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

5 **ABSTRACT**

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

11 **Location:** Worldwide.

12 **Methods:** We conducted a meta-analysis using 176 studies. They provided 411 movement
13 estimates: 175 foraging movement estimates for 101 species, 51 families and 19 orders, and
14 236 dispersal estimates for 131 species, 53 families and 16 orders. These estimates were
15 complemented by several organism functional traits: body mass, diet, locomotion mode, and
16 by environmental variables of the study sites: temperature and NDVI. We computed
17 allometric relationships between movement distances and body mass both globally and
18 separately for each taxonomic order with sufficient data. We tested the relative influence of
19 the co-variables on movement distances through model selection.

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

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

33 **Keywords**

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

40 INTRODUCTION

41 Animal movements have widespread consequences at population, community,
42 ecosystem and evolutionary levels. They alter local population density and growth rate
43 through emigration and immigration (Law *et al.*, 2003) as well as metapopulation dynamics
44 and evolution (Hanski & Gaggiotti, 2004). At the community level, previous research has
45 mainly focused on the role of dispersal limitation in metacommunity dynamics (Holyoak *et*
46 *al.*, 2005) and the associated response of biodiversity to climate changes (Lenoir *et al.*, 2020).
47 The key role of other types of movement for community dynamics has also been stressed, in
48 particular the role of foraging movements in the spatial dynamics of foodwebs (Amarasekare,
49 2008) and more generally community assembly (Schlägel *et al.*, 2020). Animal movements
50 also couple the dynamics of distinct habitats by their associated transfer of matter and energy.
51 A substantial body of theory on such meta-ecosystem dynamics has been developed
52 (Gounand *et al.*, 2018a; Guichard & Marleau, 2021), and available data demonstrate the
53 significance and breadth of such transfers (Gounand *et al.*, 2018b; McInturf *et al.*, 2019).

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

72 Movement ecology has advanced rapidly over the past few decades and a conceptual
73 framework has been proposed to unify research on all movement types within a common
74 context (Nathan *et al.*, 2008). A general understanding of the drivers and spatial extents of
75 animal movements is indeed of particular relevance for diverse research topics, including
76 ecosystem modeling (Earl & Zollner, 2017), biological control (McEvoy, 2018) or niche
77 tracking in a context of global changes (González-Varo *et al.*, 2017). To understand the
78 commonalities in movement patterns across the animal kingdom, data syntheses are needed
79 to document the magnitude and variability of movement rates among and within species, but
80 also to understand their drivers. Several syntheses revealed that interspecific variability in
81 movement distances is mostly driven by functional and life-history traits in vertebrates.
82 Among these traits, body size has been found to be the main factor that correlates positively
83 with migration (Hein *et al.* 2012), foraging (Tamburello *et al.*, 2015) and dispersal distances
84 (Sutherland *et al.*, 2000; Santini *et al.*, 2013). At a global scale, large body sizes and fast life

85 history strategies have been shown to facilitate tetrapod lineage dispersal between
86 biogeographical regions in a majority of clades (Weil *et al.*, 2023). Locomotion mode (flying,
87 walking or swimming) alters the intercept and slope of the allometries between movement
88 and body size because of the varying penetrability of the associated medium (air, land or
89 water). Larger movement distances are observed in more penetrable media (Tamburello *et al.*,
90 2015; Straus *et al.*, 2022). These studies also evidenced that diet is a significant
91 determinant of space use with carnivores foraging and dispersing over larger distances than
92 herbivores to compensate for lower resource densities (Sutherland *et al.*, 2000; Santini *et al.*,
93 2013). They have also demonstrated a significant phylogenetic inertia of movement distances
94 with taxon-specific allometric relationships with body size.

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

112

113

114 **METHODS**

115 **Literature search and data selection**

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

125 Studies were retained if they provided quantitative information about mean active
126 dispersal distance (m) and/or mean foraging distance (m) or home range size (m²) for

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

138 **Foraging and dispersal distances**

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

151 **Body mass**

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

161 **Locomotion mode**

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

168 at the time of the study, and used the corresponding body mass and trophic guild for this life
169 stage.

