Unravelling arthropod movement in natural landscapes: small-scale effects of body size and weather conditions

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Abstract

1. Arthropod movement has been noticeably understudied compared to vertebrates. A crucial knowledge gap pertains to the factors influencing arthropod movement at habitat boundaries, which has direct implications for population dynamics and gene flow. While larger arthropod species generally achieve greater dispersal distances and large-scale movements are affected by weather conditions, the applicability of these relationships at a local scale remains uncertain. Existing studies on this subject are not only scarce but often limited to a few specific species or laboratory conditions.
2. To address this knowledge gap, we conducted a field study in two nature reserves in Belgium, focusing on both flying and cursorial arthropods. Over 200 different arthropod species were captured and released within a circular setup placed in a resource-poor environment, allowing quantification of movement speed and direction. By analysing the relationship between these movement variables and morphological (body size) as well as environmental factors (temperature and wind), we aimed to gain insights into the mechanisms driving arthropod movement at natural habitat boundaries.
3. For flying species, movement speed was positively correlated with both body size and (tail)wind speed. In contrast, movement speed of cursorial individuals was solely positively related with temperature. Notably, movement direction was biased towards the vegetated areas where the arthropods were originally caught, suggesting an internal drive to move towards suitable habitat. This tendency was particularly strong in larger flying individuals and under tailwind conditions. Furthermore, both flying and cursorial taxa were hindered from moving towards the habitat by strong upwind.
4. In conclusion, movement speed and direction at patch boundaries are dependent on body size and prevailing wind conditions, and reflect an active decision-making process.

1. Background

Movement is a crucial component of the life history of many organisms. Across small and large spatial scales, it mitigates the finding of resources and mates, ultimately shaping species distributions and interactions (Bowler & Benton, 2005; Gilbert et al., 1998; McIntyre & Wiens, 1999). Studies involving animal movement tend to focus on vertebrates, leaving other groups like arthropods severely underrepresented, despite the latter constituting a substantial portion of the global biodiversity (Clark & May, 2002; Kissling et al., 2014). Admittedly, studying arthropod movement involves many inherent challenges, such as their small size and vast species diversity. Nevertheless, understanding the ecological dynamics of arthropods is crucial, as they play pivotal roles in ecosystem functioning through processes like pollination, nutrient cycling and trophic interactions (Yang & Gratton, 2014).

In mosaic landscapes, arthropods may encounter challenging environments while seeking resources or evading unfavourable conditions (Lima & Zollner, 1996; Zollner & Lima, 1999). These unfavourable zones are known as “matrix” (Ricketts, 2001; Shreeve & Dennis, 2011). Movement and orientation behaviours at habitat-matrix boundaries will therefore further influence the fate of each individual: drifting further in the matrix and losing any connection with the home patch or any other potential habitat, or returning to the home patch and remaining philopatric to the experienced environment. Unlike routine movements within a habitat, compensatory movement (Peterman et al., 2014; Schtickzelle et al., 2006) through the matrix tends to be rapid with a higher degree of directionality (Hein et al., 2003; Mola et al., 2020; Van Dyck & Baguette, 2005). Consequently, it can be expected that crossing a hostile matrix will impose substantial dispersal costs (Bonte et al., 2012), particularly for small-bodied organisms like arthropods (Hillaert et al., 2018). Behaviours at boundaries are therefore expected to have pervasive effects on population dynamics, gene flow and hence the adaptive capacities of species in fragmented landscapes (Batsleer et al., 2023; Driscoll et al., 2013).

Body size stands out as one of the most relevant factors influencing arthropod movement and orientation, due to its association with various morphological, physiological and life-history traits

(White et al., 2007; Woodward et al., 2005). Numerous arthropod taxa, ranging from cursorial groups (i.e. individuals running on the ground) like ants and beetles, to flying taxa such as butterflies, bugs and dragonflies, seem to consequently exhibit an allometric relationship between body size and mobility (Hirt et al., 2017; Hurlbert et al., 2008; Kuussaari et al., 2014; Sekar, 2012; Wootton, 2020). Larger arthropod individuals, both within and across species, generally display greater mobility, resulting in higher movement speeds and larger travelling distances. Such movement speeds and their directions can be influenced by weather conditions. The impact of local weather conditions should be most apparent for small-scale movement bouts, because of the high variability of weather conditions at small temporal and spatial scales, either because of changing weather conditions or local microclimate. A first component of local weather conditions is the prevailing temperature. Higher ambient temperatures have been shown to positively impact the activity and running speed of invertebrate ectotherms, owing to improved oxygenation rates and enhanced kinetic muscle properties (Frizzi, 2018; Hurlbert et al., 2008). Moreover, arthropod species often adjust their movement behaviour according to the local thermal conditions, with some even requiring a minimum ambient temperature to initiate movement (Frizzi, 2018; Knight et al., 2019; Knoblauch et al., 2021). However, movement responses to increased temperatures are also constrained by critical thermal upper-limits, leading to impaired movement capacity when temperatures exceed these thresholds (Chown & Nicolson, 2004; Dudley, 2000; Heinrich, 1995). A second component of local weather is wind. The direction and force of the wind exert considerable influence on movement distances and decisions, especially for flying insects undertaking long-distance dispersal (Knoblauch et al., 2021). Additionally, many arthropods possess anemotactic reception, allowing them to accurately estimate the direction of prevailing winds by sensing air currents, and consequently, make informed choices regarding movement trajectories (Buehlmann et al., 2020; Knoblauch et al., 2021).

Most of the previously mentioned research on the relationships between arthropod movement, body size and weather conditions focuses on large-scale distances, and usually involves only a limited number of large and highly mobile species (Frick et al., 2013; Knight et al., 2019; Knoblauch et al.,

2021). Small-scale movement studies investigating biometeorological relationships in arthropod movement are scarce (Aikman & Hewitt, 1972; Eguagie, 1974; Merckx et al., 2008) and especially lacking when considering behaviour at habitat boundaries. Traditional methods, such as capture-mark-recapture or tracking devices, have limitations in achieving large sample sizes, often leading to a narrow focus on individual species and hindering generalizations across taxa and life history traits (Goodwin & Fahrig, 2002; Jonsen et al., 2001). Moreover, concerns have been raised about the use of such tracking devices, as the impact of these tags on arthropods is often neglected, ultimately biasing data (Batsleer et al., 2020). While some notable efforts have been made to study arthropod exploratory movement through image-based tracking under laboratory conditions, the applicability of these findings to natural field conditions remains uncertain (Hirt et al., 2017; Terlau et al., 2023).

