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

- Thibaut Rota^{1,2,3*}, Allan Raffard^{4,5}, Iris Lang^{1,6}, Quentin Petitjean^{1,7}, Lisa Jacquin^{1,8}, Olivier
 Dézerald⁹, Simon Blanchet¹⁰, Andrew P. Hendry¹¹ and Régis Céréghino¹
- 5 ¹ Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS,
- 6 IRD, Toulouse INP, Université Toulouse 3 Paul Sabatier (UT3), Toulouse, France
- ² Institute of Microbiology, University of Applied Sciences and Arts of Southern Switzerland, Mendrisio,
 Switzerland
- 9 ³ Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
- ⁴ Université catholique de Louvain, Earth and Life Institute, Biodiversity Research Centre, Louvain-la Neuve, Belgium
- 12 ⁵ Univ. Savoie Mont Blanc, INRAE, CARRTEL, 74200 Thonon-les-Bains, France
- ⁶ Conservatoire d'espaces naturels d'Occitanie, 26 allées de Mycènes, 34000 Montpellier, France
- ⁷ INRAE Nouvelle-Aquitaine Bordeaux Centre, UR EABX, 50 Avenue de Verdun, 33612, Cestas Cedex,
 Nouvelle-Aquitaine, France
- ⁸ Institut Universitaire de France (IUF), Paris, France
- ⁹ DECOD, L'Institut Agro, IFREMER, INRAE, 35000 Rennes, France
- 18 ¹⁰ Centre National de la Recherche Scientifique, Station d'Ecologie Théorique et Expérimentale, UAR
- 19 2029, 2 route du CNRS, 09200 Moulis, France
- 20 ¹¹ Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke St. W., H3A 0C4
- 21 Montréal, Québec, Canada
- 22 * Corresponding author: Dr. Thibaut Rota (thibaut.rota@supsi.ch)

23

Abstract

24 Intraspecific trait variability (ITV) is an important aspect of community ecology, but we still 25 have a poor understanding of what drives the magnitude of relationships between ITV and 26 ecological dynamics. In order to guide ecologists interested in unravelling the ecological 27 implications of ITV, we asked whether relationships' magnitudes differ (i) between intraspecific levels (among- vs. within- populations), (ii) among ecological responses spanning 28 29 levels of biological organization (from individual performances to ecosystem functioning), and 30 (iii) among trait categories (morphology, physiology and behavior). We performed a meta-31 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 32 33 range of ecological responses. The average effect size was |r| = 0.24 [0.20 - 0.27] (95%) 34 confidence intervals). Within populations, relationships' magnitudes were higher for ecological 35 performance (foraging, diet), community and ecosystem responses than for fitness 36 (reproduction). Relationships were 28% stronger for physiological and behavioral traits than 37 for morphological traits. Our meta-analysis confirms the central aspect of ITV within 38 populations of animals to drive ecological dynamics, and emphasizes physiological and 39 behavioral traits to enhance the integration between the individual component of diversity and 40 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).

43

Introduction

44 The question 'What Do Species Do in Ecosystems?' raised three decades ago by J. H. 45 Lawton (1994) has been foundational to trait-based ecology (TBE). Trait-based ecologists 46 revolve around organisms' functional traits (Violle et al., 2007) to describe and predict how 47 organisms interact altogether and with their environment. Trait-based approaches to community 48 ecology brought the promise to improve our understanding of the mechanisms driving 49 community assembly and ecosystem processes, in being complementary to, or even outpace 50 taxonomic approaches in that regard (Enquist et al. 2015). Traits can be expressed in physical 51 dimensions (e.g., mass, length, volume, energy, time), and can meaningfully express the fit of 52 organisms with their environment (Arnold 1983; Violle et al. 2007). Inferences drawn from 53 TBE are thus, ideally, transferable to other ecosystems and life forms (Funk et al. 2017). 54 General patterns include allometric scalings between body size and metabolic rate (Kleiber 55 1932), the leaf economic spectrum (Wright et al., 2004), r- and K- life history strategies (Pianka 56 1970). Trait-based approaches do not have borders. Most traits are cheap and easy to measure, 57 fostering inclusion among researchers from different horizons, as they integrate from individual 58 to ecosystem levels, and across various ecosystems (Carmona et al. 2016).