170 **Trophic guild**

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

179 **Habitat**

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

190

191 **Methodology**

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

197 **Statistical analysis**

198 Taxon-specific allometry of space use. Prior to all analyses, we log-transformed
199 (Log_{10}) body mass and movement distances to linearize movement responses. We first
200 performed ordinary least square (OLS) regressions to assess the allometry of space use for
201 each taxonomic order that presented more than seven observations in our database. Since we
202 found that movement distances estimated by *ex situ* studies are significantly larger than those
203 estimated *in situ* (dispersal: ANCOVA: $F = 76.232$, $p = 5.15$; foraging: ANCOVA: $F = 42.925$,
204 $p = 6.50e-10$), we performed our analyses on *in situ* studies only, except for the *Haplotaxida*
205 order for which we only found foraging data from laboratory studies. For each taxonomic
206 order, we performed mixed models with a species random intercept to deal with multiple data

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

209 Functional and environmental drivers of interspecific variations in space use.
210 Because of the significant differences found between the *in situ* and *ex situ* movement
211 estimates, we continued to perform our next analyses on the subset of the *in situ* studies only.
212 We first tested the influence of functional drivers on movement distances, by assessing
213 whether the locomotion mode and trophic guild influenced the coefficients of our initial
214 allometric models: “(Dispersal or foraging) Distance ~ Dry Mass”. We built mixed models to
215 test each predictor separately for both dispersal and foraging data sets, with tracking method
216 included as a random effect, and taxonomic order and species identity incorporated as a
217 nested random effect, all on the intercept value. These random effects allowed us to deal with
218 multiple tracking methods and multiple points per species while accounting for phylogenetic
219 interdependence. We tested interaction effects between body mass and locomotion mode, and
220 between body mass and trophic guild. We finally combined these two hypothesized
221 functional drivers into a “full” model. The relative support of each model was assessed with
222 the Akaike Information Criterion corrected for small samples (AICc). The marginal and
223 conditional R² of the models were calculated to assess the proportion of variance explained
224 respectively by the fixed effects alone, and by both fixed and random effects, with the
225 “r.squaredGLMM” function from the ‘MuMIn’ R package (Bartoń, 2023).

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

233 Comparison with previous vertebrate studies. Finally, we extracted dispersal and
234 foraging regression parameters for terrestrial vertebrates from previous syntheses of the
235 literature to contrast with our own regression parameters. Dispersal distance regression
236 estimates for terrestrial mammals were obtained from Santini *et al.* (2013) and transformed to
237 express movement distance from kilometers to meters. Home range allometric relationships
238 were obtained from Tamburello *et al.* (2015) for mammals, birds and reptiles, and
239 recomputed from the original database with the radius of the home range area (m²) used as a
240 proxy for foraging distance. For consistency with our invertebrate analysis, we used the
241 following k factors to convert vertebrate fresh body mass to dry body mass: mammals:
242 k=0.2845 (Schlesinger & Potter, 1974); birds: k=0.344 (Sturges *et al.*, 1974); reptiles: k=0.24
243 (Barron, 1997) where dry mass = k x fresh mass. We then compared the foraging allometry of
244 invertebrates with those of the different vertebrate groups (birds, mammals and reptiles)
245 using a Chow test implemented in the ‘gap’ package (Zhao *et al.*, 2023). The Chow test could
246 not be used for the comparison of the dispersal behavior of invertebrates and mammals, for
247 which we only had regression parameters and no raw data.

