Behavior Outpaces Form when Linking Traits to Ecological Responses within Populations: A Meta-Analysis

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Abstract

Intraspecific trait variability (ITV) is an important aspect of community ecology, but we still have a poor understanding of what drives the magnitude of relationships between ITV and ecological dynamics. In order to guide ecologists interested in unravelling the ecological implications of ITV, we asked whether relationships' magnitudes differ (*i*) between intraspecific levels (among- *vs*. within- populations), (*ii*) among ecological responses spanning levels of biological organization (from individual performances to ecosystem functioning), and (*iii*) among trait categories (morphology, physiology and behavior). We performed a meta-analysis synthesizing a thousand effect sizes from nearly two-hundred studies, encompassing relationships between traits measured among individuals or populations of animals and a broad range of ecological responses. The average effect size was $|r|$ = 0.24 [0.20 – 0.27] (95% confidence intervals). Within populations, relationships' magnitudes were higher for ecological

performance (foraging, diet), community and ecosystem responses than for fitness (reproduction). Relationships were 28% stronger for physiological and behavioral traits than for morphological traits. Our meta-analysis confirms the central aspect of ITV within populations of animals to drive ecological dynamics, and emphasizes physiological and behavioral traits to enhance the integration between the individual component of diversity and processes at community and ecosystem-levels.

Key words: *Eco-evolutionary dynamics; functional traits; individual-based approach; phenotypic traits; trait-based ecology; intraspecific trait variation (ITV).*

Introduction

The question 'What Do Species Do in Ecosystems?' raised three decades ago by J. H. Lawton (1994) has been foundational to trait-based ecology (TBE). Trait-based ecologists revolve around organisms' functional traits (Violle et al., 2007) to describe and predict how organisms interact altogether and with their environment. Trait-based approaches to community ecology brought the promise to improve our understanding of the mechanisms driving community assembly and ecosystem processes, in being complementary to, or even outpace taxonomic approaches in that regard (Enquist et al. 2015). Traits can be expressed in physical dimensions (e.g., mass, length, volume, energy, time), and can meaningfully express the fit of organisms with their environment (Arnold 1983; Violle et al. 2007). Inferences drawn from TBE are thus, ideally, transferable to other ecosystems and life forms (Funk et al. 2017). General patterns include allometric scalings between body size and metabolic rate (Kleiber 1932), the leaf economic spectrum (Wright et al., 2004), *r*- and *K*- life history strategies (Pianka 1970). Trait-based approaches do not have borders. Most traits are cheap and easy to measure, fostering inclusion among researchers from different horizons, as they integrate from individual to ecosystem levels, and across various ecosystems (Carmona et al. 2016).

Including Intraspecific Trait Variation (ITV) in Trait-Based Ecology (TBE)

Early research in TBE led to rethink community ecology (McGill et al. 2006; Petchey and Gaston 2006). Yet, an important limitation is that studies focused heavily on species' mean trait values, assuming that all conspecifics shared identical trait values (Albert 2015). This assumption was paradoxal, as intraspecific trait variation (henceforth 'ITV') was essential to the development of natural selection (Darwin and Wallace 1858), niche (Elton 1927; Hutchinson 1957), and coexistence theories (Macarthur & Levins, 1967). In fact, ITV is as large as mean trait differences between species (Lecerf and Chauvet 2008; Siefert et al. 2015; Rota et al. 2022), and matters for species coexistence (e.g., Hart et al., 2016), predator–prey (Toscano and Griffen 2014), and consumer–resource interactions (Raffard et al. 2017; Rota et al. 2018). ITV is now recognized to be an important facet of ecology (Bolnick et al. 2011; Violle et al. 2012), provoking discussions on how it affects our understanding of food webs (e.g., behavior; Moran et al., 2017) and community assembly (e.g., metabolic traits; Brandl et al., 2022). However, the inclusion of the intraspecific component remains marginal, with only 4% of TBE studies acknowledging ITV (Green et al., 2022). Intraspecific variation is, however, fundamental in community ecology. For all individualizable organisms, ecological interactions (competition, predation etc.) are occuring among conspecific or heterospecific individuals, whom their traits differ or not. A trait-based approach at the individual level may improve to understand those interactions (Bolnick et al., 2011). Ignoring ITV can lead to inferential bias (Wong and Carmona 2021) and to miss important information about diversity. For instance, not acknowledging for intraspecific variability could distort relationships between species richness and functional diversity (Cianciaruso et al. 2009). On the other hand, acknowledging the processes affecting ITV around species' averages, such as evolution in response to competition regimes, can contribute to a mechanistic understanding of diversity–function relationships (Barabás et al. 2022).

Why Assessing Relationships' Magnitude between ITV and Ecological Dynamics?

Important insights emerged from a renewed interest for ITV. First, ITV links to community assembly patterns (e.g., species richness and diversity) and ecosystem functioning (e.g., productivity or nutrient cycling) as much as mean trait variation between species (Des Roches et al. 2018; Raffard et al. 2019). Second, ITV is changing fast with human-driven disturbances (Alberti et al. 2017), including population loss (Ceballos et al. 2017), erosion of genetic diversity (Exposito-Alonso et al. 2022), and changes in phenotypic variation (Sanderson et al. 2023). There is thus now a form of urgency in studying the primary role of ITV in ecological processes, such as answering how much and when ITV matters. Conservationists can take advantage of this research agenda, to better identifying and monitoring particular facets of ITV with particular implications for ecological functions (Blanchet et al. 2020) and nature's contribution to people (Des Roches et al. 2021).

We need to improve our knowledge about what drives the magnitude of relationships between ITV and ecological dynamics. This would also help understand how evolution, by affecting trait distributions, affects ecological dynamics (i.e., eco-evolutionary dynamics*;* Pelletier et al., 2009; Hendry, 2017). Most research has focused on natural selection (Kingsolver et al. 2012), heritability (Mousseau and Roff 1987), and evolvability so far (Wheelwright et al. 2014), in providing quantitative estimates on evolutionary processes ('*evo*'). In contrast, the relationships between ITV and ecological responses ('*eco*') did not receive yet a detailed analysis, despite that evolutionary and ecological processes are often congruent (Harmon et al. 2009). Previous studies compared the ecological impacts of populations varying in key traits (e.g., gill raker's morphology in anadromous or landlocked fish populations; Post et al., 2008), but there are still very few studies having focused at both the individual and population levels (Gibert et al. 2015). Hence, it remains unclear if relationships between ITV and ecological responses show similar magnitudes at the population and individual levels. On one hand, we could expect population-

level ITV to show stronger relationships with ecological dynamics than individual-level ITV, because local adaptation can drive divergence in among-population trait values and trait matching with local ecological processes (Post et al. 2008). On the other hand, ITV among individuals has been shown to be similar or even larger than ITV among populations (Messier et al. 2010; Rota et al. 2024). It thus remains possible that ITV among individuals express similar or stronger effects on ecological processes than ITV among populations.

Predicting how much traits link to responses across levels of biological organization remains a challenging issue (Violle et al., 2007; Enquist et al., 2015; Chacón-Labella et al., 2022). There is still a debate about how the magnitude of relationships between ITV and ecological responses may vary across levels of biological organization, from individuals to ecosystem processes. Some predict stronger links with responses at low levels of biological organization (e.g., growth rate) than with responses at higher levels (e.g., ecosystem functioning; Bailey et al., 2009). Others showed an opposite pattern (Des Roches et al. 2018; Raffard et al. 2019).

Assessing Traits' Functionality

To generate meaningful insights, we assume more or less implicitly in TBE that the traits used are functional in linking to the ecological performances or to the fitness of organisms (Arnold 1983), or more generally, to ecological functions (Violle et al. 2007). Hence, the *functionality of traits* is the matter of discussions, as it influences the choice of traits by trait-based ecologists (Mlambo 2014; Lefcheck et al. 2015; Dawson et al. 2021). In biological terms, all traits are functional since they all link to one or several biological functions, making phenotypes functional living entities (Bertossa 2011). Therefore, the question may not be whether a trait is functional or not in absolute terms (for different viewpoints across disciplines, see Dawson et al., 2021 and Sobral, 2021). Without entering into this debate, we propose to investigate *traits' functionality* that we define as the magnitude of relationships between a trait and a large array

of ecological responses. Asking *how much* traits are functional may help to increase the general quality of ecological inferences at the intraspecific level in guiding further investigators in their trait choice.