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

60 Early research in TBE led to rethink community ecology (McGill et al. 2006; Petchey and 61 Gaston 2006). Yet, an important limitation is that studies focused heavily on species' mean trait 62 values, assuming that all conspecifics shared identical trait values (Albert 2015). This 63 assumption was paradoxal, as intraspecific trait variation (henceforth 'ITV') was essential to 64 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 65 large as mean trait differences between species (Lecerf and Chauvet 2008; Siefert et al. 2015; 66 67 Rota et al. 2022), and matters for species coexistence (e.g., Hart et al., 2016), predator-prev 68 (Toscano and Griffen 2014), and consumer-resource interactions (Raffard et al. 2017; Rota et 69 al. 2018). ITV is now recognized to be an important facet of ecology (Bolnick et al. 2011; Violle 70 et al. 2012), provoking discussions on how it affects our understanding of food webs (e.g., 71 behavior; Moran et al., 2017) and community assembly (e.g., metabolic traits; Brandl et al., 72 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, 73 74 fundamental in community ecology. For all individualizable organisms, ecological interactions 75 (competition, predation etc.) are occuring among conspecific or heterospecific individuals, 76 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 77 78 (Wong and Carmona 2021) and to miss important information about diversity. For instance, not 79 acknowledging for intraspecific variability could distort relationships between species richness 80 and functional diversity (Cianciaruso et al. 2009). On the other hand, acknowledging the 81 processes affecting ITV around species' averages, such as evolution in response to competition 82 regimes, can contribute to a mechanistic understanding of diversity-function relationships 83 (Barabás et al. 2022).

84 Why Assessing Relationships' Magnitude between ITV and Ecological Dynamics?

85 Important insights emerged from a renewed interest for ITV. First, ITV links to community 86 assembly patterns (e.g., species richness and diversity) and ecosystem functioning (e.g., 87 productivity or nutrient cycling) as much as mean trait variation between species (Des Roches 88 et al. 2018; Raffard et al. 2019). Second, ITV is changing fast with human-driven disturbances 89 (Alberti et al. 2017), including population loss (Ceballos et al. 2017), erosion of genetic 90 diversity (Exposito-Alonso et al. 2022), and changes in phenotypic variation (Sanderson et al. 91 2023). There is thus now a form of urgency in studying the primary role of ITV in ecological 92 processes, such as answering how much and when ITV matters. Conservationists can take 93 advantage of this research agenda, to better identifying and monitoring particular facets of ITV 94 with particular implications for ecological functions (Blanchet et al. 2020) and nature's 95 contribution to people (Des Roches et al. 2021).

96 We need to improve our knowledge about what drives the magnitude of relationships between 97 ITV and ecological dynamics. This would also help understand how evolution, by affecting 98 trait distributions, affects ecological dynamics (i.e., eco-evolutionary dynamics; Pelletier et al., 99 2009; Hendry, 2017). Most research has focused on natural selection (Kingsolver et al. 2012), 100 heritability (Mousseau and Roff 1987), and evolvability so far (Wheelwright et al. 2014), in 101 providing quantitative estimates on evolutionary processes ('evo'). In contrast, the relationships 102 between ITV and ecological responses ('eco') did not receive yet a detailed analysis, despite 103 that evolutionary and ecological processes are often congruent (Harmon et al. 2009). Previous 104 studies compared the ecological impacts of populations varying in key traits (e.g., gill raker's 105 morphology in anadromous or landlocked fish populations; Post et al., 2008), but there are still 106 very few studies having focused at both the individual and population levels (Gibert et al. 2015). 107 Hence, it remains unclear if relationships between ITV and ecological responses show similar 108 magnitudes at the population and individual levels. On one hand, we could expect population109 level ITV to show stronger relationships with ecological dynamics than individual-level ITV, 110 because local adaptation can drive divergence in among-population trait values and trait 111 matching with local ecological processes (Post et al. 2008). On the other hand, ITV among 112 individuals has been shown to be similar or even larger than ITV among populations (Messier 113 et al. 2010; Rota et al. 2024). It thus remains possible that ITV among individuals express 114 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).

