Consistent covariation of dispersal, life history and thermal niches across terrestrial arthropods

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Abstract

Arthropods, as ectotherms, are experiencing global declines, with many species facing the need to either acclimate or disperse in response to climate change. To generate general insights into such responses, a framework integrating traits on life history, dispersal and thermal niche is currently lacking. In light of this, understanding to which degree these traits covary and are organised into syndromes are key to improve distribution forecasting under climate change. We quantified life history, dispersal and thermal range covariation among 4000 Western European arthropod species spanning eight orders, considering phylogenetic relationships to account for shared ancestry. We demonstrate the existence of two independent axes of life history variation: the fast-slow continuum and the reproductive strategy axis. Notably, species at the fast end of the continuum tend to have higher dispersal capacities and broader thermal niches than slower species. The resulting syndromes were surprisingly consistent across orders, indicating a relatively uniform pattern of trait covariations across arthropod groups. These trait combinations, which generally enhance range-shifting potential, point to the emergence of two distinct groups of arthropods: those well-suited and those less equipped to mitigate the effects of future climate change.

Main

Climate change is an escalating global problem, threatening numerous species across various

taxonomic groups[1–3]. Species may cope with changing climatic conditions by acclimatisation and/or

adaptation to the experienced novel conditions, or by tracking their climate window through

dispersal[4]. The pace at which species expand or shift their distribution will critically depend on their

life histories—such as survival, reproduction and development—that determine population growth

rate and overall demography. Furthermore, this rate of range shifts will be shaped by their dispersal

capacity and ability to acclimate to novel conditions[4]. Forecasting biodiversity under climate change[5,6],

therefore, relies on our ability to incorporate accurate trait data into extinction risk projections[7,8],

thereby informing vulnerability assessments[9,10]and refining predictions of emerging community

assemblages[11,12]. For arthropods, such an approach seems to be most urgent since any detailed

species-specific assessment will fail to provide the needed insights in light of their steep global

decline[13], which potentially jeopardizes the crucial ecosystem services these organisms provide[14].

Species are expected to show intrinsic life history trade-offs, positioning them along a "slow-fast"

continuum[15–17]. Slow-living species have longer development times and lifespans, prioritizing resource

allocation toward offspring survival rather than fecundity, while fast-living species adopt the opposite

strategy[18]. In theory, slow-living species are better adapted to stable environments and have,

therefore, greater difficulty recovering from stochastic mortality events[19]. Due to similar evolutionary

pressures stemming from environmental instability, dispersal rates are expected to be lower in species

with slow life histories[20,21]. Body size, however, may have contrasting effects. While smaller body sizes

are typically linked to a fast-paced lifestyle, larger body sizes are often positively correlated with

greater dispersal ability[4,22–24]. Predicted relationships between species' dispersal and life history traits

are therefore highly variable, both among and within species[25].

Both dispersing towards new areas and staying within a changing environment comes with certain

costs, such as the risk of staying or settling in environments where conditions may be unfavourable[26].

Such limitations should be especially pronounced in ecological specialists, as they will suffer most from

local environmental changes and/or experience greater challenges in establishing populations within

unfamiliar habitats[27–30]. In the context of climate change, thermal tolerance is a particularly important

niche component in shaping distribution patterns. Species with narrow thermal niche breadths are

generally expected to be more vulnerable to climate change[31,32] and will have to face greater risks

during dispersal into new environments in order to track their optimal temperature. Given this pivotal

role of a species' thermal niche in determining both distribution ranges and dispersal costs, it can be

expected to have shaped the evolution of both life histories[33,34] and dispersal[35,36].

Traits underlying life history variation can show complex covariation and are integrated into so-called

syndromes[37–39]. Similarly, dispersal syndromes notify covariations between dispersal and other traits,

and have been documented across various taxonomic groups[20,21,40–42]. Understanding the organisation

of trait syndromes not only allows us to estimate missing trait data[21,43] in understudied taxa, but also

allows more accurate forecasting of species distributions under environmental change[44]. Given the

urgency to understand and predict arthropod distributions under future climate change, we aim to

identify covariations between dispersal, life history and thermal niche widths across a wide range of

Western European species. If dispersal and thermal range are independent of life history traits, they

should form separate axes of variation alongside the fast-slow continuum. Conversely, if dispersal and

thermal range covary with life history traits, their inclusion will reshape the existing life history axes.

Given the vast diversity in arthropod morphology, lifestyles and dispersal modes, we expect different

taxa to exhibit significant variation in both the direction and strength of these trait covariations.

Additionally, we explore whether these syndromes are phylogenetically conserved, as shared

evolutionary history may drive similar trait associations in closely related species, eventually shaping

their responses to environmental changes and range shifts.