A good example of high trait functionality is body size. Body size is used in the vast majority of TBE studies (Green et al. 2022). It spans several orders of magnitude across and within taxa and integrates many biological and ecological processes with often a great predictive power (Peters 1993). Nevertheless, functional diversity is multi-dimensional (de Bello et al., 2021), and it stays poorly known which traits are the most linked to ecological dynamics when we consider individuals within a same cohort or size class (Brandl et al. 2022). As several authors argue (Gordon 2011; Toscano et al. 2016; Moran et al. 2017; Brandl et al. 2022; Schleuning et al. 2023), we need to look beyond body size to improve our understanding of the implications of ITV (e.g., morphology, physiology, behavior varying among individuals).

Morphology, physiology and behavior are different facets depicting an individual phenotype. Morphology reflects the abilities of an individual to perform in its environment given biomechanical constraints (Van Valen 1965; Arnold 1983). For instance, the relative mass of metabolically-active organs is used as an energetic proxy (Careau et al. 2008). Yet, energetic currencies such as metabolic rates (i.e., energy loss) should link closer to ecological performances such as feeding rates (i.e., energy intakes) and growth rates (i.e., energy not allocated to maintenance nor reproduction; Biro & Stamps, 2008; Careau & Garland, 2012). Through trophic and ecological interactions, it is expected that metabolic traits are involved in community assembly patterns and ecosystem functioning (Brandl et al., 2022; fig. 1A). Some examples suggest that behavioral traits have a close link to ecological interactions (Gordon, 2011; Toscano et al., 2016; for chosen examples from our literature review, see table S1). Behavioral variation among individuals can strongly affect the outcomes of predator-prey interactions (McGhee et al. 2013). Behavioral traits such as locomotion activity,

aggressiveness, or boldness are involved in energetic trade-offs (Careau et al., 2008), and hormones regulate metabolism and behavior (Ricklefs & Wikelski, 2002). Physiological and behavioral traits such as those, as well as other energy and matter currencies (e.g., stoichiometry; Elser et al., 2000) – perhaps as opposed to more structural, morphological traits – are therefore expected to exert strong links with ecological performances, fitness, and hence ecological dynamics (Gordon 2011; Moran et al. 2017; Brandl et al. 2022). However, to date, no study synthesized the functionality of morphological, behavioral and physiological traits on various ecological responses.

Questions and Hypotheses

We aimed filling this gap with a meta-analysis exploring the magnitude of relationships between ITV and various ecological responses (fig. 1B) across a large diversity of traits, systems, and species in the animal realm. We tested three main hypotheses:

(*Q1/H1*) Does the strength of relationships between ITV and ecological responses (hereafter 'effect sizes') differ within populations ($\boldsymbol{i_a}$) versus among populations ($\boldsymbol{i_b}$). We expected that $\boldsymbol{i_a} < \boldsymbol{i_b}$, because individuals should show stronger phenotypic divergences among- than within-populations. An alternative expectation is that $\boldsymbol{i_a} = \boldsymbol{i_b}$, if for instance the populations ($\boldsymbol{i_a}$) have large sizes or are inter-connected populations, making them phenotypically representative of the entire meta-population ($\boldsymbol{i_b}$) (Messier *et al.*, 2010; Rota *et al.*, 2024).

(*Q2/H2*) How do effect sizes vary among ecological responses at different levels of biological organization? We ranked ecological responses from ($\boldsymbol{ii_a}$) proximal responses to the focal organism (e.g., foraging performance, growth, diet, and fitness) to ($\boldsymbol{ii_b}$) distal responses as community assembly (further abbreviated "community") and ecosystem functioning (further abbreviated "ecosystem"; see fig. 1B). We expected that effect sizes would decrease from

proximal to distal responses (***ii_a*** > ***ii_b***; as the width of grey arrows in fig. 1B), as the strength of relationships between traits and responses should dissipate as the number of intermediate relationships increases (black arrows in fig. 1B; see the algebraic rationale in Bailey et al., 2009). Effect sizes could on the contrary, be stronger for distal than for proximal ecological responses (***ii_a*** < ***ii_b***) if intermediate relationships' strength shows additivity or multiplicativity through biological scales (Bailey *et al.*, 2009).

(*Q3/H3*) How do effect sizes vary among trait types? Effect sizes were divided into (***iii_m***) morphology (e.g., body shape, relative length of functional body parts), (***iii_p***) physiology (e.g., metabolic rate, hormone levels, elemental stoichiometry), and (***iii_b***) behavior (e.g., activity, boldness, sociability). We hypothesized that behavioral and physiological traits would show the strongest correlations with ecological responses (i.e., ***iii_m*** < ***iii_p*** ~ ***iii_b***). However, it could be relaxed when morphological differences occur between morphotypes having diverged from hundreds to thousands of generations, and for which large phenotypic variation can match ecological differences (e.g.; ecological radiation between limnetic and benthic eco-morphs within a same lake population; Harmon *et al.*, 2009).