122

Assessing Traits' Functionality

123 To generate meaningful insights, we assume more or less implicitly in TBE that the traits used 124 are functional in linking to the ecological performances or to the fitness of organisms (Arnold 125 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 126 127 (Mlambo 2014; Lefcheck et al. 2015; Dawson et al. 2021). In biological terms, all traits are 128 functional since they all link to one or several biological functions, making phenotypes 129 functional living entities (Bertossa 2011). Therefore, the question may not be whether a trait is 130 functional or not in absolute terms (for different viewpoints across disciplines, see Dawson et 131 al., 2021 and Sobral, 2021). Without entering into this debate, we propose to investigate traits' 132 *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.

136 A good example of high trait functionality is body size. Body size is used in the vast majority 137 of TBE studies (Green et al. 2022). It spans several orders of magnitude across and within taxa 138 and integrates many biological and ecological processes with often a great predictive power 139 (Peters 1993). Nevertheless, functional diversity is multi-dimensional (de Bello et al., 2021), 140 and it stays poorly known which traits are the most linked to ecological dynamics when we 141 consider individuals within a same cohort or size class (Brandl et al. 2022). As several authors 142 argue (Gordon 2011; Toscano et al. 2016; Moran et al. 2017; Brandl et al. 2022; Schleuning et 143 al. 2023), we need to look beyond body size to improve our understanding of the implications 144 of ITV (e.g., morphology, physiology, behavior varying among individuals).

145 Morphology, physiology and behavior are different facets depicting an individual phenotype. 146 Morphology reflects the abilities of an individual to perform in its environment given 147 biomechanical constraints (Van Valen 1965; Arnold 1983). For instance, the relative mass of 148 metabolically-active organs is used as an energetic proxy (Careau et al. 2008). Yet, energetic 149 currencies such as metabolic rates (i.e., energy loss) should link closer to ecological 150 performances such as feeding rates (i.e., energy intakes) and growth rates (i.e., energy not 151 allocated to maintenance nor reproduction; Biro & Stamps, 2008; Careau & Garland, 2012). 152 Through trophic and ecological interactions, it is expected that metabolic traits are involved in 153 community assembly patterns and ecosystem functioning (Brandl et al., 2022; fig. 1A). Some 154 examples suggest that behavioral traits have a close link to ecological interactions (Gordon, 155 2011; Toscano et al., 2016; for chosen examples from our literature review, see table S1). 156 Behavioral variation among individuals can strongly affect the outcomes of predator-prey 157 interactions (McGhee et al. 2013). Behavioral traits such as locomotion activity,

158 aggressiveness, or boldness are involved in energetic trade-offs (Careau et al., 2008), and 159 hormones regulate metabolism and behavior (Ricklefs & Wikelski, 2002). Physiological and 160 behavioral traits such as those, as well as other energy and matter currencies (e.g., 161 stoichiometry; Elser et al., 2000) – perhaps as opposed to more structural, morphological traits 162 - are therefore expected to exert strong links with ecological performances, fitness, and hence 163 ecological dynamics (Gordon 2011; Moran et al. 2017; Brandl et al. 2022). However, to date, 164 no study synthesized the functionality of morphological, behavioral and physiological traits on 165 various ecological responses.

166

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:

170 (*Q1/H1*) Does the strength of relationships between ITV and ecological responses (hereafter 171 'effect sizes') differ within populations (i_a) versus among populations (i_b). We expected that i_a 172 $< i_b$, because individuals should show stronger phenotypic divergences among- than within-173 populations. An alternative expectation is that $i_a = i_b$, if for instance the populations (i_a) have 174 large sizes or are inter-connected populations, making them phenotypically representative of 175 the entire meta-population (i_b) (Messier *et al.*, 2010; Rota *et al.*, 2024).