Results

Results

Data on dispersal capacity, life history traits and thermal niche were obtained from an existing dataset

described by Logghe et al. (2024). From this dataset, we selected eight arthropod orders with

sufficiently high data quality, resulting in a refined dataset comprising over 4000 species and nine

functional traits. As a first exploration of these data, we conducted a phylogenetically corrected PCA

on a subset of species with complete data for all traits. This analysis revealed no distinct separation

among orders, suggesting that covariations may be consistent across taxonomic groups (Figure 1). PC1

shows a strong positive relationship with voltinism and dispersal, while it is also strongly negatively

correlates with development time (Appendix S.1). Additionally, it exhibits a positive correlation with

thermal mean and range, though this relationship is not as strong as with the other traits. In contrast,

PC2 is strongly positively correlated with fecundity and size. These results indicate the existence of

covariations between dispersal, life history, body size and thermal niche across arthropod orders.

Figure 1: PCA results for arthropod species for which data on all traits was available (n=200). Dots represent species with

symbol colour and shape according to their taxonomic order. Arrows represent the direction and magnitude of each variable's

contribution to the principal components.

Next, we employed Bayesian Generalized Linear models to identify trait covariations within each of

the eight arthropod orders. These models accounted for phylogenetic relatedness between species,

ensuring that observed relationships reflect ecological and evolutionary patterns. Our results reveal

multiple trait syndromes within various arthropod orders (Figure 2 for an example, all in Appendix S.2).

In most orders, there is a clear positive relationship between fast development, voltinism and dispersal

(Figure 3). Additionally, temperature niche components tend to covary positively with dispersal

capacity, fecundity and size in the majority of orders. Covariations between other trait combinations

are always present within at least one order. However, these are highly order specific and, therefore,

not generalizable across arthropod orders.

Figure 2: Pairwise posterior distributions for trait covariations (slopes of the linear regressions) within Araneae. Column names represent independent variables, while row names denote dependent
variables. Negative covariations are highlighted in red and positive covariations in blue. Effect sizes that are clearly determined (i.e. the 95% interval does not include zero) are outlined in the
corresponding colour.

Figure 3: Overview of trait covariations across each order, represented as a correlation matrix. Each grid of the matrix is divided into eight cells, with each cell representing one order. The taxa are, from left to right and top to bottom: Araneae, Coleoptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera, Odonata and Orthoptera. Red cells indicate a clearly determined (0 not included in the 95 credibility interval) negative relationship, blue cells indicate a clearly determined positive relationship, and grey cells show that the relationship was not clearly determined. White cells denote that this trait combination was not assessed for the given order, due to either an absence of data for one of the traits or convergence issues.

In order to estimate how much trait values are determined by shared ancestry between species, we

calculated the phylogenetic signal for every trait and arthropod order (Figure 4). On average, body size

and development time showed very strong phylogenetic signals, suggesting these traits are generally

strongly influenced by phylogeny. In contrast, thermal niche and fecundity appeared largely

independent of phylogeny in most arthropod orders. Finally, the phylogenetic signal for dispersal

displayed considerable variation, indicating that the influence of phylogenetic relationships differs

substantially between orders (Appendix S.3).

Figure 4: Overview of the phylogenetic signal (Pagel's Lambda) for every assessed trait for each arthropod order. Arthropod orders
are from top to bottom: Lepidoptera, Coleoptera, Hymenoptera, Hemiptera, Orthoptera, Odonata, Isopoda and Araneae. Colours
represent the strength of phylogenetic signal, with higher values (darker red) indicating that trait values are more explained by
phylogenetic relationships. The grey squares indicate that the phylogenetic signal was not calculated for that trait and order
due to a lack of data.

124   Discussion

Our quantitative synthesis across a wide range of Western European arthropods indicates that

dispersal, life history and thermal niche are tightly connected, implying similar evolutionary pressures

on these traits. While there are notable differences between orders, these relationships remain largely

consistent across taxa, suggesting that trait covariations can be generalized to a broad range of

arthropod species.

A considerable amount of interspecific life history trait variation in arthropods can be attributed to the

slow-fast continuum, with a clear distinction between species with fast and slow lifecycles.

Interestingly, development time appears closely tied to dispersal capacity, as we observed clear

covariations between development time, voltinism and dispersal across various orders. Previous

research has shown similar patterns, with high dispersal ability often linked with fast life history

strategies[20,21,45]. Given that most insects disperse only in their winged adult stages, this dispersal-life

history syndrome may have evolved as a bet-hedging strategy in response to unstable environments,

allowing for rapid relocation when conditions become unfavourable[46,47]. Interestingly, we found

limited evidence to suggest that fast-living species produce more offspring, a pattern that would

typically be anticipated within the slow-fast continuum framework[18]. While Lepidoptera and

Coleoptera did show a clear negative relationship between fecundity and development time, our

analyses suggest that the reproductive axis of variation is as good as independent from the

developmental axis. We thus show that the independence of these two distinct axes of life history

variation is rather a rule than an exception, as was previously reported for plants[48] and

vertebrates[16,49,50].