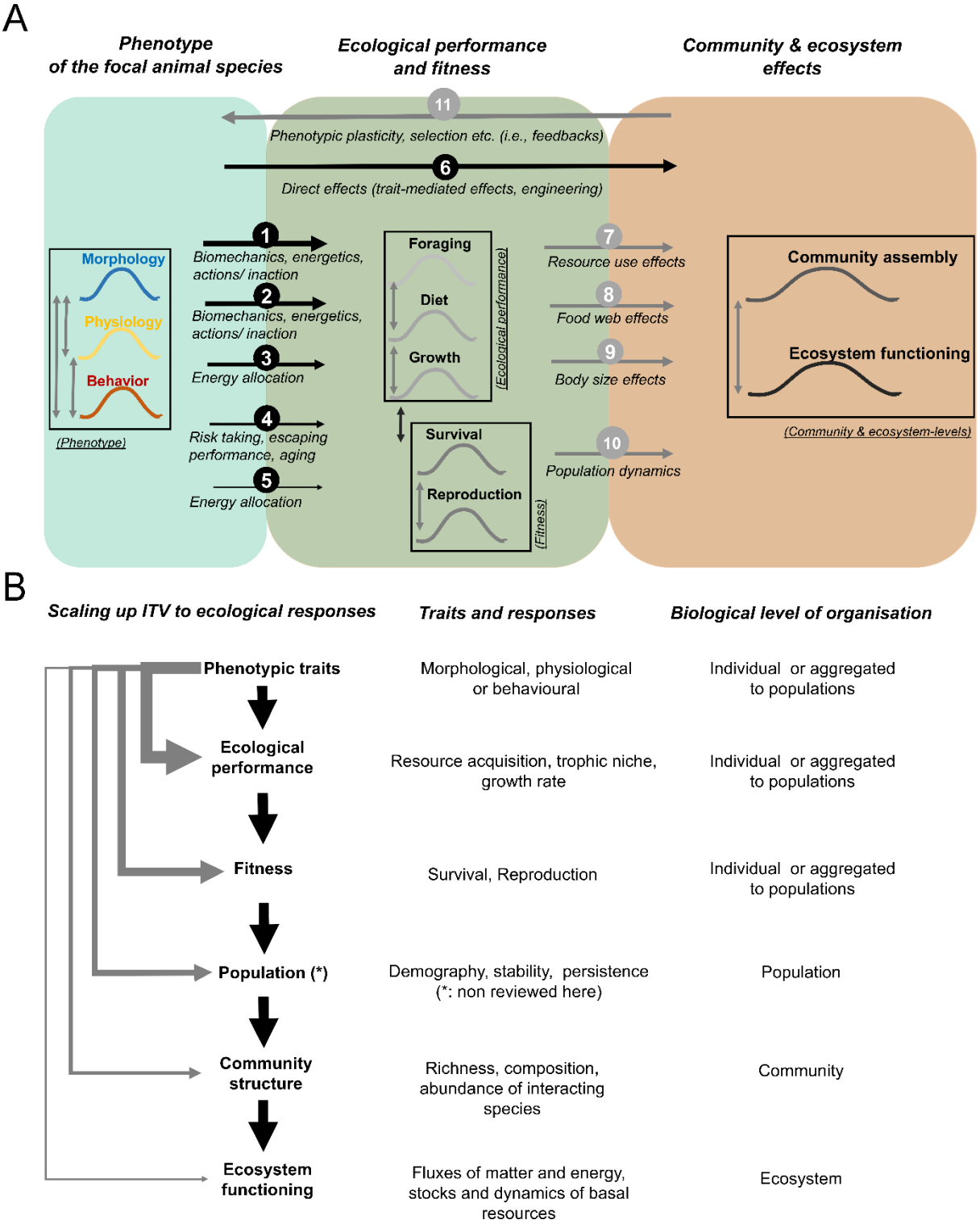

Figure 1: (A) Diagram showing how ITV could relate to various ecological responses in animals. (B) The magnitude of relationships between ITV and ecological responses is expected to change across levels of biological organization. Black arrows depict intermediate relationships propagating ITV effects across biological levels of organization. Following hypothesis 2 (see main text), the magnitude of relationships between ITV and ecological responses could decrease along higher levels of biological organization (Bailey et al. 2009), from responses located on the organism itself to community and ecosystem levels (grey arrows). All the relationships depicted by grey arrows in panel B are assessed in this meta-analysis, excepting the one for populations (*). Examples of relationships are depicted in table S1, with numbers corresponding with fig. 1A.

Methods

Search Strings and Selection Criteria

We searched for thirty keyword combinations in Web of Science ('all databases'), Scopus and Google Scholar (table S2), and obtained a total of 6904 studies. After having sorted out the duplicates manually in Excel (n = 335), we obtained 6569 studies, from which 613 studies followed our scope after having scrutinized titles and abstracts. Our general scope was studies investigating relationships between animal's trait variability at the intraspecific level and various ecological responses. Exclusion criteria at this stage were studies focusing on other groups than animals, investigating other questions than traits – ecological responses, or studies at the interspecific level.

After a full-text examination of those 613 studies, 121 studies met our criteria. We considered empirical studies (*i*) on wild animals, with observations conducted either in the field, microcosms or mesocosms, (*ii*) Studies reporting quantitative relationships or comparison statistics between a phenotypic trait measured on several individuals, or averaged at the level of a group of individuals (i.e., population or colonies of eusocial animals), and a measured ecological response, (*iii*) morphological, physiological, or behavioral traits are categorical or continuous, (i*v*) we did not include ecological responses reflecting population dynamics or population persistence since those are long-term phenomena for which relationships with ITV are difficult to estimate with empirical studies, (*v*) studies focused on the 'identity' of phenotypes (i.e., one phenotype versus another) not 'diversity' (i.e., statistics from treatments including mixtures of phenotypes were excluded), (*vi*) we did not define life history traits as "trait types", since they were categorized as ecological responses (e.g., growth, survival and reproduction), and (*vii*) we did not include body size since we aimed to focus on often neglected traits beyond body size (see justification in the Introduction section). We therefore ensured that

effect sizes were the least influenced by body size (for a detailed description, see Box1 in Supplementary Materials).

We finally scrutinized the references of these 121 papers and added 49 additional studies meeting our selection criteria. We further added 22 studies from our personal libraries (fig. S1). Studies reporting undetailed statistics (e.g., only *P*-values) or for which notes of concerns have been recently published were excluded from the final dataset. We kept the effect sizes (*r* values) from Bolnick & Paull (2009) despite they retracted their paper, since the error was an incorrect calculation of the *P*-values, not the *r* coefficients, hypotheses, nor methods.

Intraspecific Level, Trait Types, Ecological Responses, and Covariates

We noted the intraspecific level from which the relationships belonged (i.e., among individuals, among populations, among colonies of eusocial animals). We considered the following seven types of ecological response: '*Foraging efficiency*' (resource consumption or feeding rates); '*trophic niche*' (trophic niche position, trophic level, and degree of specialization inferred from either stable isotopes or diet assessments); '*growth*' (size-standardized growth rates over time based on body length or body mass); '*survival'* (survival rates obtained from capture-mark-release-recapture in the wild or from controlled experiments); *'reproduction'* (number of mates, egg numbers, clutch sizes, or sibling survival); '*community*' (abundances, biomasses, diversity and structures of communities of organisms of at least two species interacting with the focal phenotypes); '*ecosystem*' (standing stocks or dynamics of basal resources such as primary producers or detritus, as well as energy and matter cycling as C and N cycling). We then categorized traits into morphology, physiology, and behavior. Morphological traits included body shape, trophic apparatus shape, and linear morphometrics on specific features, locomotion traits, coloration, body condition, reproductive organ relative size, brain relative size, and morphotypes. Physiological traits were either assimilation, energy reserves, excretion,

metabolic traits, elemental stoichiometry, hormone levels, immunity, or physiological syndromes. Behavioral traits reflected differences in aggressiveness, exploration, boldness, sociability, activity or cognitive abilities. Finally, we considered the trophic level (i.e., primary consumers feeding on basal resources or predators feeding on other animals), the ecosystem type (i.e., freshwater and/or marine or terrestrial), the methodological approach (i.e., field observations, mesocosm, or microcosms), and the year of publication as covariates.

Calculation of Effect Sizes

We collected correlation coefficients (r) or statistics (e.g., F or t statistics) corresponding to each trait-to-ecological response relationship. The original estimates were transformed to correlation coefficients r and then to Fischer's Z-transformed correlation coefficients Zr, following established procedures (Nakagawa & Cuthill, 2007; see table S3). Since we aimed to quantify the magnitude of ITV – ecological response relationships, and to perform comparisons among trait and ecological response categories, the direction of the relationship was not meaningful here. We used absolute values of correlation coefficients $|Zr|$ in further analyses (Bailey et al. 2009). For each effect size $|Zr|$, we computed a sampling variance (vi) that we used in our models (detailed below) (Nakagawa and Cuthill 2007; Nakagawa et al. 2022).

Statistical Analyses

We performed statistical analyses using R, version 4.3.2. (R Development Core Team, 2023). We used hierarchical multi-level models accounting for phylogeny (function '*rma.mv()*' in the R package '*metafor*'; Viechtbauer, 2010, see the package's website: https://www.metafor-project.org/doku.php/metafor). These models take random-effects accounting for between- and within-study variance, as well as a matrix of phylogenetic relatedness among species in the error structure. They acknowledge the three usual sources of non-independence of meta-analyses in ecology and evolution (Noble et al., 2017; see also a guide by S. Nakagawa and M.

Lagisz (2016) here: https://environmentalcomputing.net/statistics/meta-analysis/meta-analysis-3/). In addition, this approach allowed us to account for a variance – covariance matrix reflecting the non-independent structure of sampling variances (*vi*) in our dataset, and to obtain cluster-robust point and variance estimates regarding selective reporting bias (see Yang et al. 2024*a*).

We computed phylogenetic relatedness among species following Moran et al. (2021). We extracted phylogenetic and taxonomic information from the Open Tree of Life (https://tree.opentreeoflife.org/; Hinchliff et al., 2015). We then resolved any polytomies by randomisation in the R package '*rotl*' (Michonneau et al. 2016). Branch lengths were estimated using Grafen's method (Grafen 1989) in the R package '*ape*' (Paradis and Schliep 2019), and we added a residual error term accounting for the computed phylogenetic correlation matrix in our meta-analytic models. We accounted for within-study non-independence by adding a within-study random effect term (nested with *studyID*), attributing an identifier to all effect sizes (see Noble et al. 2017; Yang et al. 2024*a*). Selective reporting bias and sources of non-independence inherent to the structure of the data can be accounted for by modelling an appropriate sampling variance – covariance matrix (*varcov*), and by following a two-step cluster-robust estimation procedure (Yang et al. 2024*a*). We computed *varcov* with the function *vcalc()* of the package '*metafor*', accounting for the basal level of our observations (*effect sizeID*), the cluster of the model (*studyID*), and a subgrouping variable regarding trait-to-response combinations (n= 468) (subgroup argument), in setting covariation among subgroups as ρ=0.6. This *varcov* ensured that the residual errors of the model accounted for the non-independence inherent to trait-to-response combinations (n= 468). This accounted for the fact that traits have shared means and errors within those categories but that those means and errors are expected to show larger differences with other traits and responses measured on other pairs of individuals, and species, in line with the multi-level structure in the data. For each model

(see fixed-effect structures below), we re-ran the output from the function *rma.mv()* to get a cluster-robust estimation of effect size estimates and their variance using the function *robust()* of the package '*metafor*' (i.e., two-step procedure described in fig. 7 in Yang et al. 2024*a*).