176 (Q2/H2) How do effect sizes vary among ecological responses at different levels of biological 177 organization? We ranked ecological responses from (ii_a) proximal responses to the focal 178 organism (e.g., foraging performance, growth, diet, and fitness) to (ii_b) distal responses as 179 community assembly (further abbreviated "community") and ecosystem functioning (further 180 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).

187 (Q3/H3) How do effect sizes vary among trait types? Effect sizes were divided into (iii_m) 188 morphology (e.g., body shape, relative length of functional body parts), (iii_p) physiology (e.g., 189 metabolic rate, hormone levels, elemental stoichiometry), and (*iii*_b) behavior (e.g., activity, 190 boldness, sociability). We hypothesized that behavioral and physiological traits would show the 191 strongest correlations with ecological responses (i.e., $iii_m < iii_p \sim iii_b$). However, it could be 192 relaxed when morphological differences occur between morphotypes having diverged from 193 hundreds to thousands of generations, and for which large phenotypic variation can match 194 ecological differences (e.g.; ecological radiation between limnetic and benthic eco-morphs 195 within a same lake population; Harmon et al., 2009).





197 Figure 1: (A) Diagram showing how ITV could relate to various ecological responses in animals. (B) The 198 magnitude of relationships between ITV and ecological responses is expected to change across levels of biological 199 organization. Black arrows depict intermediate relationships propagating ITV effects across biological levels of 200 organization. Following hypothesis 2 (see main text), the magnitude of relationships between ITV and ecological 201 responses could decrease along higher levels of biological organization (Bailey et al. 2009), from responses located 202 on the organism itself to community and ecosystem levels (grey arrows). All the relationships depicted by grey 203 arrows in panel B are assessed in this meta-analysis, excepting the one for populations (*). Examples of 204 relationships are depicted in table S1, with numbers corresponding with fig. 1A.

205

206

Methods

Search Strings and Selection Criteria

207 We searched for thirty keyword combinations in Web of Science ('all databases'), Scopus and 208 Google Scholar (table S2), and obtained a total of 6904 studies. After having sorted out the 209 duplicates manually in Excel (n = 335), we obtained 6569 studies, from which 613 studies 210 followed our scope after having scrutinized titles and abstracts. Our general scope was studies 211 investigating relationships between animal's trait variability at the intraspecific level and 212 various ecological responses. Exclusion criteria at this stage were studies focusing on other 213 groups than animals, investigating other questions than traits – ecological responses, or studies 214 at the interspecific level.

215 After a full-text examination of those 613 studies, 121 studies met our criteria. We considered 216 empirical studies (i) on wild animals, with observations conducted either in the field, 217 microcosms or mesocosms, (ii) Studies reporting quantitative relationships or comparison 218 statistics between a phenotypic trait measured on several individuals, or averaged at the level 219 of a group of individuals (i.e., population or colonies of eusocial animals), and a measured 220 ecological response, (iii) morphological, physiological, or behavioral traits are categorical or 221 continuous, (iv) we did not include ecological responses reflecting population dynamics or 222 population persistence since those are long-term phenomena for which relationships with ITV 223 are difficult to estimate with empirical studies, (v) studies focused on the 'identity' of 224 phenotypes (i.e., one phenotype versus another) not 'diversity' (i.e., statistics from treatments 225 including mixtures of phenotypes were excluded), (vi) we did not define life history traits as 226 "trait types", since they were categorized as ecological responses (e.g., growth, survival and 227 reproduction), and (vii) we did not include body size since we aimed to focus on often neglected 228 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 inSupplementary 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.