248 **Phylogenetic signal**

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

261

262 **RESULTS**

263 **Datasets**

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

280

281 **Allometry of space use**

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

291 When looking at the different taxonomic orders separately, we confirm a strong
292 phylogenetic signal in movement distances with a wide variation of regression estimates
293 among taxonomic orders for both foraging (**Figure 2**) and dispersal (**Figure 3**) movements.
294 We recover a positive relationship between body mass and movement distances for most
295 taxonomic orders, but with variable slopes (**Table 1**). Only *Odonata* show a non-significant
296 negative correlation between body mass and both dispersal and foraging distances (**Table 1**).
297 We also note a strong dispersion of data points of Coleoptera and Hemiptera dispersal
298 distances around the regression line, whose slope coefficients are almost null ($b = 0.03$ and
299 0.00 , respectively, **Table 1**).
300

301 **Effects of functional traits and environmental factors on movement** 302 **distances**

303 We found that locomotion mode is the most influential driver of interspecific variations in
304 movement distances. The effect size of locomotion on foraging movement is particularly
305 strong, about 3.6 times larger than its effect size on dispersal (**Figure 4**). The other drivers
306 have comparatively low effects with partial- η^2 values below 0.1. Body mass is the second
307 most influential driver of foraging distance (partial- $\eta^2 = 0.10$), followed by trophic guild,
308 while temperature and NDVI have almost null effects. For dispersal distance, body mass,
309 temperature and NDVI have low but comparable effect sizes (partial- $\eta^2 = 0.076$, 0.071 and
310 0.078 , respectively) and trophic guild ranks last among the tested dispersal predictors. For
311 consistency with the other analyses, **Figure 4** includes taxonomic order, species identity and
312 tracking method as random effects. However, phylogeny predominates all other factors of
313 dispersal distance, and ranks second for foraging movements when tested as a fixed effect
314 (**Figure S4 in Appendix 2**).

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

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

331

332 **Comparison with terrestrial vertebrates**

333 Invertebrate body mass in our study spans eight orders of magnitude, exceeding vertebrate
334 body mass range in Tamburello *et al.* (2015) and Santini *et al.* (2013) by two and three orders
335 of magnitude, respectively (**Figure 6**). The observed overlap of body weights between
336 vertebrates and invertebrates comes from the 25 vertebrate species, mostly passerines and
337 rodents, that have lighter dry masses than the heaviest invertebrate in our database, which is
338 the Giant African land snail (*Lissachatina fulica*, Férussac 1821). We find clearly different
339 dispersal allometries between invertebrates and mammals, the latter having an intercept value
340 two orders of magnitude above that of invertebrates ($\log_{10}(a) = 3.40$ versus 1.62) and a
341 regression slope 3.6 times steeper ($b = 0.68$ versus 0.19). We also find that the allometry of
342 foraging of invertebrates is significantly different from that of birds and mammals (Chow-test
343 invertebrates-birds: $F = 4.77$, $p = 9.07e-03$; invertebrates-mammals: $F = 8.40$, $p = 2.66e-04$),
344 but not significantly different from the foraging allometry of reptiles (Chow-test: $F = 0.14$, p
345 $= 0.87$) (see **Figure S5 in Supplementary information**).

346 **DISCUSSION**

347 We assembled the first global database of movement patterns of terrestrial invertebrates,
348 focusing on active dispersal and foraging movements. Using this database, we documented
349 allometric relationships between body mass and foraging and dispersal movement distances
350 across major terrestrial invertebrate taxonomic orders. We then assessed whether invertebrate
351 movements were driven by the same functional traits as those evidenced for vertebrate taxa.
352 The relatively low contribution of body mass to the variability of invertebrate movement
353 distance strongly contrasts with previous results on vertebrates. While 24% and 20% of
354 variability is explained by invertebrates' body mass for dispersal and foraging movements
355 respectively in simple linear models, these values fall down to 7% and 10% (marginal R-
356 squared values) when considering taxonomy and tracking method as random effects. In a
357 similar analysis conducted on vertebrate species, Tamburello *et al.* (2015) evidenced that
358 body mass alone explained up to 44% of home range variability when controlling for
359 taxonomy and tracking method. Regarding the dispersal distance of mammals, Santini *et al.*
360 (2013) evidenced that body mass alone explained up to 64% of variance using a simple linear
361 regression model.

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

374 We further reported different allometries between invertebrates and vertebrates, except
375 regarding the foraging of reptiles (Figure 6) which share ectothermic metabolism with
376 invertebrates. Taken together, vertebrates have larger movement distances for a given body

377 mass and steeper allometric curves. A possible explanation for this discrepancy between
378 vertebrates and invertebrates may lie in differences between these groups in their mode of
379 thermoregulation, terrestrial vertebrates being in majority endothermic while invertebrates are
380 ectothermic. The energetic cost of endothermy may explain larger foraging distances of
381 endotherms to cope with this energy expenditure.