Sampling variance (*vi*) and mean-centered year of publication are indicators of small study effects and publication time-lag bias, respectively (Nakagawa et al., 2022). We assessed and accounted for these two bias in adding these terms as fixed-effects in our models, so effect size estimates are given for *vi* = zero, and for the average year in our dataset which was 2012.5 (Nakagawa et al., 2022). Using the same error and random-effects terms model structure as mentioned above, we first estimated the grand-mean effect size with an intercept-only model. We then setted intraspecific level as a fixed effect (*H1*). Here we tested if effect sizes obtained among individuals vs. among populations differed, in merging 'populations' and 'colonies of eusocial animals', to reduce the unbalancing of effect sizes between 'individual-level' (n=952) and 'population-level' (n=56). We then tested our hypotheses regarding differences among trait types and ecological response types (*H2* and *H3*) on data at the individual level, with n=952 effect sizes (94% of the dataset), to avoid any confounding effects of the intraspecific level on those two hypotheses. We also tested H_2 and H_3 using all the dataset, to see if it would change our conclusions (see table S4). In both cases, we built a model including ecological response type as a fixed effect and adding trait type as a random effect (*H2*). We then tested for differences between trait types, in adding ecological response type as a random effect (*H3*).

The conversion of correlation coefficients *Zr* to their absolute values $|Zr|$ can cause $|Zr|$ to be biased upward, since when *Zr* is close to zero, any estimation error will increase $|Zr|$ (Morrissey 2016). Moreover, since $|Zr| \geq 0$, we cannot directly test its departure from zero. We therefore generated null effect sizes $|Zr|_{null}$ (Raffard et al. 2019). For each 1008 effect size in our dataset, we randomly simulated a distribution of 1000 *t* statistics based on sample sizes *N* of each effect size under the null of no correlation. We then converted these *t* statistics into absolute $|Zr|$ values

and averaged them for each effect size. Using the same model structure as above, we estimated equivalent $|Zr|_{null}$ effect sizes. We obtained unbiased $|Zr|$ estimates and their 95% confidence intervals, and subtracted the estimated $|Zr|_{null}$ from the modelled estimates of $|Zr|$. We back-transformed $|Zr|_{unbiased}$ to $|r|_{unbiased}$ effect sizes for reporting magnitude estimates in the main text using a popular statistic in empirical ecology (correlation coefficient).

As developed above, we accounted for selective reporting bias with a cluster-robust estimation. We also assessed publication bias with a funnel plot on *Zr* from the intercept-only model including all the dataset. We corrected effect sizes estimates by their null equivalent, therefore accounting at our maximum for known sources of bias. We computed total heterogeneity and tested its significance with a *Q*-test of total heterogeneity, as we computed between-, within-study, and phylogenetic heterogeneity (I^2) using Viechtbauer's method (Viechtbauer, 2010; see R code).

For all hypotheses, we considered statistical significance among groups using comparison tests and *P*-values accounting for the multi-level structure of the dataset, with an alpha threshold of 5%. We visualized effect size raw distributions with orchard plots (package '*OrchaRd2.0*'; (Nakagawa et al. 2023), but we modified the function so that lower prediction and confidence intervals at 95% were bounded to zero, as by definition, absolute effect sizes cannot extend below zero. Our alignment with the PRISMA guidelines for ecology and evolutionary biology meta-analysis reporting (O'Dea et al., 2021) is shown in table S5.

Results

Our dataset comprised 1008 effect sizes from 188 studies, covering 126 animal species across seven major taxonomic groups and a vast range of ecological contexts. Morphology, physiology, and behavior were represented by 351, 204, and 453 effect sizes, respectively (fig.

2). Effect sizes expressed ecological relationships among individuals (94%), among populations (4%) or among colonies of eusocial animals (2%; fig. 2B).

Heterogeneity and Covariates

Total heterogeneity in our meta-analysis was high (87%; $Q_{df=1005}$ = 6238.7; P < .0001). Phylogenetic relatedness among species accounted for 4.8% of the total heterogeneity in effect sizes. Most of the heterogeneity was within studies (45.7%), rather than among studies (36.5%). We did not observe any statistical difference among categories of covariates, and accordingly, distributions were undistinguishable between systems (aquatic *vs.* terrestrial; z = 0.2; P = .841), trophic levels (consumers *vs.* predators; z = 1.58; P = .114), and methodological approaches (field observations, mesocosms, and microcosms; z < 1.18; P > .239; fig. S2–S4). It is noteworthy that the two levels ‘colonies of social animals’ and ‘populations’ that we merged to test for differences among intraspecific levels (among-population vs. within-populations) shared very similar effect sizes in average (fig. S5).