Our results suggest that thermal niche breadth has played a role in shaping the evolution of dispersal

in arthropods, with most orders showing a positive relationship between realised thermal niche

breadth and dispersal ability. This relationship likely arises from the costs associated with dispersing

to new environments, where the risk of encountering unfavourable climatic conditions is high[26]. A

broader thermal niche breadth reduces this risk by increasing the chances that newly colonised areas

fall within the species' tolerable thermal range. However, the causal relationship could also work in

reverse, as limited dispersal capacity may constrain a species' realised thermal niche by restricting

access to potentially suitable regions, despite physiological tolerance to those climates[51]. In other

words, the realised thermal niche, as considered in this study, would be narrower than the

fundamental thermal niche, simply because of dispersal limitations. Implementation of other niche

components such as diet or habitat specialisation could have provided a more holistic view on the

relationship between dispersal and ecological generalisation. It is worthwhile to notice that the

retrieved thermal niche-body size relationships were predominantly negative, which aligns with

experimentally derived patterns of lower thermal tolerance in large-bodied animals[52].

Besides thermal niche breadth, thermal optima also covary with dispersal ability. Across nearly all

assessed arthropod orders, species adapted to warmer climates exhibit higher dispersal capacities.

Although cold-adapted species may face greater risks from climate change and thus might benefit

more from range shifting as a mitigation strategy, their generally lower dispersal capacities make

spreading a less viable option[53]. Furthermore, our findings indicate that low dispersal capacity often

covaries with slower life histories, which hampers colonization success due to slower population

growth rates and, therefore, elevated vulnerability to stochastic extinction[54]. Consequently, the

arthropod species most at risk from temperature changes due to climate change are also those least

equipped to mitigate its effects through range shifts - a trend also noted in European mammals[55].

Phylogenetic signals were highly variable and strongly influenced by both the specific trait and

arthropod order being assessed. Body size and development time showed strong phylogenetic

conservation in most orders, while thermal niche was largely independent of shared ancestry.

Dispersal and fecundity present an interesting pattern, being strongly conserved in some orders but

showing minimal phylogenetic influence in others. A strong phylogenetic signal in body size was

expected, as closely related species often share a similar morphology. Development time is typically

linked to size, as larger species require more time to accumulate tissue[56,57]. However, our data do not

fully support the idea that larger arthropod species develop more slowly, as only Coleoptera showed

a clear positive relationship between body size and development time. Instead, it appears that closely

related arthropod species have evolved similar pace-of-life strategies due to comparable life cycle

characteristics[58]. The weak phylogenetic signal in thermal traits aligns nicely with earlier findings

suggesting directional selection driven by physiological constraints and experienced thermal

conditions within species' range over evolutionary history[59]. The variable phylogenetic signal for

dispersal capacity likely reflects the diverse dispersal mechanisms across arthropod orders. For

example, dispersal in flying insects like Lepidoptera and Odonata tends to be body size-dependent,

with larger species typically showing higher mobility[24,60,61]. In Coleoptera and Hemiptera, dispersal

capacity is closely tied to hind wing development, a trait that is also strongly phylogenetically

conserved[62–64]. For taxa with more passive dispersal mechanisms, a lower phylogenetic signal in

dispersal capacity is expected, as dispersal is less directly linked to specific morphological traits. In

Araneae, for instance, nearly all species show ballooning behaviour regardless of size, with larger

species typically ballooning as juveniles. Dispersal propensity in spiders is thus more strongly

correlated with habitat stability and specialization, factors that are generally independent of

phylogenetic lineage[65].

One of the most unexpected findings of this study was the remarkable consistency across arthropod

orders in terms of covariations between dispersal, life history and thermal niche. Given the

extraordinary diversity within this phylum, we expected significant differences in these covariations

between groups. Although all trait combinations had at least one order that lacked a clearly

determined relationship, the overall consistency across orders remains noteworthy. This uniformity

could have important implications for modelling the future effects of climate change, suggesting that

detailed trait information for every species might not be as necessary as previously suggested[66].

Instead, many missing trait values could potentially be inferred from accessible trait data, facilitating

broader, more efficient predictions.

Methods

Data description

The data used for this study was sourced from the dataset described by Logghe et al. (2024), which contains information on 28 life history and ecological traits for 4874 terrestrial arthropod species. We focused on eight arthropod orders for which data on both dispersal and life history was available: Araneae, Coleoptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera, Odonata and Orthoptera. Two orders, Diptera and Opiliones, were excluded due to lacking data. This resulted in a dataset containing 4343 species. From this dataset, we selected nine traits deemed particularly relevant for predicting range shifts under climate change[66,68]. These included four life history traits (development time, dispersal, fecundity and voltinism), four thermal traits (mean, maximum, minimum and range of temperatures), and body size, which is often correlated with both life history and thermal limits (e.g. Berger et al., 2008; Hillaert et al., 2018; Klockmann et al., 2017). Appendix S.4 shows the data coverage of traits for each order.