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

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

405 Some other potentially influential co-variables could not be assembled for our dataset.
406 Habitat and vegetation structure have been found to significantly affect mean displacement
407 range in some invertebrate taxa (Crist *et al.*, 1992) as for vertebrates (Bowers *et al.*, 1996).
408 However, the limited resolution of spatial products available at the global scale and for
409 ancient dates did not allow capturing relevant habitat and vegetation structure metrics for
410 most invertebrate species of our database that have movement distances below 250 meters
411 (foraging distance: median - 3rd quartile = 6 - 21m; dispersal distance: median - 3rd quartile
412 = 107 - 592m). We were neither able to collect enough diet and habitat specialization data to
413 explore the links between specialization level and movement distances that have been
414 evidenced in some taxa. For instance, carabid beetles that are strict specialists of woodlands
415 move much more slowly than habitat generalist species (Brouwers & Newton, 2008).
416 Differences in dispersal distance have also been evidenced between habitat specialists and
417 generalists, the latter ones being more explorative and dispersing further than specialists in
418 gastropods (Dahirel *et al.*, 2015).

419 Our synthesis reveals an over-representation of arthropods in invertebrate movement studies
420 (themselves being dominated by Coleopterans), while extensive data on the space use of

421 annelids, molluscs, nematodes and more generally of the tiniest species are still needed.
422 Tracking methods initially designed for vertebrates, like telemetry or harmonic-radar, have
423 only recently become suitable for studying the movement of the largest invertebrate species
424 (Chapman *et al.*, 2004; Kissling *et al.*, 2014). The development of innovative tracking
425 methods should improve the spectrum of animals whose movements might be studied in
426 future years (see for example Cointe *et al.*, 2023). For the tiniest invertebrates however, the
427 contribution of active movements to overall displacements is likely to strongly decrease
428 compared to the contribution of passive phoretic movements, especially for dispersal. The
429 exact mechanisms and the spatial extent of phoresy processes remain unclear (Bartlow &
430 Agosta, 2021). It would thus be inaccurate and misleading to extrapolate our dispersal data to
431 phoretic animals following our allometric equations.

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

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602 DATA ACCESSIBILITY STATEMENT

603 The compiled database and accompanying R script are available on Zenodo:

604 <https://zenodo.org/records/10230297>

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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]	0.37
	 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, 3.53]	-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
	<i>All orders</i>	<i>In situ : CMR</i>	175	<i>Sp. + Met.</i>	<i>0.46 [-0.27, 0.47]</i>	<i>0.35 *** [0.23, 0.48]</i>	<i>0.92</i>
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
		<i>All orders</i>	<i>In situ : CMR</i>	236	<i>Sp. + Met.</i>	<i>1.44 * [0.29, 1.81]</i>	<i>0.19 *** [0.08, 0.30]</i>

620 ession parameter estimates for body mass across separate taxonomic orders with $n \geq 7$
621 observations. Global regressions (*'All orders'*) include all taxonomic orders in our databases
622 without constraint on minimal number of data. Mixed linear models are of the form $\log_{10}(D)$
623 $\sim \log_{10}(a) + b \times \log_{10}(M)$ where D: movement distance and M: dry mass. Mixed linear models
624 include the tracking method as a random effect. Mixed linear models include the species
625 (*'Sp.'*) and the tracking method (*'Met.'*) when needed as a random effect. We used the most
626 frequently used tracking method as the reference for each taxonomic order. $\log_{10}(a)$:
627 intercept; b: slope; 95% CI: 95% confidence interval. R^2 corresponds to the conditional R^2 for
628 mixed models. Significance (p-values) codes: 0 *'***'* 0.001 *'**'* 0.01 *'*'* 0.05 *'.'* 0.1 *' '*.