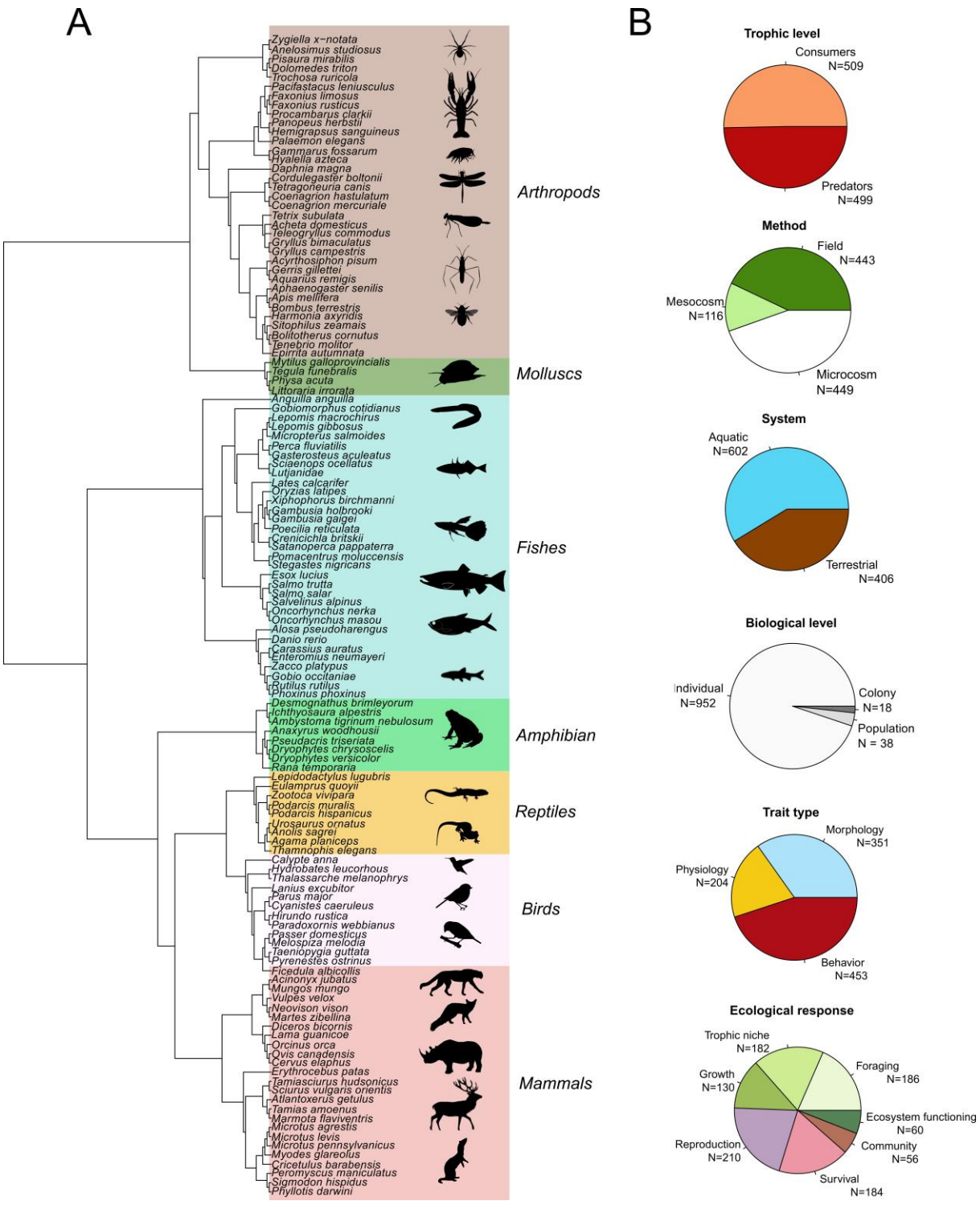

Figure 2: (A) Phylogenetic tree of species in our dataset, with species' names and taxonomic groups, with silhouettes of iconic taxa within each group. (B) Pie charts of main factors accounted for in the meta-analysis, with respective sample sizes of |*Zr*| effect sizes.

Publication Bias

The funnel plot of *Zr* effect sizes was roughly symmetric (fig. S6), suggesting minor publication bias. Raw effect sizes indicated that the most extreme relationships varied between $-3 \leq Zr \geq 3$, which is similar to $-0.99 \leq r \geq 0.99$. Effect sizes $|Zr|$ being comprised between 1 and 2 or equivalently $|r|$ between 0.76 and 0.96 were not rare, while most part of effect sizes *Zr* were comprised between –1 and 1, or equivalently $|r|$ between 0 and 0.76 (fig. S6). We did not observe temporal bias ($t = -1.200$; $P = .230$), but as we worked with absolute effect sizes, the effect of sampling variance *vi* was strongly positive ($t = 5.24$; $P < .0001$).

Estimated Effect Sizes

The global effect size of relationships between traits and ecological responses was non-null ($|r|_{\text{unbiased}} = 0.24$) as its 95% confidence intervals (further abbreviated '95% CI') excluded zero ([0.20 – 0.27] 95% CI; table 1). Effect sizes among populations were twice higher than among individuals (fig. S7), but it was not significant (table 1).

Effect sizes for reproduction were twice lower than for foraging performance and trophic niche (fig. 3, table 1). Effect sizes for community were twice higher than effect sizes for reproduction (fig. 3, table 1). The same analysis performed on the whole dataset led to similar estimates, at the difference that responses at the ecosystem-level appeared significantly higher than reproduction (table S4).

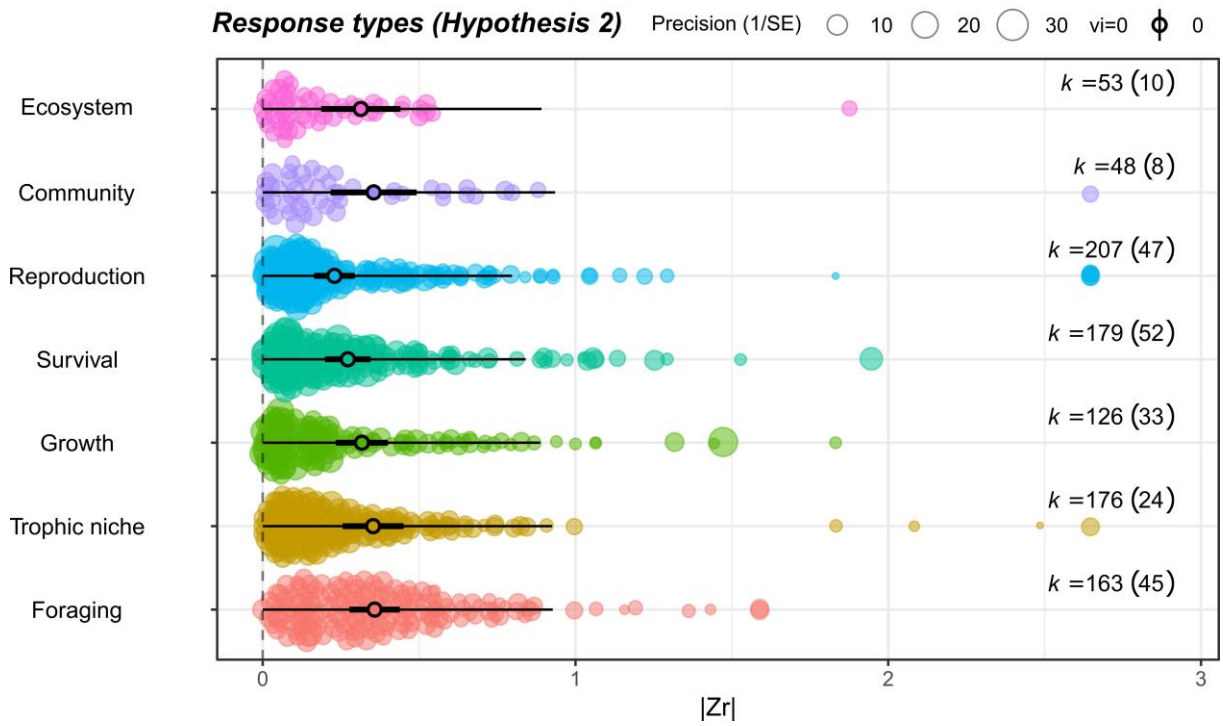

Figure 3: Orchard plot of model estimates of |*Zr*| effects sizes estimated for each ecological response at the among-individual level (n=952 effect sizes). The size of each point is proportional to the precision of the effect size (1/SE). Thick and thin error bars give 95% confidence and prediction intervals, respectively. Sample sizes (k) and number of studies (in brackets) are given for each category of ecological responses. Model estimates are reported in table 1.

Physiological and behavioral traits showed effect sizes 28% higher than morphological ones (fig. 4, table 1). The difference between physiology and morphology was not significant when tested on the whole dataset (i.e., including both individual and among-population observations; table S4). Differences among trait type categories were not reflected in the relative frequencies of trait types included in the first quartile range (25th percentile) of effect sizes distribution (morphological: 37% physiological: 19%, and behavioral traits: 44%; fig. 4), but effect sizes with large magnitudes in the dataset were corroborating statistical results, as morphological (17%) and physiological traits (17%) were less represented than behavioral traits (66%) in the third quartile (75th percentile) of the effect sizes distribution (fig. 4).