This study aims to understand the interplay between movement, body size and weather conditions at habitat boundaries by conducting field release experiments on a diverse range of arthropod species. Two different nature reserves consisting of dune and heathland habitats were used as field sites, which differed in spatial heterogeneity. This allowed us to assess whether arthropods choose to move towards suitable habitat areas when venturing in the matrix. The realised movement speed and direction of arthropods at the patch boundary—without relying on tracking devices—was measured and correlated with individual body size and prevailing weather conditions. Movement behaviours after release represent movements that we consider to be relevant for short-term displacements when organisms leave their habitat and enter the matrix. Such release experiments have been conducted to understand perceptual ranges and movement at boundary responses in single species (Bonte et al., 2004; Kallioniemi et al., 2014; Merckx & Van Dyck, 2007; Schultz et al., 2012). Here we build on this earlier work but scale-up to multiple species thereby constraining release distances to a single relevant point in the landscape. We expect (i) a positive correlation between movement and body size, (ii) the strengthening of this effect under warmer temperatures and stronger tailwinds, (iii) an influence of wind conditions on the movement direction of flying insects, and (iv) a biased movement direction

towards suitable environments due to the perception (correct interpretation by the individual) of the environment and avoidance of risks when crossing the hostile matrix.

2. Methods

2.1 Experimental field work

The field work for this study was conducted during the summer of 2021 at two distinct locations in Belgium. The first site was a coastal dune grassland in De Panne, while the second site encompassed both dry and wet heathland patches in Kalmthout (details in Appendix S.1). Both sites differed in structural heterogeneity of the landscape. In the coastal dune site at De Panne, large areas of open sand (representing the matrix) bordered large areas of dense shrubland, thus creating a kind of "binary" landscape. In Kalmthout, patches of open sand were considerably smaller, and were embedded within a dense heath landscape, thereby creating a patchier landscape where matrix and habitat surrounded each other. By selecting these two distinct sites, we aimed to determine whether arthropod movement direction at habitat boundaries is either random or biased towards vegetated areas. If arthropods indeed show an internal drive to move towards habitat patches, we should find a strong bias towards one direction in De Panne, while movement should be more random at Kalmthout (see Appendix S.1).

Within the vegetated areas at both sites, arthropod individuals from various species were randomly captured either by hand or by sweep netting. Each captured individual was assigned a unique ID and photographed in the field with a graph paper (1 mm squares) as background. To assess the movement behaviour of these arthropods, separate set-ups were designed for flying and cursorial (i.e. running on the ground) individuals, as we anticipated different movement speeds and perceptual abilities. In a large area of open sand, which was assumed to be matrix for species living in vegetated areas, two circular set-ups were demarcated by placing coloured flags at five different radii with uniform interval distances (2 metres for flying individuals and 20 centimetres for cursorial individuals). Movement speed was measured using a chronometer, whereby the movement time was recorded as the duration

144 an individual took to traverse either 10 meters (for flying locomotion) or 1 meter (for cursorial
145 locomotion), or when an individual came to stop at a specific distance. The directions of movement
146 and wind were categorised using cardinal directions (N, NE, E, SE, S, SW, W or NW), and then converted
147 into angles in degrees, with west serving as the zero degrees reference (see further). By comparing the
148 movement and wind angles, we were able to determine whether the movement was aligned with the
149 wind or not, and to differentiate between movement upwind and movement assisted by tailwinds.
150 Specifically, we defined tailwind movements when the direction of movement deviated by a maximum
151 of 45 degrees from both sides of the prevailing wind direction, while upwind movements deviated by
152 at least 135 degrees from both sides of the prevailing wind direction (or 45 degrees from both sides of
153 the direction of the tail; Figure 1). West was chosen as the zero degrees reference, as the vegetated
154 areas at De Panne were located in this direction relative to the experimental set-up (Figure 1). This
155 decision assumed that the arthropods would exhibit a preference for returning to the location where
156 they were initially caught, since they were released in a matrix with very few available resources. The
157 surface area of the matrix was sufficiently large to assume that moving through it would bring a high
158 energetic cost and uncertainty for the released arthropod. By adopting the orientation as shown in
159 Figure 1, we aimed to gain insights in navigation behaviour, as movement patterns would likely reflect
160 the tendency and ability to return to the habitat of origin.

161 During measurements, the captured arthropods were temporarily housed in dark boxes to minimize
162 stress and prevent mortality due to overheating. Each individual spent a maximum of thirty minutes in
163 these boxes. Subsequently, the arthropods were taken out one by one and released in the open sand.
164 To mitigate the likelihood of an escaping movement response and directional bias arising from the
165 researchers' presence, cursorial animals were released at a distance of 1 meter from the observer,
166 whereas flying animals were released above the head of the observer. Individuals were not chased by
167 the researchers and had complete freedom to decide when and where to move. By doing this, we
168 aimed to minimize stress and present the option to actively choose movement directions. In total,

1355 arthropod individuals from 255 different species were tested. Among these individuals, 762 exhibited flying locomotion, while the remaining 593 displayed cursorial locomotion.

