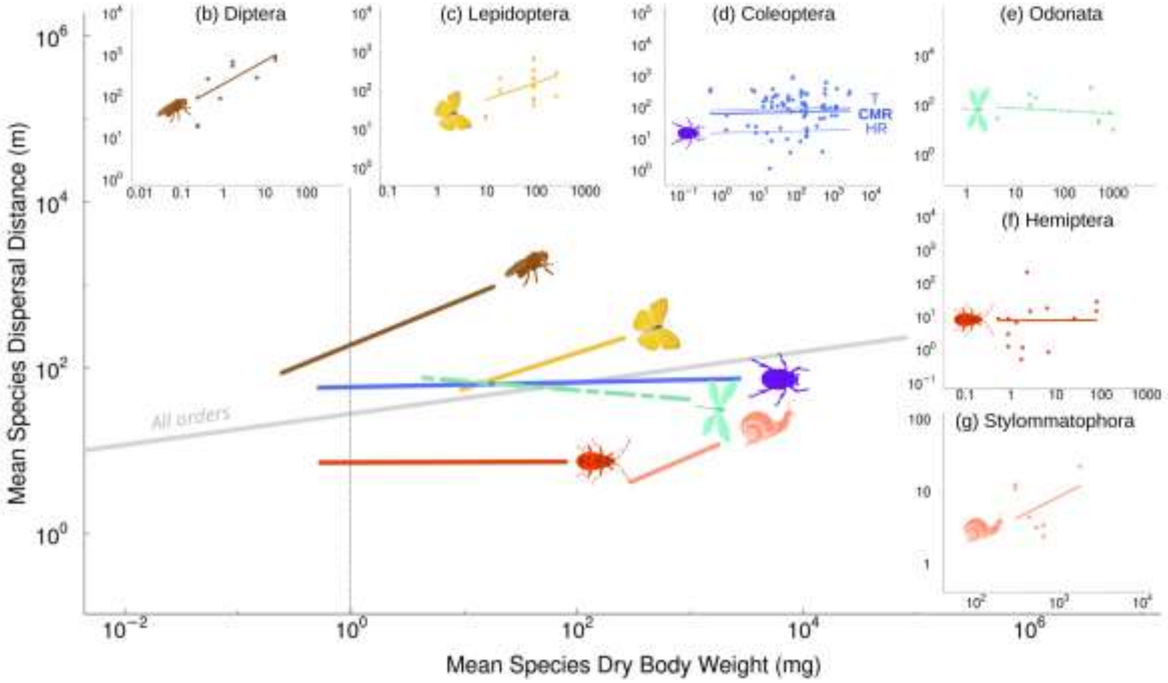


Figure 1. Tested predictions: *(a)* Positive scaling of dispersal and foraging distances with body mass; *(b)* Carnivores are expected to forage further than herbivores and decomposers; *(c)* Flying individuals move further than walkers, both moving further than crawlers; *(d)* Phylogenetic signal in dispersal and foraging movement distances; *(e)* Higher local temperature leads to larger movement distances. Higher NDVI leads to lower movement distances.



<u>Figure 2.</u> Allometry of foraging distances in terrestrial invertebrates across taxonomic orders (n ≥ 7 obs.). Regressions are performed on *in situ* data only, except for panel (h) (lab studies only). (a) Summary of taxonomic order-specific regression lines of capture-mark-recapture (CMR) data; (b) flying (wasps and bees) and walking (ants) Hymenoptera; (c) dragonflies and damselflies (Odonata); (d) true bugs (Hemiptera); (e) grasshoppers, locusts and crickets (Orthoptera); (f) spiders (Aranea); (g) beetles (Coleoptera); (h) annelid worms (Haplotaxida); (i) snails and slugs (Stylommatophora). In panels b, c, e and h, regression lines of alternative tracking methods are also reported: T: telemetry; VM: visual monitoring. Solid lines: positive regression slope; Dashed lines: negative regression slope.



<u>Figure 3.</u> Allometry of dispersal distances in terrestrial invertebrates across taxonomic orders (n ≥ 7 obs.). Regressions are performed on *in situ* data only. (a) Summary of taxonomic order-specific regression lines of capture-mark-recapture (CMR) data; (b) Diptera; (c) butterflies (Lepidoptera); (d) beetles (Coleoptera); (e) dragonflies and damselflies (Odonata); (f) true bugs (Hemiptera); (g) snails and slugs (Stylommatophora). In panel d, regression lines of alternative tracking methods are also reported: T: telemetry; HR: harmonic radar.