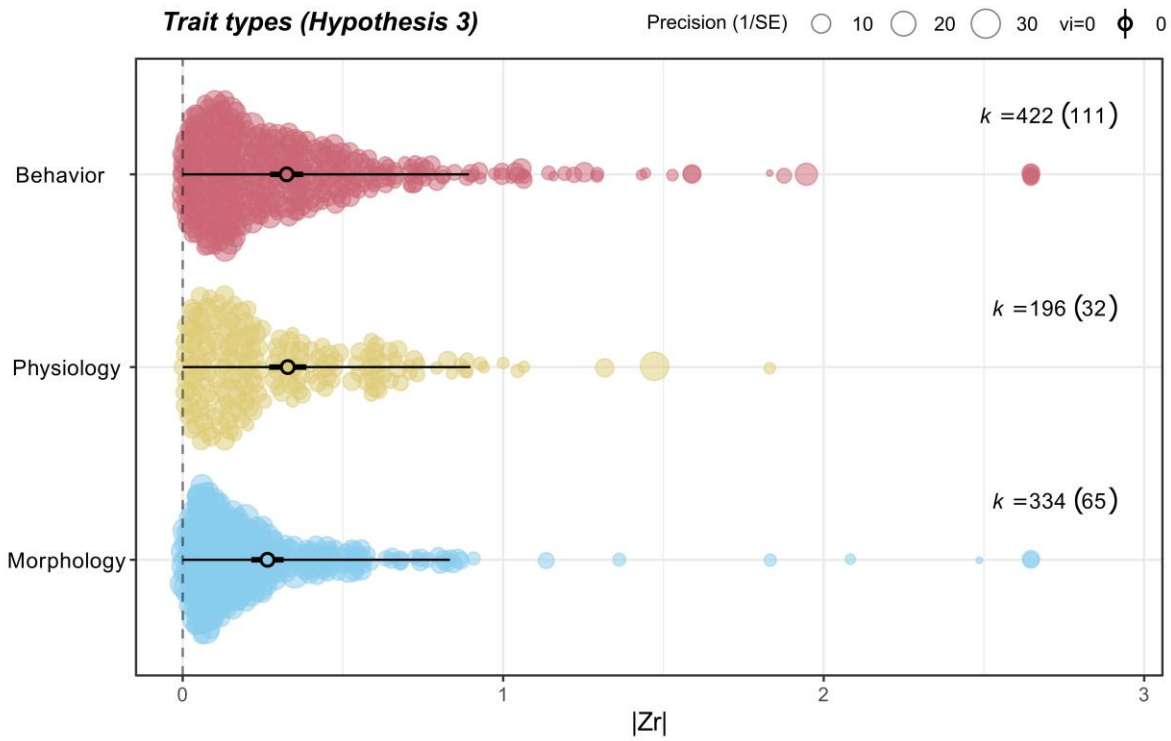

Figure 4: Orchard plot of model estimates of |*Zr*| effects sizes estimated for each trait type category at the among-individual level (n=952 effect sizes). The size of each point is proportional to the precision of the effect size (1/SE). Thick and thin error bars give 95% confidence and prediction intervals, respectively. Sample sizes (*k*) and number of studies (in brackets) are given for each trait type category. Model estimates are reported in table 1. Categories are shown in blue, yellow, and orange for morphological, physiological and behavioral traits, respectively.

Reproductive organ relative size (n=1), immunity (n=3), morphotypes (n=75), hormone levels (n=11), and assimilation (n=4) were the three sub-trait categories maintaining the strongest relationships (fig. 5). Effect size with large values and estimated with sufficient sample sizes were then activity (n=133), metabolism (n=89), boldness (n=91), stoichiometry (n=52), exploration (n=92), and aggressiveness (n=57) (fig. 5). Some sample sizes were small and expressed large 95% CIs. We therefore advocate for caution when interpreting those results, as we refrained to perform direct statistical comparisons among sub-trait categories. In ranking effect sizes by their magnitudes, we instead aimed at a semi-quantitative analysis.

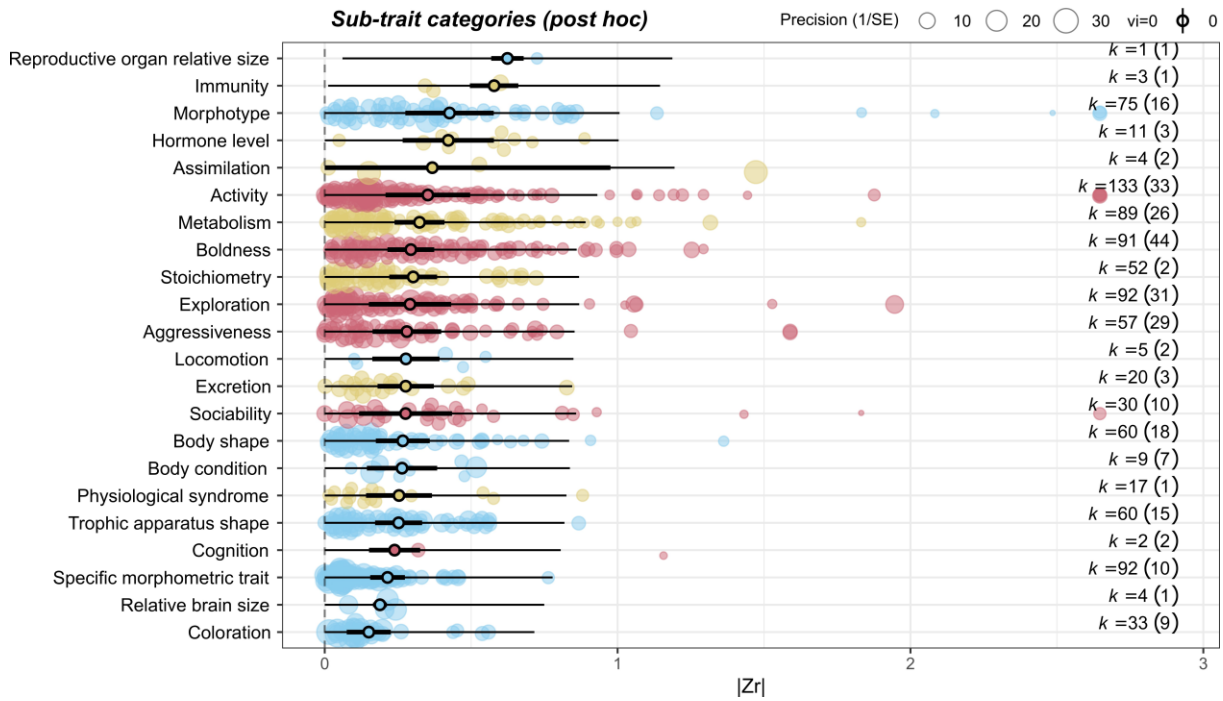

Figure 5: Orchard plot of model estimates of |*Zr*| effects sizes for each sub-trait type, ranked from highest (top) to lowest estimates (bottom). The size of bubbles is proportional to the precision of the effect sizes (1/SE). Thick and thin error bars give 95% confidence and prediction intervals, respectively. Sample sizes (k) and number of studies in brackets are given for each trait type category. Categories are shown in blue, yellow, and orange for morphological, physiological and behavioral traits, respectively.

Table 1: Mean effect sizes and 95% confidence intervals for (A) the intercept-only model (global estimate, H_0), and the model for intraspecific levels (among- and within populations; H_1) for all the dataset. (B) Estimates given for response types (H_2) and trait types (H_3), are based on a subset of the data, including only effect sizes at the individual level (n=952; 94% of the dataset). Raw estimated effect sizes are given as $|Zr|$ and $|r|$, as well as with their unbiased estimates ($|Zr| - |Zr|_{null}$). Confidence intervals at 95% are given in brackets. For each model, (†) indicates the category with the lowest estimated effect size, and the categories shown in bold (*****) are those with significantly higher estimates compared to (†). Pairwise comparison statistics (*z*- and *P*- values) are given accordingly.