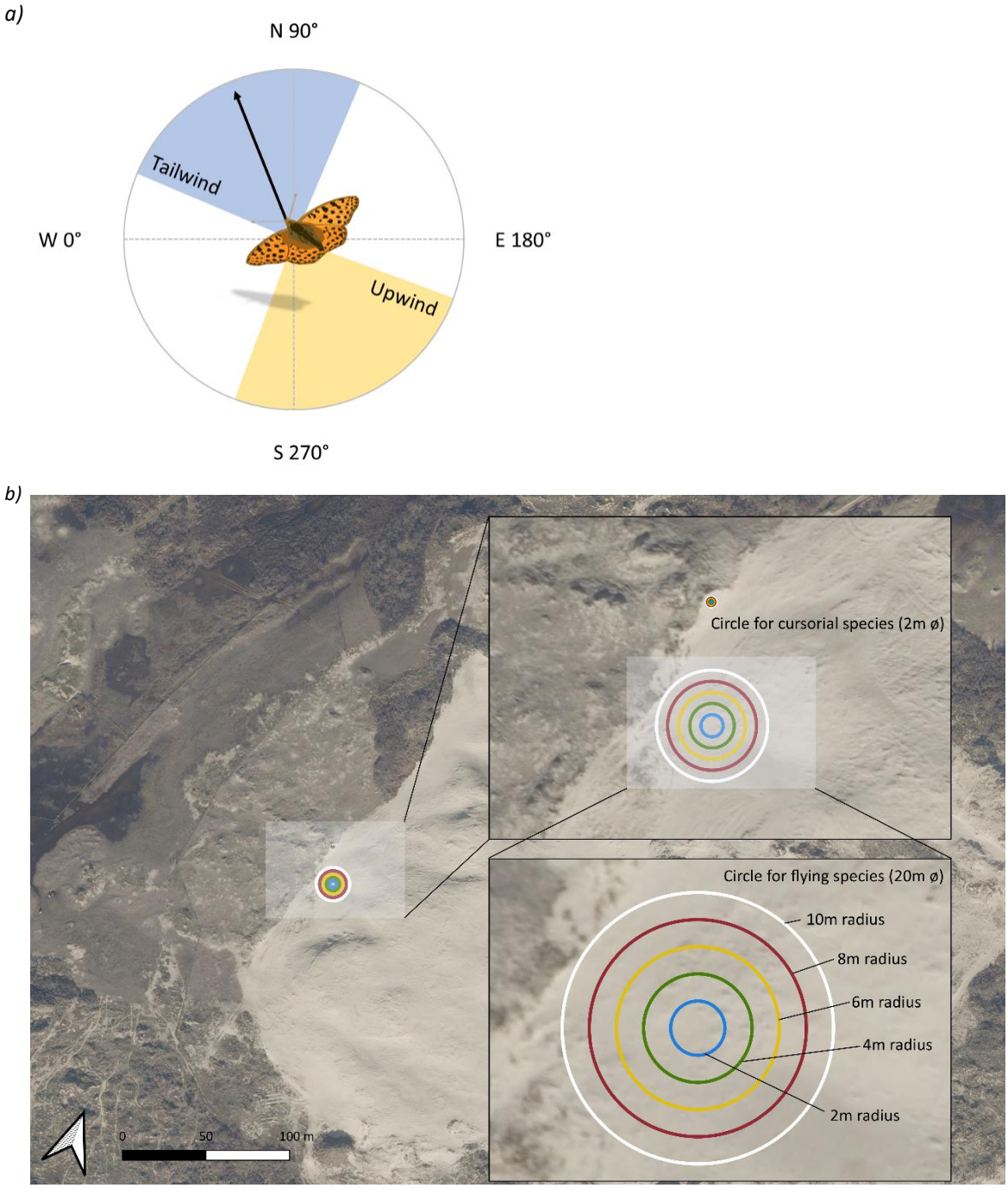


Figure 1: a) Schematic representation of how the cardinal directions were converted into angles. The black arrow indicates the direction of the movement. The blue area indicates all wind directions that can be classified as tailwind in this specific example, while the yellow area indicates upwind. b) Map of the experimental set-up at De Panne, with the vegetated areas to the west. Circular setups were drawn at a realistic scale. The illustrations in this figure were created by author Charlotte Taelman, aerial photograph (winter 2022) obtained from Agency for Information Flanders (geopunt.be).

172 Every half-hour of the release experiments, wind direction, wind speed and temperature were
173 recorded at an average height of 1.5 to 1.8 metres, using a weather station equipped with a built-in
174 thermometer and anemometer. Wind speed was calculated as the average of the minimum and
175 maximum values measured within a half-minute interval. Sampling days were carefully selected to
176 ensure suitable weather conditions for representative arthropod movement: a cloud cover below 60%
177 and temperatures between 15°C and 34°C.

178 Due to practical constraints, determining the dry weight of individual arthropods was not feasible.
179 Body length was used instead as an alternative proxy for body size (Ganihar, 1997; Martin et al., 2014;
180 Moretti et al., 2017). The photos of the arthropods taken in the field were analysed using ImageJ
181 version 1.52a (Schneider et al., 2012). The grid pattern in the background of the photos was used as
182 reference to measure the length of each individual's body, starting from the cephalon (excluding the
183 antennae) and extending to the tip of the abdomen.

184 **2.2 Statistical analyses**

185 All data analyses were conducted using R version 4.2.2 (R Core Team, 2021). The "dplyr" package
186 (Wickham et al., 2022) was used for general data manipulation and organization. All visuals were
187 created with the "ggplot2" (Wickham, 2016), "RcolorBrewer" (Neuwirth, 2022) and "showtext" (Qiu,
188 2023) packages.

189 ***2.2.1 Movement speed***

190 As a first explorative analysis, a Principal Component Analysis (PCA) was conducted, separately for
191 flying and cursorial species to understand how species movement behaviours group according to their
192 traits, phylogeny and the prevalent environmental conditions.

193 To confirm any observed relationships between movement speed, body size and weather conditions
194 in flying and cursorial arthropods, a distinct Bayesian Generalized Linear model was employed for each
195 group ("brms" package (Bürkner, 2021)). The dependent variable in these models was movement

speed, while the independent variables were body size, temperature and wind speed (all standardized to a mean of zero and a standard deviation of one). The models were fitted with a Gaussian distribution using 4 chains and 4000 iterations to ensure reliable results. Non-informative flat priors were used for the model parameters. As we expected wind speed to have opposing effects depending on its orientation relative to an individual's movement, we constructed additional models by splitting the dataset into individuals that moved either tail- or upwind, and ran two separate models. This approach was used to test potential differences in responses and proved to be more efficient than the incorporation of an interaction between two circular variables to the Bayesian models.

Since the models did not account for the potential influence of phylogenetic relationships between species, additional models were constructed to address this issue. For this purpose, phylogenetic trees were created by linking the species names to the Open Tree Taxonomy database, establishing a tree based on the known phylogenetic relationships between species ("rotl" package (Michonneau et al., 2016)). Branch lengths were calculated with the "ape" package (Paradis & Schliep, 2019) using the "Grafen" method (Grafen, 1989), leading to the construction of a phylogenetic covariance matrix ("geiger" package (Matthew et al., 2014)). First of all, this tree was used to calculate Pagel's lambda, a measure for the phylogenetic signal in a specific trait, for movement speed and direction of both flying and cursorial species ("phytools" package (Revell, 2012)). Secondly, the phylogenetic distances between species were incorporated into all Bayesian Generalized Linear models (similar to those above) as blocking factors. By doing so, the models considered the phylogenetic relationships between species when analysing the correlation between movement speed and the other variables.

2.2.2 Movement direction

The analysis of arthropod movement behaviour in different wind scenarios involved several circular statistics tests ("circular" package (Agostinelli & Lund, 2022)). These analyses were performed separately for both sampling sites to analyse the effect of structural heterogeneity within the landscapes.