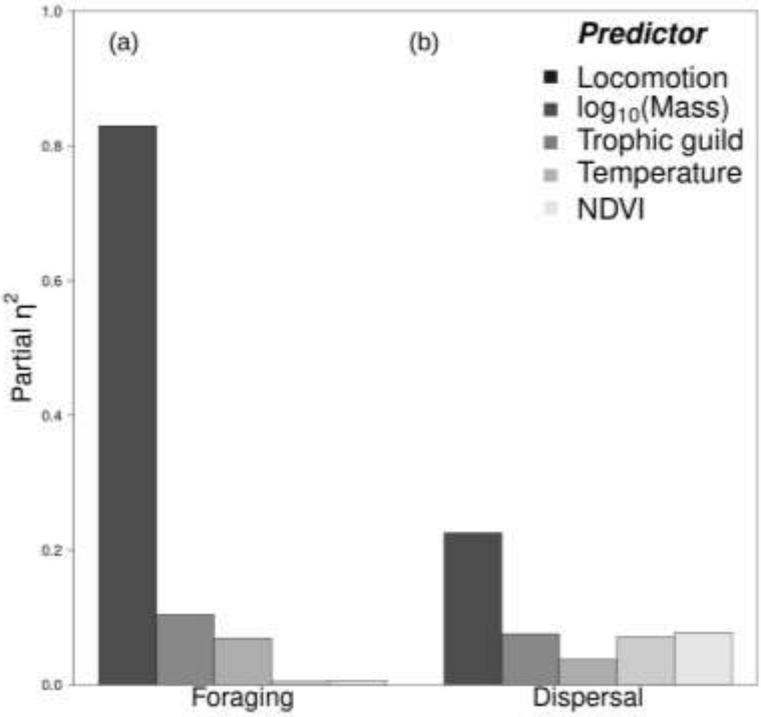


Figure 4. Effect sizes of locomotion mode, body dry mass, diet, temperature and NDVI as drivers of invertebrate foraging (a) and dispersal (b) movements. Tracking method and a nested taxonomic order/species effect are included in the models as random effects. Note that *in situ* studies only have been considered for this figure to allow the inclusion of the two environmental variables, temperature and NDVI.

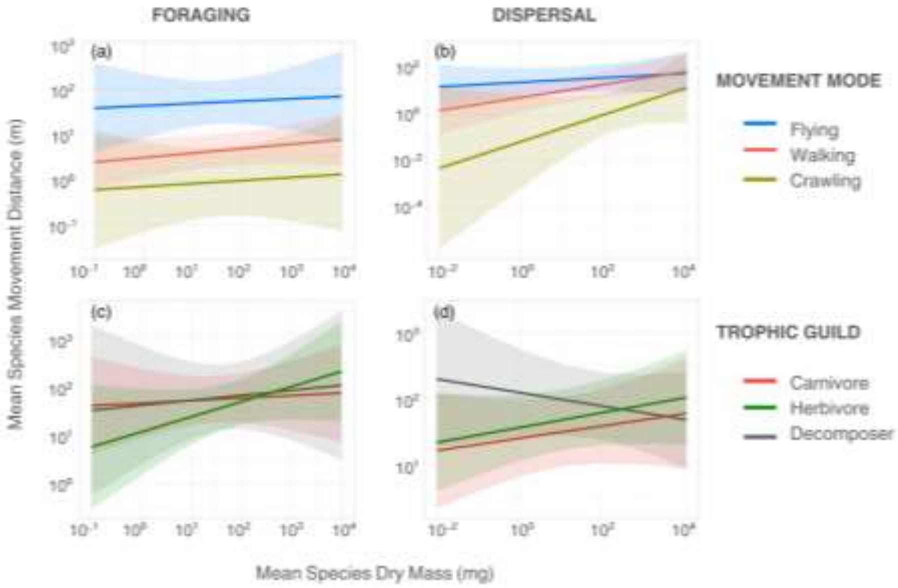


Figure 5. Allometry of space use across trophic guilds and species with similar locomotion strategies, taking taxonomic order and tracking method random effects into account. Regression line coefficients are reported in Table 2 (*Full models* parameters).

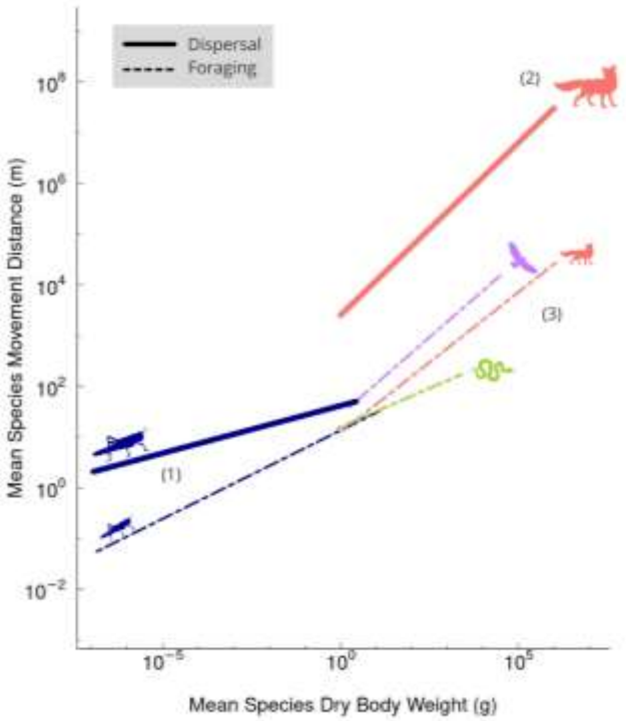


Figure 6. Comparative plot of the allometries of dispersal (thick, solid lines) and foraging (thin, dashed lines) movement distances between terrestrial invertebrates (dark blue lines) and terrestrial vertebrates (pink: mammals, purple: birds, green: reptiles). Sources: (1) this study; (2) Santini *et al*. (2013); (3) Tamburello *et al*. (2015).

SUPPORTING INFORMATION

Appendix 1 – Calculation details for the database compilation.

Appendix 2 – Full literature search strategy and additional figures.