Parameters *(/model)*	$\|Zr\|$	$\|r\|$	$\|Zr\|_{null}$	$\|Zr\|_{unbiased}$	$\|r\|_{unbiased}$	z	*P*
(A) *(/Intercept-only)*							
Global estimate	0.30 (0.25 – 0.34)	0.29 (0.25 – 0.33)	0.05 (0.05 – 0.06)	0.25 (0.20 – 0.28)	0.24 (0.20 – 0.27)	–	–
(/Intraspecific levels)							
Within-populations **(†)** *(individuals)*	0.28 (0.24 – 0.33)	0.28 (0.24 – 0.32)	0.06 (0.05 – 0.06)	0.22 (0.19 – 0.27)	0.22 (0.19 – 0.25)	–	–
Among-populations	0.51 (0.28 – 0.75)	0.47 (0.27 – 0.64)	0.04 (0.03 – 0.05)	0.47 (0.25 – 0.70)	0.43 (0.24 – 0.59)	1.90	.0572
(B) *(/Trait types model)*							
Morphology **(†)**	0.25 (0.21 – 0.30)	0.25 (0.20 – 0.29)	0.05 (0.05 – 0.06)	0.20 (0.17 – 0.24)	0.20 (0.16 – 0.23)	–	–
Physiology (*)	**0.32 (0.27 – 0.38)**	**0.31 (0.26 – 0.36)**	**0.06 (0.04 – 0.07)**	**0.26 (0.23 – 0.31)**	**0.26 (0.22 – 0.29)**	**2.42**	**.0157**
Behavior (*)	**0.32 (0.27 – 0.37)**	**0.31 (0.26 – 0.36)**	**0.06 (0.05 – 0.07)**	**0.26 (0.22 – 0.30)**	**0.25 (0.21 – 0.29)**	**2.55**	**.0108**
(/Response types)							
Foraging (*)	**0.34 (0.26 – 0.42)**	**0.33 (0.25 – 0.40)**	**0.07 (0.05 – 0.08)**	**0.27 (0.21– 0.34)**	**0.26 (0.20 – 0.32)**	**2.32**	**.0204**
Trophic niche (*)	**0.35 (0.25 – 0.45)**	**0.34 (0.25 – 0.42)**	**0.06 (0.05 – 0.07)**	**0.29 (0.20 – 0.38)**	**0.28 (0.20 – 0.35)**	**2.19**	**.0284**
Growth	0.31 (0.23 – 0.39)	0.30 (0.23 – 0.37)	0.06 (0.05 – 0.07)	0.25 (0.18 – 0.32)	0.24 (0.18 – 0.30)	1.80	.0717
Survival	0.27 (0.20 – 0.35)	0.26 (0.19 – 0.33)	0.05 (0.04 – 0.06)	0.22 (0.16 – 0.29)	0.22 (0.15 – 0.27)	1.21	.2271
Reproduction **(†)**	0.22 (0.15 – 0.29)	0.21 (0.14 – 0.28)	0.05 (0.04 – 0.06)	0.17 (0.11 – 0.23)	0.16 (0.10 – 0.22)	–	–
Community (*)	**0.37 (0.23 – 0.50)**	**0.35 (0.22 – 0.47)**	**0.08 (0.07 – 0.09)**	**0.29 (0.16 – 0.41)**	**0.27 (0.16 – 0.37)**	**2.00**	**.0466**
Ecosystem	0.33 (0.20 – 0.46)	0.32 (0.19 – 0.43)	0.08 (0.07 – 0.09)	0.25 (0.13 – 0.37)	0.24 (0.13 – 0.33)	1.53	.1264

Discussion

With this meta-analysis, we analyzed four decades of studies in ecology and evolution with the aim to improve our knowledge of the magnitude of relationships between ITV and ecological dynamics (Des Roches et al. 2018; Raffard et al. 2019). Not only our analysis emphasized that ITV matters for ecology, but also that the intraspecific level (among populations vs. among individuals), the type of ecological response, and the type of trait (morphology, physiology, and behavior) are three important factors driving the strength of relationships between traits and

ecological responses within species of animals. Our synthesis focusing largely on trait differences among individuals provides the first broad sense estimates for the magnitude of relationships between traits and ecological responses. This opens new avenues to improve our knowledge of the links between individual traits and ecosystem processes, which we will distill through this discussion.

Global Effect Sizes for Relationship Magnitudes between ITV and Ecological Responses

The global effect size we report ($|r|_{\text{unbiased}}$ = 0.24 [0.20 – 0.27] 95% CI; table 1) might be considered small to moderate in absolute terms (Nakagawa and Cuthill 2007). However, it falls in the upper range of effect sizes reported in ecology and evolution (*ca.* 95% of $|r|$ values are between 0.14 and 0.26; Møller & Jennions, 2002). This remains true when emphasizing only among-individual variability ($|r|_{\text{unbiased}}$ = 0.22 [0.19 – 0.25] 95% CI; table 1).

Effect sizes among populations and groups of eusocial animals were strong in absolute terms ($|r|_{\text{unbiased}}$ = 0.43 [0.24 – 0.59] 95% CI; table 1), and twice stronger than effect sizes collected among individuals. However, this difference was not significant (P = .0572), as our test surely suffered from a too low sample size in the among-population category (fig. S7). While more data are needed to reach a conclusion, the twofold difference tends to support our first hypothesis. Populations whom phenotypically diverged, or expressed local trait matching with ecological processes show links between their traits and ecological responses of a greater magnitude. However, the alternative hypothesis that relationships assessed among individuals could be as large as the ones obtained among populations, remains a possibility as well. In a world where genetic and phenotypic diversity are eroding and changing fast (Exposito-Alonso et al. 2022; Sanderson et al. 2023), ITV has important implications for the conservation and management of intraspecific diversity (Blanchet et al. 2020; Des Roches et al. 2021). Management and conservation plans should consider that both ITV within and among

populations are relevant biological levels, as these two levels are nested, meaning that changes in ITV within populations are ultimately changing among population ITV, with overlooked consequences for ecological dynamics.

The heterogeneity in our dataset was large (87%), as were the prediction intervals at 95% around our estimates (fig. 3–5). Despite the extensive scope of our meta-analysis, the 95% confidence intervals around point estimates stays small, meaning that the multi-level structure of our models accounted well for this heterogeneity. Accordingly, all the covariates that we tested were not significant, suggesting that our results may generalize across years of publication, aquatic and terrestrial realms, consumers and predators, as well as methodological approaches (field, mesocosms, microcosms). Meta-analyses in ecology and evolution often consider that large total heterogeneities (often inherent to both disciplines) should inevitably lower the generality of findings, but this might not be always the case in multi-level meta-analyses. The within-study heterogeneity can comprise a substantial part of total heterogeneity (as in the present meta-analysis), which would need to be accounted for when evaluating the generality of findings, which lies more on the between-study heterogeneity (Yang et al. 2024*b*).

How ITV Relates to Ecological Responses across Biological Levels?

We expected that the overall strength of a cascade of indirect relationships between ITV and an ecological response would decrease from low levels to high levels of biological organization. Effects of ITV could dissipate due to the accumulation of intermediate relationships among distal relationships, for instance between a given phenotypic trait and a response at the community or ecosystem level (*H2*; see Bailey et al., 2009). Our results did not support this hypothesis. We rather observed large magnitudes for organismal performance and community-level responses, while relationships with fitness (survival and reproduction) displayed the

smallest magnitudes. The same analysis performed on the whole dataset showed that both community and ecosystem-level responses were higher than reproduction.

Effect sizes were larger for foraging and trophic niche responses than for reproduction. This can be explained since reproduction outcomes are still complex to predict, as they are influenced by intrinsic (genetic and phenotypic), and extrinsic processes such as varying environmental conditions and random events (Merilä & Sheldon, 2000). Then, effect sizes for community-level responses were larger than for reproduction. This could arise because of methodological differences. In our dataset, most studies investigating fitness took place in nature (*ca.* 70%), whereas most studies investigating responses at the community and ecosystem levels were conducted in mesocosms (*ca.* 75%). A dampening of effect size magnitude can occur because of a greater complexity in nature compared to controlled conditions (Hendry 2019). Nevertheless, we did not find differences between estimates from field, mesocosm or microcosm studies. Thus, we are left with the result already reported by others (Des Roches et al., 2018; Raffard et al., 2019) that the magnitude of the links between ITV and ecological responses are substantial for community dynamics, even when they arise from phenotypic differences among individuals of similar body sizes (this study).

The effect sizes for fitness proxies reported here are of similar nature to linear estimates of directional selection (Hendry 2017). Indeed, our estimates for reproduction ($|r|_{\text{unbiased}} = 0.16$ for among-individuals and 0.16 for the whole dataset) matched accurately with those reported elsewhere for linear directional selection ($|\beta| = 0.15$; see Kingsolver et al., 2012). One potential reason for the relatively small effect sizes of ITV on fitness related responses is that past adaptation of individuals to the local environment has already shaped ITV near their optima (i.e., stabilising selection). Another mechanism can be fluctuating selection regimes averaging over time (Wright et al., 2019). As such, the estimated selection on traits is no longer strong: "*selection erases its traces*" (Haller and Hendry 2014). By contrast, ITV effects on community

and ecosystem dynamics do not reflect adaptations *per se* and are not under selection to eliminate such effects, which might explain why the effect sizes we observed at these levels were larger than on reproduction. Yet, this does not mean that selection is weaker than the links between ITV and community/ ecosystem responses. Subtle rates of changes in trait distributions, when scaled up to population dynamics and higher numbers of generations, can lead to large eco-evolutionary dynamics (Hansen et al. 2011).