To assess the correlation between wind direction and movement direction, the Jammalamadaka-Sarma correlation coefficient (Jammalamadaka & Sarma, 1988) was calculated for both flying and cursorial arthropods within different taxonomic orders, limited to orders represented by 8 or more samples. Additionally, the Rayleigh's test of Uniformity (Pewsey et al., 2013) was performed to examine whether there was a unimodal directional bias in the distribution of arthropod movement directions. The significance of the results from these tests was evaluated by correcting for multiple testing using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995), addressing potential issues of false positives.

Furthermore, several Bayesian Generalized Linear Models were fitted to explore the relationship between body size and movement direction. For these analyses, only data from De Panne was used since the difference in direction between habitat and matrix was much clearer compared to the site at Kalmthout. A binary value (0 or 1) was assigned to indicate whether or not an individual had moved towards the habitat from where they were initially caught. Deviations greater than 45 degrees from the zero-degree point (west) were considered as not moving towards the habitat and were assigned a value of 0. Body size and wind speed were used as independent variables, while this binary value was the dependent variable, modelled using a binomial distribution with a logit link function. Temperature was omitted from these models because we considered it irrelevant in the context of navigation. As with movement speed, the datasets were again split to test whether different responses were present under upwind or tailwind conditions. Each model was again corrected for phylogenetic relationships, which involved constructing phylogenetic trees using Open Tree Taxonomy and incorporating phylogenetic distances as blocking factors in the models.

3. Results

3.1 Movement speed

The PCA (Figure 2) shows Odonata, having larger body sizes, to be separated from the other studied arthropod orders. That the first axis explains respectively 36% of the variation in flying species and 34% of the variation in cursorial species, shows that weather conditions are indeed an important determinant of movement. We further explore interspecific variation more into detail by means of (phylogenetically corrected) linear models.

In flying species, large species generally exhibited higher movement speeds compared to smaller ones (Figure 3a, left). However, this relationship appears to reach an optimal point around 15 mm body size, beyond which a further increase in body size does not lead to higher movement speeds (Appendix S.2.2). The overall positive impact of body size and wind speed on movement speed of flying species (Figure 3a, left) remains when only tailwind movements are considered, but disappears when movement occur upwind (Figure 3b,c, left). For tailwind speed, the correlation also demonstrated a saturation point, which occurred around 3 m/s wind speed, beyond which movement speed did not increase further (Appendix S.2.1). The overall positive effect of wind speed on movement speed is thus primarily driven by the effects found under tailwind conditions (Figure 3, left). Temperature did not exhibit a clearly determined effect on the movement speed of the studied flying insects (Figure 3, left). Pagel's lambda of movement speed was notably high (λ=0.733), indicating a strong phylogenetic signal. Nevertheless, as expected from the overlap among taxa in the PCA, phylogenetic corrections had no substantial qualitative impact on the posterior distributions of the effect sizes and their interpretation (Figure 3).

The movement speed of cursorial species was, in contrast, only affected by temperature (Figure 3, right), with the positive effect indicating higher speeds reached under warmer conditions. The Pagel's lambda of movement speed for the cursorial species was considerably smaller compared to flying species (λ=0.357).

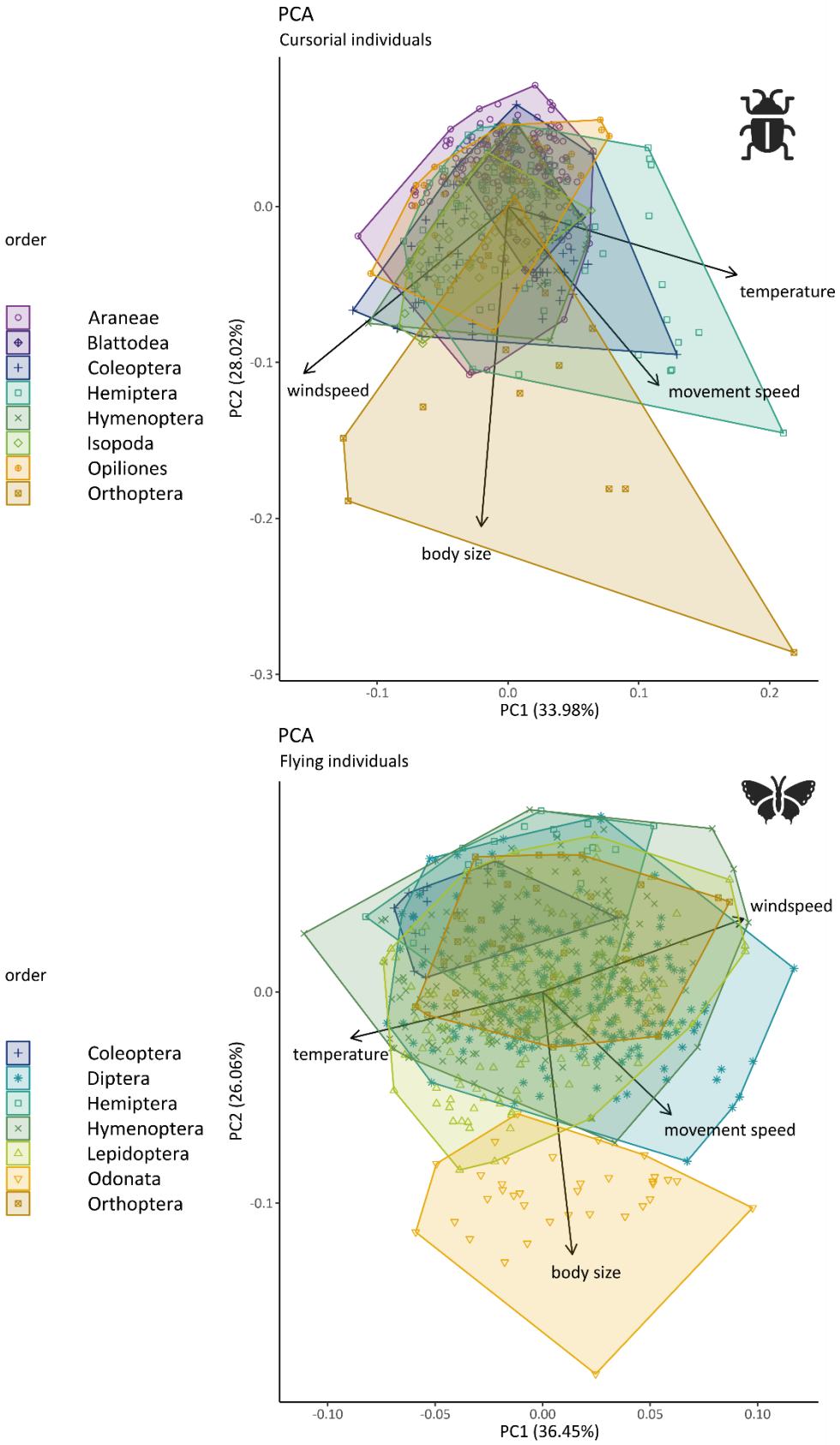


Figure 2: PCA results for flying (top) and cursorial (bottom) individuals. Dots represent individuals with symbol colour and shape according to their taxonomic order. A convex polygon is drawn around individuals of the same taxonomic order, by connecting the most extreme values.