237 Intraspecific Level, Trait Types, Ecological Responses, and Covariates

238 We noted the intraspecific level from which the relationships belonged (i.e., among individuals, 239 among populations, among colonies of eusocial animals). We considered the following seven 240 types of ecological response: '*Foraging efficiency*' (resource consumption or feeding rates); 241 'trophic niche' (trophic niche position, trophic level, and degree of specialization inferred from 242 either stable isotopes or diet assessments); 'growth' (size-standardized growth rates over time 243 based on body length or body mass); 'survival' (survival rates obtained from capture-mark-244 release-recapture in the wild or from controlled experiments); 'reproduction' (number of mates, 245 egg numbers, clutch sizes, or sibling survival); 'community' (abundances, biomasses, diversity 246 and structures of communities of organisms of at least two species interacting with the focal 247 phenotypes); 'ecosystem' (standing stocks or dynamics of basal resources such as primary 248 producers or detritus, as well as energy and matter cycling as C and N cycling). We then 249 categorized traits into morphology, physiology, and behavior. Morphological traits included 250 body shape, trophic apparatus shape, and linear morphometrics on specific features, locomotion 251 traits, coloration, body condition, reproductive organ relative size, brain relative size, and 252 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.

259

Calculation of Effect Sizes

260 We collected correlation coefficients (r) or statistics (e.g., F or t statistics) corresponding to 261 each trait-to-ecological response relationship. The original estimates were transformed to 262 correlation coefficients r and then to Fischer's Z-transformed correlation coefficients Zr, 263 following established procedures (Nakagawa & Cuthill, 2007; see table S3). Since we aimed to 264 quantify the magnitude of ITV – ecological response relationships, and to perform comparisons 265 among trait and ecological response categories, the direction of the relationship was not 266 meaningful here. We used absolute values of correlation coefficients |Zr| in further analyses 267 (Bailey et al. 2009). For each effect size |Zr|, we computed a sampling variance (vi) that we 268 used in our models (detailed below) (Nakagawa and Cuthill 2007; Nakagawa et al. 2022).

269

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.metaforproject.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 metaanalyses 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/metaanalysis-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*).

282 We computed phylogenetic relatedness among species following Moran et al. (2021). We 283 extracted phylogenetic and taxonomic information from the Open Tree of Life 284 (https://tree.opentreeoflife.org/; Hinchliff et al., 2015). We then resolved any polytomies by 285 randomisation in the R package 'rotl' (Michonneau et al. 2016). Branch lengths were estimated 286 using Grafen's method (Grafen 1989) in the R package 'ape' (Paradis and Schliep 2019), and 287 we added a residual error term accounting for the computed phylogenetic correlation matrix in 288 our meta-analytic models. We accounted for within-study non-independence by adding a 289 within-study random effect term (nested with *studyID*), attributing an identifier to all effect 290 sizes (see Noble et al. 2017; Yang et al. 2024a). Selective reporting bias and sources of non-291 independence inherent to the structure of the data can be accounted for by modelling an 292 appropriate sampling variance – covariance matrix (varcov), and by following a two-step 293 cluster-robust estimation procedure (Yang et al. 2024*a*). We computed *varcov* with the function 294 *vcalc()* of the package '*metafor*', accounting for the basal level of our observations (*effect* 295 *sizeID*), the cluster of the model (*studyID*), and a subgrouping variable regarding trait-to-296 response combinations (n = 468) (subgroup argument), in setting covariation among subgroups 297 as $\rho=0.6$. This varcov ensured that the residual errors of the model accounted for the non-298 independence inherent to trait-to-response combinations (n = 468). This accounted for the fact 299 that traits have shared means and errors within those categories but that those means and errors 300 are expected to show larger differences with other traits and responses measured on other pairs 301 of individuals, and species, in line with the multi-level structure in the data. For each model

302 (see fixed-effect structures below), we re-ran the output from the function *rma.mv()* to get a
303 cluster-robust estimation of effect size estimates and their variance using the function *robust()*304 of the package '*metafor*' (i.e., two-step procedure described in fig. 7 in Yang et al. 2024*a*).