As a measure for body size, adult arthropod's body length in millimetres is used. Development time is defined as the duration between egg laying and adult emergence, expressed in days. Fecundity is defined as the number of offspring a female could produce during her lifetime, while voltinism refers to the maximum number of generations a species could complete in a single year. Note that the maximum value for voltinism is used, as the number of generations can vary annually and across regions. Dispersal is defined as the movement of a species from its place of birth to their location of reproduction[71], with significant variation in modes and proxies both across and within orders. To enable comparison, Logghe et al. (2024) rescaled dispersal capacity on a relative scale from 0.1 to 1 within each order, where 0.1 represented the least dispersive species and 1 the most dispersive. Thermal mean, minimum and maximum represent the average, minimum and maximum annual temperatures (in °C) across the species' geographic range (see Logghe et al., 2024 for details on the

calculation of these metrics). Finally, thermal range was calculated as the difference between thermal

minimum and maximum.

Statistical analysis

To account for the shared evolutionary history among species, which can influence trait similarities,

we controlled for phylogenetic relatedness in all our analyses. This approach ensured that observed

relationships between traits reflected ecological or evolutionary patterns, rather than being influenced

by shared ancestry. To achieve this, we constructed a phylogenetic tree including all species in the

dataset, which served as the basis for subsequent analyses. The tree was built by linking species names

to the Open Tree Taxonomy database, which contains data on known phylogenetic relationships ("rotl"

package)[72]. Branch lengths were added to the tree using the "ape" package[73] and calculated with the

"Grafen" method[74].

To examine how life history and thermal traits are distributed across arthropod orders, we performed

a phylogenetic principal component analysis (PCA) using the "phyl.pca" function from the "phytools"

package[75]. Unlike standard PCA, this method incorporates phylogenetic relationships, correcting for

the lack of independence between species due to shared ancestry. The analysis was conducted on a

subset of the dataset that included only the 145 species for which complete data on all traits were

available.

Bayesian Generalized Linear models were employed to assess whether covariations were present

between the selected traits ("brms" package)[76]. Given the strong phylogenetic signal across the tree

of life, the variation in data quantity and quality among orders, and our aim to detect and understand

potential divergence in the covariations across arthropod orders, we analysed every order separately.

Trait data on body size, fecundity and development time underwent log transformation before analysis

to reduce skewness of the data. For every order, each trait combination was run two times, with the

dependent and independent variable interchanged. Each model was fitted with a distribution

depending on the independent variable: zero-one-inflated beta for voltinism, binomial for dispersal

and Gaussian for the remaining variables. The models were run using 4 chains and 4000 iterations,

with a burn-in period of 1000. Non-informative flat priors were used for the model parameters.

Phylogenetic distances between species were derived from a phylogenetic distance matrix derived

from the previously mentioned phylogenetic tree ("geiger" package)[77]. These distances were

incorporated into every Bayesian model as blocking factors, to ensure that phylogenetic relationships

were considered when the covariation between traits is estimated. Convergence of the models was

checked by examining the effective sample size (>1000) for each chain as well as Gelman-Rubin statistic

(Rhat < 1.1) among chains. Effect sizes were deemed clearly determined when 0 was not included in

the 95% credibility intervals of the posteriors.

Finally, we assessed the phylogenetic signal using Pagel's Lambda for each considered trait and

arthropod order[78]. This is a metric that estimates how much closely related species resemble each

other compared to expectations under a Brownian motion model of evolution. Pagel's Lambda

typically ranges from 0 (indicating no influence of phylogenetic relationships on trait values) to 1

(indicating trait values are entirely explained by phylogenetic relationships). We calculated this metric

using the "phylosig" function from the "phytools" package[75].

R version 4.0.4[79] was used to perform all data analyses.

Data availability

266 The complete dataset on arthropod life histories and ecological traits can be found on GBIF:

267 https://doi.org/10.15468/75g5z9. The filtered dataset specific to this study can be accessed on

268 Zenodo: 10.5281/zenodo.14527806.

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Author contributions

Garben Logghe, Femke Batsleer, Dirk Maes and Dries Bonte conceived the framework of the study.
Garben Logghe collected the trait data. Guillermo Fandos and Garben Logghe developed the statistical

449   analysis. Garben Logghe wrote the first draft of the manuscript. All authors contributed substantially

450   to interpretation of the results and revision of the manuscript.

451   ## Ethics declarations

452   The authors declare that they have no competing interests.