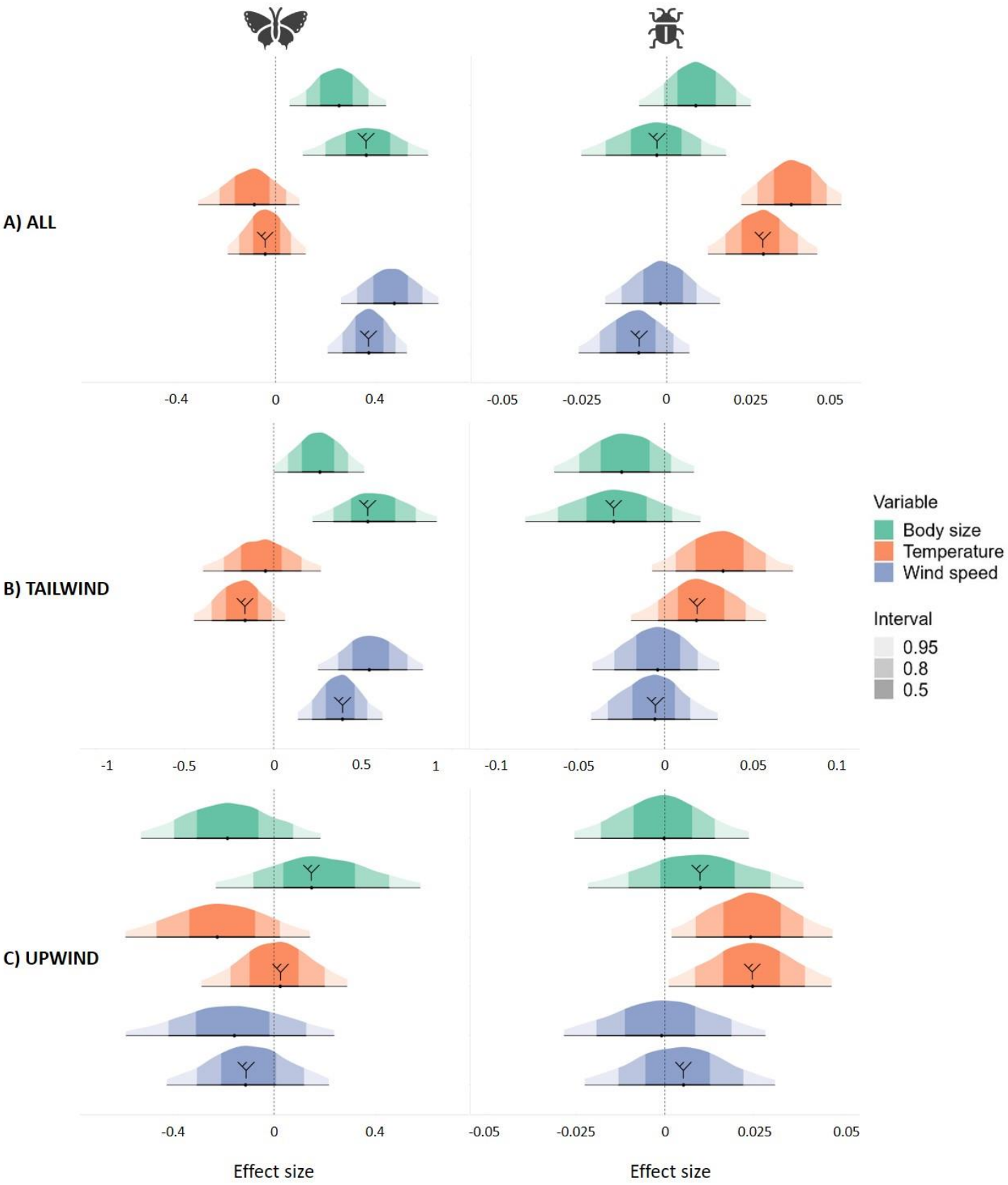


Figure 3: Posterior distributions of the effect sizes between movement speed as dependent variable and body size, temperature and wind speed as independent variables. For a) all wind conditions, b) tailwind conditions (n=527) and c) upwind conditions (n=281). Posterior distributions that are marked with a phylogenetic tree resulted from the phylogenetically corrected models. Effect sizes were deemed clearly determined when 0 was not included in the 95% credibility intervals of the posteriors.