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MOVEMENT	HYPOTHESIS	MODEL	$\log_{10}(a)$ (95% CI range)	b (95% CI range)	R ² marg.	R ² cond.	Δ AICc	
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 (flying)	1.47 *** [0.91, 1.98]	0.14 . [0.00, 0.28]	0.39	0.88	-26.05
			(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	(flying)	1.55 *** [0.81, 2.26]	0.09 [-0.25, 0.43]	0.40	0.88	-21.69	
		(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	(carnivore)	0.31 [-0.32, 0.93]	0.25 ** [0.09, 0.42]	0.06	0.91	-4.28
			(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	(carnivore)	0.39 [-0.24, 1.00]	0.16 . [-0.03, 0.36]	0.11	0.92	-4.90
			(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]			
	<i>Full model</i>	- M + L + TG + M:L + M:TG	(flying)	1.62 *** [0.90, 2.33]	0.05 [-0.31, 0.41]	0.40	0.88	-15.82
			(walking)			
(crawling)			0.48 **	0.10				
(carnivore)			-0.16 **	0.07				
(herbivore)						
(decomposer)			1.04 .	0.31				
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 (flying)	1.51 *** [0.91, 2.06]	0.13 * [0.00, 0.26]	0.23	0.90	-20.07
			(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	(flying)	1.55 *** [0.94, 2.10]	0.07 [-0.07, 0.21]	0.22	0.86	-18.85	
		(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	(carnivore)	1.04 ** [0.31, 1.71]	0.10 [-0.04, 0.24]	0.08	0.92	-1.97
			(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]			
	<i>Full model</i>	- M + L + TG + M:L + M:TG	(flying)	1.36 *** [0.61, 2.02]	0.10 [-0.15, 0.35]	0.26	0.89	-15.48
			(walking)			
(crawling)			0.71 ***	0.28 *				
(carnivore)			-1.18 **	0.58				
(herbivore)						
(decomposer)			1.53	0.12				
			2.06 *	-0.10				

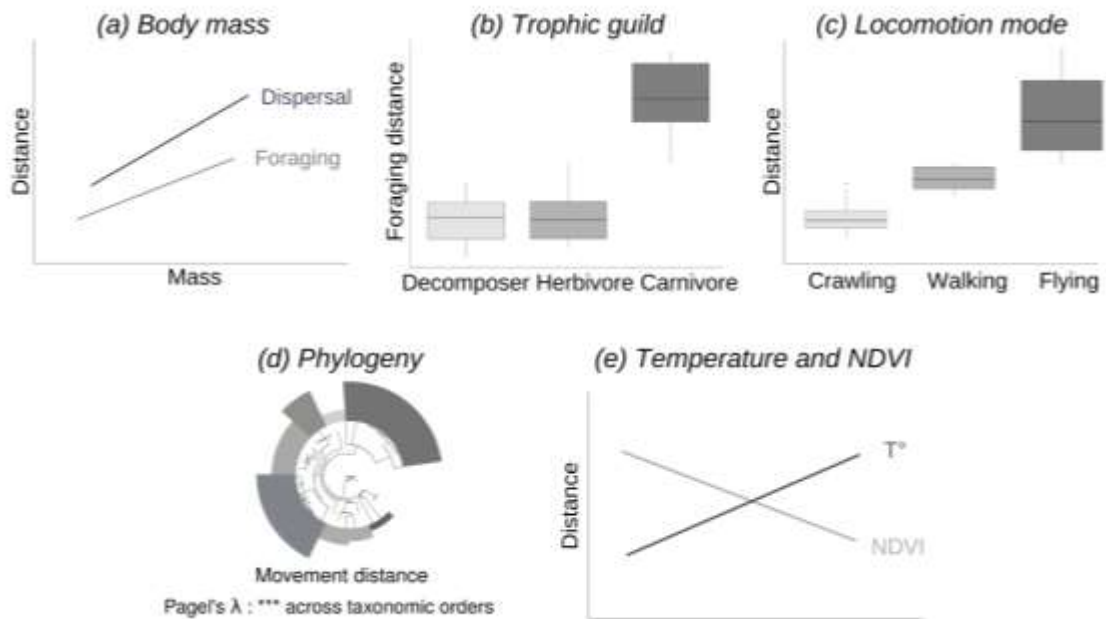
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Table 2. Allometric regression results for linear mixed-effect models. Taxonomic order and species were included in all models as nested random effects, and tracking method was included as a simple random effect. $\log_{10}(a)$: intercept; b : slope; R² marg.: marginal R²; R² cond.: conditional R²; 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 ' '.