305 Sampling variance (vi) and mean-centered year of publication are indicators of small study 306 effects and publication time-lag bias, respectively (Nakagawa et al., 2022). We assessed and 307 accounted for these two bias in adding these terms as fixed-effects in our models, so effect size 308 estimates are given for vi = zero, and for the average year in our dataset which was 2012.5 309 (Nakagawa et al., 2022). Using the same error and random-effects terms model structure as 310 mentioned above, we first estimated the grand-mean effect size with an intercept-only model. 311 We then setted intraspecific level as a fixed effect (H1). Here we tested if effect sizes obtained 312 among individuals vs. among populations differed, in merging 'populations' and 'colonies of 313 eusocial animals', to reduce the unbalancing of effect sizes between 'individual-level' (n=952) 314 and 'population-level' (n=56). We then tested our hypotheses regarding differences among trait 315 types and ecological response types (H2 and H3) on data at the individual level, with n=952316 effect sizes (94% of the dataset), to avoid any confounding effects of the intraspecific level on 317 those two hypotheses. We also tested H_2 and H_3 using all the dataset, to see if it would change 318 our conclusions (see table S4). In both cases, we built a model including ecological response 319 type as a fixed effect and adding trait type as a random effect (H2). We then tested for 320 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 $|Zr| \ge 0$, 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 backtransformed $|Zr/_{unbiased}$ 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-, withinstudy, and phylogenetic heterogeneity (*P*) 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.

346

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).

352

Heterogeneity and Covariates

353 Total heterogeneity in our meta-analysis was high (87%; $Q_{df=1005} = 6238.7$; P < .0001). 354 Phylogenetic relatedness among species accounted for 4.8% of the total heterogeneity in effect 355 sizes. Most of the heterogeneity was within studies (45.7%), rather than among studies (36.5%). 356 We did not observe any statistical difference among categories of covariates, and accordingly, 357 distributions were undistinguishable between systems (aquatic vs. terrestrial; z = 0.2; P = .841), 358 trophic levels (consumers vs. predators; z = 1.58; P = .114), and methodological approaches 359 (field observations, mesocosms, and microcosms; z < 1.18; P > .239; fig. S2–S4). It is 360 noteworthy that the two levels 'colonies of social animals' and 'populations' that we merged to 361 test for differences among intraspecific levels (among-population vs. within-populations) 362 shared very similar effect sizes in average (fig. S5).



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

3	6	7
~	~	

377

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 $-3 \le Zr \ge$ 3, which is similar to $-0.99 \le r \ge 0.99$. 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).

375 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

379 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.

392 Physiological and behavioral traits showed effect sizes 28% higher than morphological ones 393 (fig. 4, table 1). The difference between physiology and morphology was not significant when 394 tested on the whole dataset (i.e., including both individual and among-population observations; 395 table S4). Differences among trait type categories were not reflected in the relative frequencies 396 of trait types included in the first quartile range (25th percentile) of effect sizes distribution 397 (morphological: 37% physiological: 19%, and behavioral traits: 44%; fig. 4), but effect sizes 398 with large magnitudes in the dataset were corroborating statistical results, as morphological 399 (17%) and physiological traits (17%) were less represented than behavioral traits (66%) in the 400 third quartile (75th percentile) of the effect sizes distribution (fig. 4).



401

402 **Figure 4**: Orchard plot of model estimates of |Zr| effects sizes estimated for each trait type 403 category at the among-individual level (n=952 effect sizes). The size of each point is 404 proportional to the precision of the effect size (1/SE). Thick and thin error bars give 95% 405 confidence and prediction intervals, respectively. Sample sizes (*k*) and number of studies (in 406 brackets) are given for each trait type category. Model estimates are reported in table 1. 407 Categories are shown in blue, yellow, and orange for morphological, physiological and 408 behavioral traits, respectively.

409 Reproductive organ relative size (n=1), immunity (n=3), morphotypes (n=75), hormone levels 410 (n=11), and assimilation (n=4) were the three sub-trait categories maintaining the strongest 411 relationships (fig. 5). Effect size with large values and estimated with sufficient sample sizes 412 were then activity (n=133), metabolism (n=89), boldness (n=91), stoichiometry (n=52), 413 exploration (n=92), and aggressiveness (n=57) (fig. 5). Some sample sizes were small and 414 expressed large 95% CIs. We therefore advocate for caution when interpreting those results, as 415 we refrained to perform direct statistical comparisons among sub-trait categories. In ranking 416 effect sizes by their magnitudes, we instead aimed at a semi-quantitative analysis.