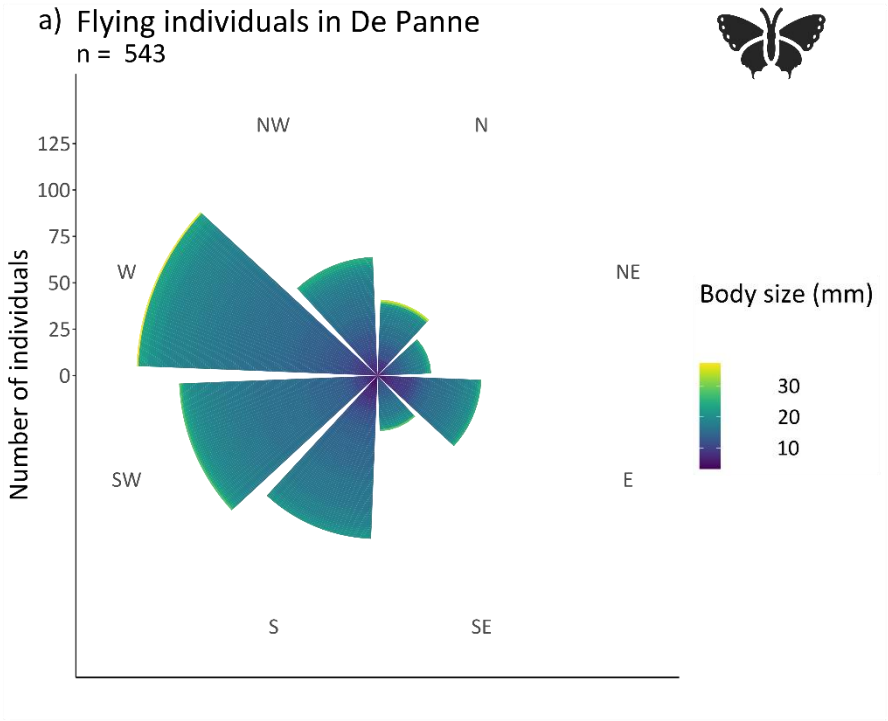
3.2 Movement direction

Arthropod movement exhibited a noticeable directional bias, indicating that individuals did not move randomly (Figure 4). The R-values, representing concentration of movement and thus directional bias, were significant after correction for multiple testing for most taxonomic orders (Appendix S.6). In addition, the Jammalamadaka-Sarma correlation coefficients between wind and movement direction did not show a general pattern across taxa, with some orders following the wind more than others (Appendix 2.7). However, these correlations where only significant for Lepidoptera (Kalmthout, r=0.36), Araneae (De Panne, r=0.34) and Diptera (De Panne, r=0.19).

At De Panne, where the habitat of the arthropod species was clearly located in one direction (northwest to southwest), movement direction was mostly oriented towards habitat areas across all observations (Figure 4). The lowest R-value at this site (R=0.19; p=0.05) was associated with a south-west wind opposite to the habitat direction, indicating lack of any directionality of movements under these wind conditions. In contrast, the highest R-value and hence strongest directionality prevailed under south-east winds, which largely aligned with the orientation towards the habitat (R=0.71, p<0.01). Furthermore, the Jammalamadaka-Sarma coefficient across all observations was positive (r=0.07), indicating a minor effect of wind direction on movement direction. In contrast, at the Kalmthout site, which was surrounded by suitable habitat in multiple directions, movement directional bias was only significant under NE winds (R=0.44; p<0.01). This indicates that arthropod movement was more random compared to the site at De Panne. Additionally, the Jammalamadaka-Sarma coefficient was larger (r=0.14) compared to De Panne, suggesting that movement direction was more positively aligned with wind direction.

Movement direction did not only correlate to wind direction, but additionally to wind speed as well. We ran Bayesian generalized linear models for the experiments in De Panne only, which showed that higher wind speeds reduce the efficiency of flying individuals to move towards habitat (Figure 5a, left). This effect was mainly steered by individuals tested under upwind conditions (Figure 5c, left). Similarly,

cursorial species only showed a negative correlation between wind speed and movement direction under upwind conditions (Figure 5, right). This indicates that strong upwinds lower the propensity of both groups to navigate back to the habitat. These patterns remained conserved under phylogenetic correction ($\lambda < 0.001$). Habitat-directed movements also differed with body size. Larger flying species are more prone to move towards habitat, while the pattern is reversed for cursorial species (Fig 5a, right). Additionally, the effect of wind speed on cursorial navigation only holds under upwind conditions when phylogenetically corrected ($\lambda = 0.210$).



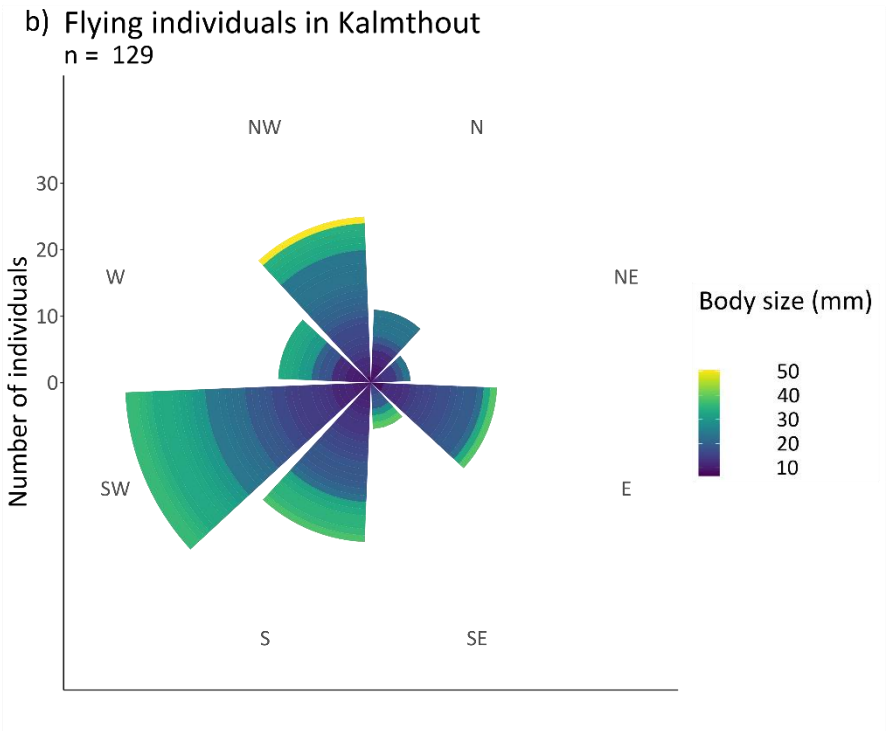


Figure 4: Circular bar plots of movement directions of flying species for both a) De Panne and b) Kalmthout site. Each concentric slice on the bar represents an individual, and is coloured according to its body size. Similar figures for cursorial and flying species under the different wind directions can be found in Appendix S.5.