645 **FIGURES**

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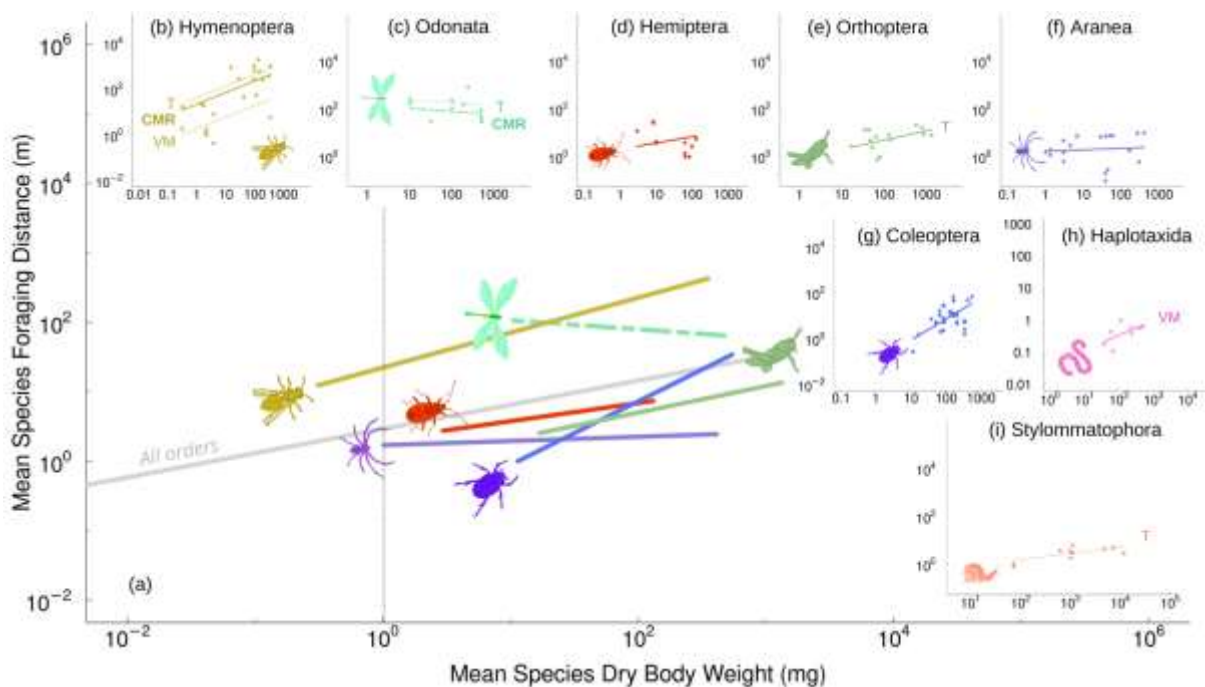
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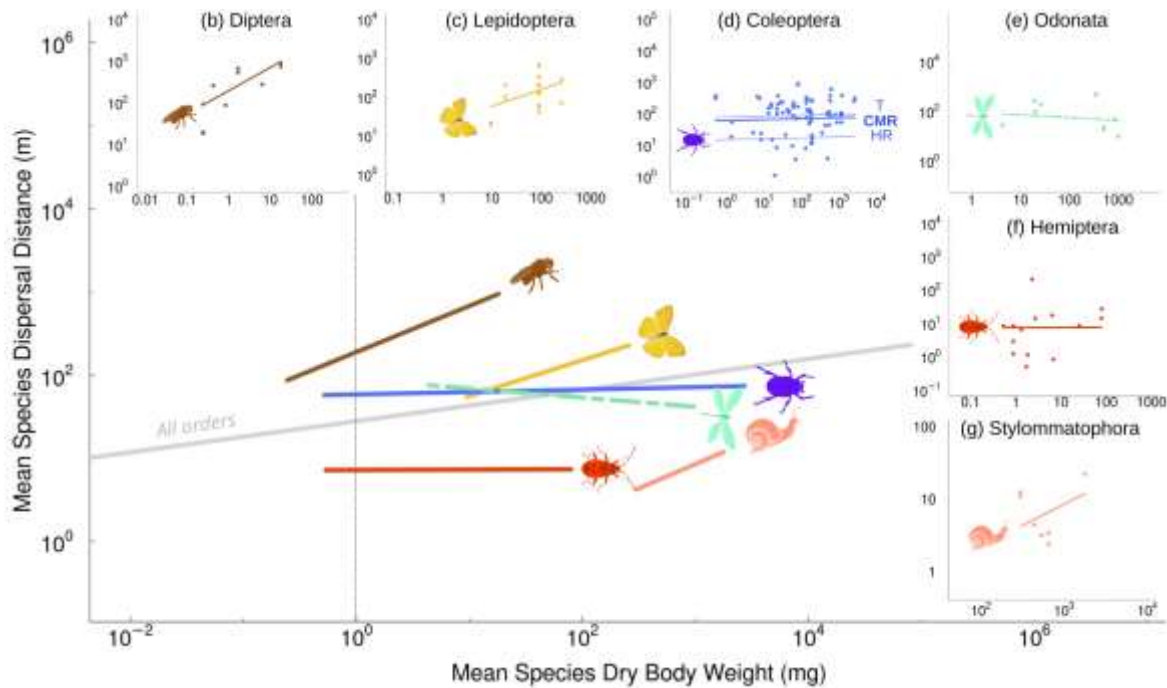
654 Figure 1. Tested predictions: (a) Positive scaling of dispersal and foraging distances with
 655 body mass; (b) Carnivores are expected to forage further than herbivores and decomposers;
 656 (c) Flying individuals move further than walkers, both moving further than crawlers; (d)
 657 Phylogenetic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