418 **Figure 5**: Orchard plot of model estimates of |Zr| effects sizes for each sub-trait type, ranked 419 from highest (top) to lowest estimates (bottom). The size of bubbles is proportional to the 420 precision of the effect sizes (1/SE). Thick and thin error bars give 95% confidence and 421 prediction intervals, respectively. Sample sizes (k) and number of studies in brackets are given 422 for each trait type category. Categories are shown in blue, yellow, and orange for 423 morphological, physiological and behavioral traits, respectively.

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

Parameters (/model)	Zr	r	$ \mathbf{Z}r _{\mathrm{null}}$	Zr unbiased	r unbiased	Z	Р
(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
433							

434

435

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 442 ecological responses within species of animals. Our synthesis focusing largely on trait 443 differences among individuals provides the first broad sense estimates for the magnitude of 444 relationships between traits and ecological responses. This opens new avenues to improve our 445 knowledge of the links between individual traits and ecosystem processes, which we will distill 446 through this discussion.

447 Global Effect Sizes for Relationship Magnitudes between ITV and Ecological 448 Responses

The global effect size we report ($|r|_{unbiased} = 0.24 [0.20 - 0.27] 95\%$ 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 ($|r|_{unbiased} = 0.22 [0.19 - 0.25] 95\%$ CI; table 1).

454 Effect sizes among populations and groups of eusocial animals were strong in absolute terms 455 $(|r|_{\text{unbiased}} = 0.43 [0.24 - 0.59] 95\%$ CI; table 1), and twice stronger than effect sizes collected 456 among individuals. However, this difference was not significant (P = .0572), as our test surely 457 suffered from a too low sample size in the among-population category (fig. S7). While more 458 data are needed to reach a conclusion, the twofold difference tends to support our first 459 hypothesis. Populations whom phenotypically diverged, or expressed local trait matching with 460 ecological processes show links between their traits and ecological responses of a greater 461 magnitude. However, the alternative hypothesis that relationships assessed among individuals 462 could be as large as the ones obtained among populations, remains a possibility as well. In a 463 world where genetic and phenotypic diversity are eroding and changing fast (Exposito-Alonso 464 et al. 2022; Sanderson et al. 2023), ITV has important implications for the conservation and 465 management of intraspecific diversity (Blanchet et al. 2020; Des Roches et al. 2021). 466 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.

470 The heterogeneity in our dataset was large (87%), as were the prediction intervals at 95% 471 around our estimates (fig. 3-5). Despite the extensive scope of our meta-analysis, the 95% 472 confidence intervals around point estimates stays small, meaning that the multi-level structure 473 of our models accounted well for this heterogeneity. Accordingly, all the covariates that we 474 tested were not significant, suggesting that our results may generalize across years of 475 publication, aquatic and terrestrial realms, consumers and predators, as well as methodological 476 approaches (field, mesocosms, microcosms). Meta-analyses in ecology and evolution often 477 consider that large total heterogeneities (often inherent to both disciplines) should inevitably 478 lower the generality of findings, but this might not be always the case in multi-level meta-479 analyses. The within-study heterogeneity can comprise a substantial part of total heterogeneity 480 (as in the present meta-analysis), which would need to be accounted for when evaluating the 481 generality of findings, which lies more on the between-study heterogeneity (Yang et al. 2024b).

482

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 communitylevel responses, while relationships with fitness (survival and reproduction) displayed the

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

492 Effect sizes were larger for foraging and trophic niche responses than for reproduction. This 493 can be explained since reproduction outcomes are still complex to predict, as they are 494 influenced by intrinsic (genetic and phenotypic), and extrinsic processes such as varying 495 environmental conditions and random events (Merilä & Sheldon, 2000). Then, effect sizes for 496 community-level responses were larger than for reproduction. This could arise because of 497 methodological differences. In our dataset, most studies investigating fitness took place in 498 nature (ca. 70%), whereas most studies investigating responses at the community and 499 ecosystem levels were conducted in mesocosms (ca. 75%). A dampening of effect size 500 magnitude can occur because of a greater complexity in nature compared to controlled 501 conditions (Hendry 2019). Nevertheless, we did not find differences between estimates from 502 field, mesocosm or microcosm studies. Thus, we are left with the result already reported by 503 others (Des Roches et al., 2018; Raffard et al., 2019) that the magnitude of the links between 504 ITV and ecological responses are substantial for community dynamics, even when they arise 505 from phenotypic differences among individuals of similar body sizes (this study).