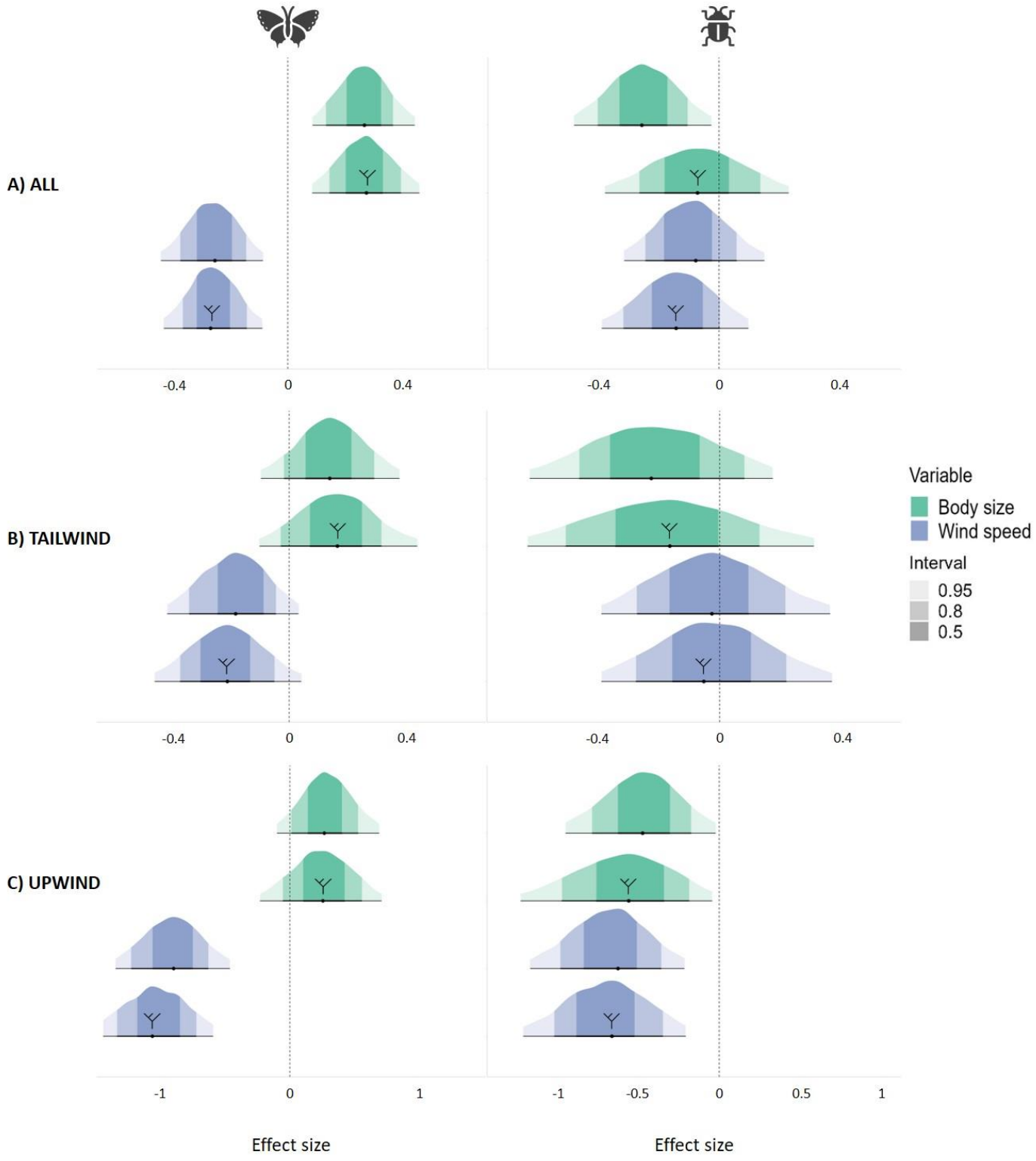


Figure 5: Poster distributions of the effect sizes between movement direction as dependent variable and body size and wind speed as independent variables. For a) all wind conditions, b) tailwind conditions (n=440) and c) upwind conditions (n=248). Only data from the De Panne site was used for this analysis. Posterior distributions that are marked with a phylogenetic tree resulted from the phylogenetically corrected models. Effect sizes were deemed clearly determined when 0 was not included in the 95% credibility intervals of the posteriors.

4. Discussion

We used release experiments to gain insights on the condition-dependency of small-scale arthropod movement at their patch boundary. Movements at this spatiotemporal scale can determine the future trajectories within or back from the matrix in fragmented habitats. These fundamental movement elements are anticipated to eventually shape large scale canonical and lifetime movement patterns (Getz & Saltz, 2008), and thus patterns of gene flow, colonisation-extinction dynamics and species assembly in fragmented landscapes (Batsleer et al., 2023; Jeltsch et al., 2013). Using a standardised approach under natural conditions, we demonstrate the importance of phylogeny, body size and weather conditions on arthropod movement in the hostile matrix close to the patch boundary. Larger flying arthropods exhibited greater movement speeds compared to their smaller counterparts, while the presence of strong tailwinds further increased their movement speed. In contrast, the movement speed of cursorial arthropods appeared unrelated to body size but displayed an increase in response to elevated temperatures. Notably, our observations revealed a clear directional bias towards habitat, indicating an internal drive among arthropods to move towards suitable environments. However, species showed varying levels of navigational proficiency, with larger flying and smaller cursorial arthropods displaying a greater tendency to move in the direction of suitable habitat. Furthermore, our study identified strong upwinds as a hindrance to both groups, impeding the capacity for navigation towards suitable habitat.

The positive correlation between movement speed and body size in flying arthropods was in alignment with our expectations. Previous studies already established that—within a taxon—larger arthropods tend to move faster (Kuussaari et al., 2014; Wootton, 2020). Our study emphasizes that this effect remains consistent across multiple taxa, even after accounting for phylogenetic relationships. Consequently, this means that there is a difference in movement speed between taxa, but the positive relationship between movement speed and body size is conserved. For example, larger bees are

generally faster than smaller bees or smaller butterflies, but do not necessarily surpass the pace of a larger dragonfly.

In contrast, the absence of a correlation between movement speed and body size in cursorial arthropods does not match the positive relationship retrieved in previous studies (Foellmer et al., 2011; Hirt et al., 2017; Hurlbert et al., 2008). A first possible explanation is that a relatively limited range of body sizes were tested, spanning from 1.21 mm to 21.31 mm, making it hard to detect a signal when effects are mainly determined by very large species. Secondly, our proxy for body size could obscure true relationships. For instance, harvestmen may appear small in our dataset due to their compact body length, but their long legs could enable faster running compared to species with similar body length (Arnold et al., 2017; Kaspari & Weiser, 1999; Smith et al., 2012). The use of a relative measure (e.g. leg or wing length relative to body length) remains, however, hard to generalize across taxa and thus limits the applicability for across taxa comparisons. A third potential explanation is linked to the interaction between the body mass of an individual and the texture of the surface on which it moves. Sand is a porous substance, in which heavier objects might sink faster compared to smaller objects. This could hamper movement of arthropods who do not have the morphological adjustments to move agilely on coarse-grained surfaces.