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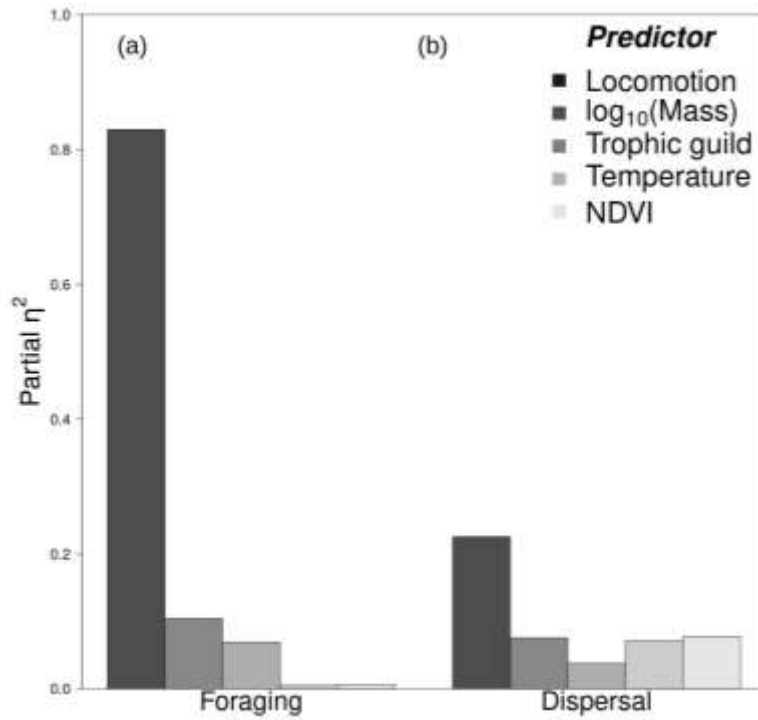
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Figure 2. Allometry of foraging distances in terrestrial invertebrates across taxonomic orders ($n \geq 7$ obs.). Regressions are performed on *in situ* data only, except for panel (h) (lab studies only). (a) Summary of taxonomic order-specific regression 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.