Other factors may explain why effect sizes were the largest at the community level. First, many relationships in ecology are non-linear. Because of Jensen's inequality (Bolnick et al. 2011), concave-up intermediate relationships can amplify the effects of ITV at high levels of biological organization (see Bailey et al., 2009). Second, large effects of ITV can occur through direct effects on community and ecosystem responses (i.e., 'trait-mediated effects'; Schmitz et al., 2004), which could be particularly strong as they may not dissipate through many intermediate relationships (fig. 1a). This can be particularly true when focal animals are keystone (Paine 1980), foundation (Ellison 2019), engineer species (Romero et al. 2015), or are prone to niche construction (Laland et al. 1999). A great example comes from the Yellowstone, where a small subset of wolf individuals within a pack are specialized on beavers (i.e., some individuals are hunting ~200% more beavers; Bump et al., 2022), and therefore, are contributing disproportionately to wetland appearance/loss dynamics (Gable et al. 2020).

Do Trait Types Showed Different Relationship Magnitudes with Ecological Responses?

We hypothesized that physiological and behavioral traits would maintain stronger ecological relationships than morphological ones (*H3*). Accordingly, physiological and behavioral trait variation among individuals showed 28% stronger relationships with ecological responses than did morphological traits. This confirms that traits reflecting energetic tradeoffs and interactions among individuals matter for our understanding of ecological processes. For instance,

functional responses of predator crabs (*Panopeus herbstii*) on mussel prey (*Brachidontes exustus*) are mediated by consistent variation among individuals in their activity levels, suggesting strong ecosystem-level effects given that mussels are famous ecosystem engineers (Toscano and Griffen 2014). Physiological traits showed strong relationship strengths across ecological responses (fig. 4&5). An example is how variations in corticosterone levels among individuals predict long-term reproductive performances in wandering albatross (*Diomedea exulans*; Angelier et al., 2010). This is consistent with the fact that variations in metabolic, immune, hormonal, and stoichiometric traits are all believed to be strongly related with fitness, community and ecosystem responses (Elser et al. 2000; Ricklefs and Wikelski 2002; Brandl et al. 2022).

Understanding how different phenotypic dimensions relate to ecological differences among individuals or populations is a priori challenging, and this motivated the present work. From a general standpoint, morphology could express a *potential* for ecological effects, where physiological and behavioral traits might be closer to *realized* effects (Wainwright and Reilly 1994). Our results are in agreement with this general view, albeit the average difference among large categories of traits were rather small in absolute (table 1). Morphological traits that showed the largest effect sizes were also the most *a priori* functionally-relevant (fig. 5). The category with the highest effect size and sufficient sample size was '*Morphotype*', which refers to dimorphic populations, or ecotypes which diverged ecologically hundreds to thousands of generations ago (Harmon et al., 2009). '*Locomotion*' designates morphological traits linked to the capacity for an individual to perform locomotion ('*activity*'), the behavioral sub-category showing the strongest effect size (fig. 5). The trait coined '*body condition*' is a proxy for physiological status (energy reserve). Morphological traits with the less general functional relevance for a broad range of ecological responses, such as linear morphometric traits (labelled 'specific morphometric traits') exhibited unexpectedly, lower effect sizes (fig. 5).

Our results at the intraspecific level are contrasting with the strong reliance on morphological traits in TBE (Dawson et al. 2021). This popularity for morphology may hold into that those traits are easily measured on immobilized or dead animals. Another reason for the popularity of morphology could be its low flexibility (i.e., low intra-individual variation) and high heritability compared to physiology and behavior (Mousseau and Roff 1987). Although morphological traits do not maintain the strongest ecological relationships in average (this meta-analysis), since they are less labile and more heritable in comparison to physiological or behavioral traits, they could maintain more persistent eco-evolutionary dynamics than physiology and behavior. This idea would need to be investigatred. However, the lability of physiological and behavioral traits does not mean randomness, as it should not prevent their use in TBE. Those trait types show moderate to high repeatability among individuals (Bell et al. 2009), and in some cases, large heritabilities as well (Dochtermann et al. 2014). Moreover, recent advances show that the residual intra-individual variation for those traits can be structured, with predictable *vs.* unpredictable individuals (Stamps et al. 2012). Finally, if we aim at quantifying the propensity of traits to be involved in eco-evolutionary dynamics, it would be promising to compare the evolvabilities (Hansen et al. 2011) of those trait types with metrics expressing their propensity to alter ecological dynamics.

General formulations have been suggested to explore theoretically the links between traits, abundances, and ecosystem functions (Violle et al. 2007). Our trait functionality estimates can help to parametrize eco-evolutionary or trait-based models intended to assess how shifts in trait distributions through evolution, selection, patch dynamics, etc. can affect various ecological responses from ecological performances to ecosystem functioning (Govaert et al. 2019). Therefore, we invite to investigate how changes in the moments of traits distribution (mean, variance, skewness and kurtosis), for instance under selection (Kingsolver et al. 2012) and various ecological functionality estimates available for different traits (our approach), can

change the outcomes on ecological processes (Norberg et al. 2001; Barabás et al. 2022). In addition, we invite to continue refining empirical estimates for trait selection rates, evolutionary potentials, and trait's functionality for different trait categories, and to assess how those metrics covary or not. This would help identify particular facets of ITV showing both large evolutionary change potential, as well as large potential to link to ecosystem functions (Blanchet et al. 2020; Des Roches et al. 2021).

Concluding Remarks

Ideal traits to move forward TBE of animals should meet two criteria: (*i*) link to a vast range of ecological functions operating at different levels, and (*ii*) be 'universal', i.e., can be measured across intra- and interspecific levels of various animal taxonomic groups (Carmona et al. 2016). Here, several continuous traits showed relatively strong links with ecological responses, as they can meet the second criterion (e.g., hormone levels, activity, metabolism, boldness, stoichiometry, excretion, sociability, body condition, and cognitive abilities; fig. 5). Technological developments should facilitate the measurement of such traits at the individual level, allowing multi-trait approaches. Telemetry and camera traps, coupled with artificial intelligence (AI) algorithms, are improving the study of movements, activity and stereotypic behaviors of vertebrates in the field (Suraci et al. 2017; Salama AbdELminaam et al. 2020). Flow cytometry, (-thermal) imagery, and respiration chambers are facilitating the measurement of shape and size, metabolism, and behavior on aquatic invertebrates (Réveillon and Becks 2022). In a similar way, the continuous miniaturization of telemetry allows collecting behavioral data on insects as small as bumblebees (Hagen et al. 2011).

We advocate the assessment of the functionality of traits used in TBE. This effort should parallel their harmonisation towards a universal set of continuous individual-based traits and their inclusion in databases. In the face of global changes, this information should help towards

a better appraisal of the implications of biodiversity changes at the levels of individuals, populations, species, communities and ecosystems. To unravel the ecological implications of animal intraspecific diversity, we encourage ecologists not to neglect physiological and behavioral traits. Future studies at the intraspecific level will gain in predictive abilities by addressing simultaneously all the facets of a phenotype and their covariations. Multiple morphological, physiological, and behavioral traits are integrated into one phenotype, and acknowledging this would inform about ecological and fitness trade-offs (Arnold 1983; Violle et al. 2007). Such an approach at the individual level will improve our integration of biological scales, evolutionary and ecological processes, as well as predictions of the effects of global changes on ecosystems.

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Authorship

T.R. assembled the first ideas. T.R. designed the study with the guidance of A. R., S. B., A. P. H., and R. C.. T. R. and A. R. performed the systematic review of the literature in parallel, deleted duplicates and validated selected studies. T.R. extracted the data from the selected papers, did the statistical analyses and wrote a first draft of the manuscript. All co-authors then contributed to the discussion of the results and to the editing of the manuscript until its publication.

Data accessibility

The data and R code supporting the results and their reproducibility can be accessed through a public repository (Figshare) [https://doi.org/10.6084/m9.figshare.27377529.v1].

Conflicts of interest

The authors have no conflict of interest to declare.

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