In addition to body size, wind speed also positively influenced the movement speed of flying individuals. Conversely, when individuals faced upwind, the effect reversed. This implies that movements away from habitat boundaries may be more pronounced when arthropods fly with the wind, which can assist them in traversing the matrix (DiLeo et al., 2022). However, under natural conditions, the prospect of winds blowing arthropods out of their habitat might deter them from departing, as for instance found in ballooning spiders (Bonte et al., 2007). In our study, however, individuals initiated movement in the local matrix after they had been placed there involuntarily. Release experiments as conducted by us with many species, or similar work on single species (Bonte et al., 2004; Kallioniemi et al., 2014; Merckx & Van Dyck, 2007; Schultz et al., 2012), are therefore

364 representative for movements at boundaries, when species accidentally or through routine behaviours
365 cross the habitat boundary. It is known that movement rules cause variability in movement
366 trajectories, but also conversely, that conditions experienced during different parts of the trajectory
367 affect the movement rules through e.g. ecophysiological feedbacks (Goossens et al., 2020). Insights
368 from our work are therefore mainly relevant for movement trajectories and consequent behaviour at
369 boundaries, but likely less for routine behaviours within suitable habitat or special dispersal behaviours
370 when crossing the matrix (Bonte et al., 2012; Clobert et al., 2009).

371 Surprisingly, temperature did not impact the movement speed of flying individuals. This can potentially
372 be attributed to the capacity of many flying arthropods to elevate their body temperature through
373 wing movement (Heinrich, 1974). Moreover, our dataset lacked extreme (hot or cold) temperatures
374 and we used an approximative measure for temperature, measured at the height of the observer, not
375 in the direct surroundings of the individuals. Both can potentially mask any trend between
376 temperature and movement of flying arthropods. In contrast, cursorial individuals demonstrated the
377 opposite pattern: temperature exerted a positive effect and wind did not. Given that cursorial species
378 remain in direct contact with the bare sand, they experience higher temperatures compared to flying
379 species due to the fast and more extreme heating of sandy surface. However they do not have specific
380 mechanisms in order to thermoregulate body temperature (Maes et al., 2006; Mutiibwa et al., 2015)
381 and it is thus expected that their movement is more directly linked to the temperatures within their
382 close environment. Our measurements reflect this, on condition that temperature measured at
383 observer height is directly related to surface temperature. Nevertheless, extremely high temperatures
384 can potentially become detrimental when a certain thermal threshold is reached, and consequently
385 impede any movement (Heinrich, 1995). We did not observe such conditions.

386 The movement direction of both flying and cursorial species exhibited a clear bias towards habitat
387 areas, indicating that the intention of moving towards suitable environments is a more important
388 driver for orientation than wind direction (Acevedo & Fletcher, 2017). This was supported by the data

389 from Kalmthout, where the movement direction should not matter that much since the set-up was
390 surrounded by habitat in multiple directions. At this site, we indeed observed that movement was
391 more random and correlated with wind direction, indicating that the arthropods at De Panne actively
392 chose to move towards suitable habitat. Homing behaviour and side fidelity have been shown in
393 Hymenoptera, Lepidoptera and Blattodea, indicating that insects are indeed able to actively navigate
394 the landscape and determine where suitable areas are located (Boeddeker et al., 2015; Moura et al.,
395 2022; Rivault & Durier, 2004).

396 Although the direction of movement is clearly related to the location of habitat, movement direction
397 was not completely decoupled from wind conditions. For both flying and cursorial species, strong
398 upwind negatively impacted the returning rates towards the habitat patch, indicating the wind's ability
399 to divert individuals away from patch boundaries, even if they are able to navigate. Nonetheless, the
400 preference for a specific direction persisted despite wind resistance, implying that arthropods are
401 willing to endure, at least at small spatial scales, the energetic costs associated with navigating towards
402 hospitable patches. Similarly, tailwind assistance could minimize energy expenditure during
403 movement, which is in line with much larger-scale observations from migratory species (Knight et al.,
404 2019; Knoblauch et al., 2021). Only when winds were aligned with the habitat direction, a clear-cut
405 positive correlation between movement and wind direction was observed, indicating that arthropods
406 opportunistically harness winds to facilitate movement towards their intended destinations. Tailwinds
407 are known to drive large scale migratory events (Åkesson, 2016), but are thus equally important for
408 small-scale movement behaviours at patch boundaries.

409 Larger flying arthropods moved more towards the habitat compared to smaller individuals and species.
410 Large body sizes provides advantages in handling upwind movement (Kuenen & Cardé, 1993) and is
411 potentially related to a better developed perceptual ranges (i.e. the distance at which an individual
412 can sense its suitable environment). For cursorial arthropods, only phylogenetically uncorrected
413 models showed that smaller taxa are more inclined to move towards habitat. This might imply that

414 certain taxa with generally small species, such as spiders, possess more extensive perceptual ranges,
415 potentially because they rely more on non-visual cues in order to navigate the environment (Foelix,
416 2011).

417 Movement behaviours at patch boundaries are condition dependent, non-random (Goicolea et al.,
418 2021), and reflect an active decision-making process (Bonte et al., 2012; Clobert et al., 2009; Poethke
419 et al., 2011). Nevertheless, the tendency (often interpreted as success when costs of entering the
420 matrix are high) of actively returning to a suitable habitat patch depends heavily on both body size and
421 prevailing weather conditions. Larger body sizes and the ability to fly provide advantages for
422 arthropods navigating through the matrix, enhancing their efficiency and propensity to move in the
423 desired direction. Moreover, ambient temperatures and wind speeds can either augment or impede
424 small-scale movement efficiency, depending on factors like wind direction and thermal thresholds. The
425 looming influence of climate change introduces another layer of complexity, with expected potential
426 changes in body sizes (Daly et al., 2024; Davies, 2019; Polidori et al., 2020) and wind patterns (Greene
427 et al., 2010). This implies that changes in local weather conditions, associated with global warming,
428 will not only influence population sizes by increasing stress on a local scale, but might also exert a
429 direct impact on behaviours at boundaries, thereby propagating or constraining subsequent
430 movements among habitat patches.

431 Declarations

432 **Availability of data and materials**

433 The raw data are available via Zenodo at https://doi.org/10.5281/zenodo.8232574.

434 **Competing interests**

435 The authors declare that they have no competing interests.

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Author's contributions

Garben Logghe, Charlotte Taelman, Florian Van Hecke and Dries Bonte designed the experiments. Charlotte Taelman, Florian Van Hecke and Garben Logghe conducted the practical work. Garben Logghe and Charlotte Taelman analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to the interpretation of the results and revision of the manuscript.

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