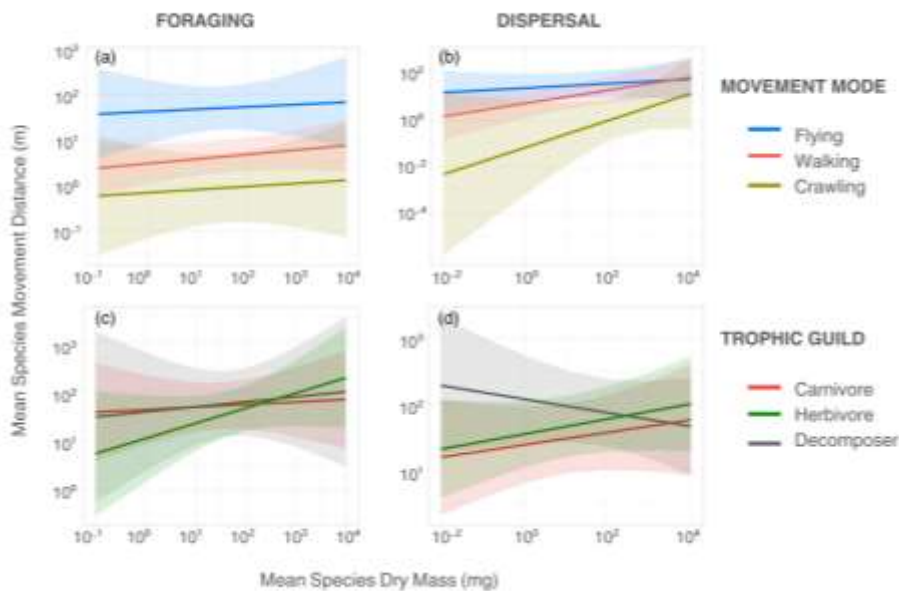
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Figure 3. Allometry of dispersal distances in terrestrial invertebrates across taxonomic orders ($n \geq 7$ obs.). Regressions are performed on *in situ* data only. (a) Summary of taxonomic order-specific regression lines of capture-mark-recapture (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.



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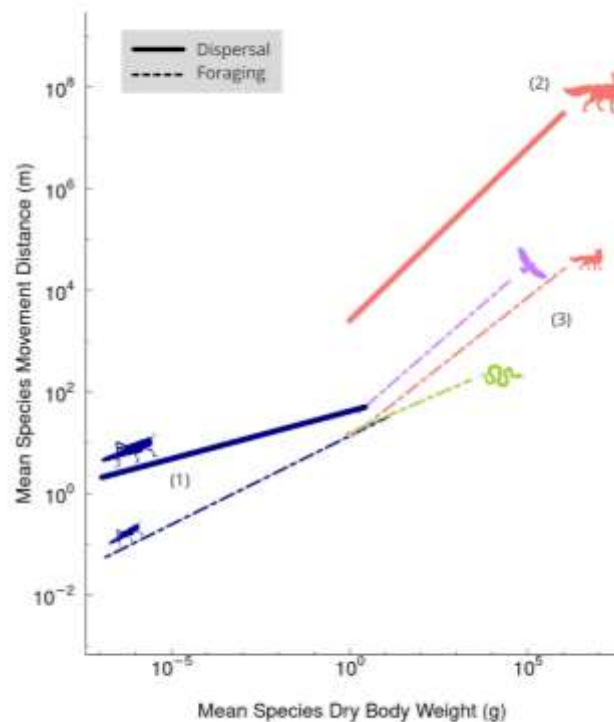


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723 Figure 5. Allometry of space use across trophic guilds and species with similar locomotion
724 strategies, taking taxonomic order and tracking method random effects into account.
725 Regression line coefficients are reported in Table 2 (*Full models*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

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

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755 SUPPORTING INFORMATION

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757 **Appendix 1** – Calculation details for the database compilation.

758 **Appendix 2** – Full literature search strategy and additional figures.

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