506 The effect sizes for fitness proxies reported here are of similar nature to linear estimates of 507 directional selection (Hendry 2017). Indeed, our estimates for reproduction ($|r|_{unbiased} = 0.16$ for 508 among-individuals and 0.16 for the whole dataset) matched accurately with those reported 509 elsewhere for linear directional selection ($|\beta| = 0.15$; see Kingsolver et al., 2012). One potential 510 reason for the relatively small effect sizes of ITV on fitness related responses is that past 511 adaptation of individuals to the local environment has already shaped ITV near their optima 512 (i.e., stabilising selection). Another mechanism can be fluctuating selection regimes averaging 513 over time (Wright et al., 2019). As such, the estimated selection on traits is no longer strong: 514 "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).

521 Other factors may explain why effect sizes were the largest at the community level. First, many 522 relationships in ecology are non-linear. Because of Jensen's inequality (Bolnick et al. 2011), 523 concave-up intermediate relationships can amplify the effects of ITV at high levels of biological 524 organization (see Bailey et al., 2009). Second, large effects of ITV can occur through direct 525 effects on community and ecosystem responses (i.e., 'trait-mediated effects'; Schmitz et al., 526 2004), which could be particularly strong as they may not dissipate through many intermediate 527 relationships (fig. 1a). This can be particularly true when focal animals are keystone (Paine 528 1980), foundation (Ellison 2019), engineer species (Romero et al. 2015), or are prone to niche 529 construction (Laland et al. 1999). A great example comes from the Yellowstone, where a small 530 subset of wolf individuals within a pack are specialized on beavers (i.e., some individuals are 531 hunting ~200% more beavers; Bump et al., 2022), and therefore, are contributing 532 disproportionately to wetland appearance/loss dynamics (Gable et al. 2020).

533 Do Trait Types Showed Different Relationship Magnitudes with Ecological 534 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, 540 functional responses of predator crabs (Panopeus herbstii) on mussel prey (Brachidontes 541 exustus) are mediated by consistent variation among individuals in their activity levels, 542 suggesting strong ecosystem-level effects given that mussels are famous ecosystem engineers 543 (Toscano and Griffen 2014). Physiological traits showed strong relationship strengths across 544 ecological responses (fig. 4&5). An example is how variations in corticosterone levels among 545 individuals predict long-term reproductive performances in wandering albatross (Diomedea 546 exulans; Angelier et al., 2010). This is consistent with the fact that variations in metabolic, 547 immune, hormonal, and stoichiometric traits are all believed to be strongly related with fitness, 548 community and ecosystem responses (Elser et al. 2000; Ricklefs and Wikelski 2002; Brandl et 549 al. 2022).

550 Understanding how different phenotypic dimensions relate to ecological differences among 551 individuals or populations is a priori challenging, and this motivated the present work. From a 552 general standpoint, morphology could express a *potential* for ecological effects, where 553 physiological and behavioral traits might be closer to *realized* effects (Wainwright and Reilly 554 1994). Our results are in agreement with this general view, albeit the average difference among 555 large categories of traits were rather small in absolute (table 1). Morphological traits that 556 showed the largest effect sizes were also the most *a priori* functionally-relevant (fig. 5). The 557 category with the highest effect size and sufficient sample size was 'Morphotype', which refers 558 to dimorphic populations, or ecotypes which diverged ecologically hundreds to thousands of 559 generations ago (Harmon et al., 2009). 'Locomotion' designates morphological traits linked to 560 the capacity for an individual to perform locomotion (*'activity'*), the behavioral sub-category 561 showing the strongest effect size (fig. 5). The trait coined 'body condition' is a proxy for 562 physiological status (energy reserve). Morphological traits with the less general functional 563 relevance for a broad range of ecological responses, such as linear morphometric traits (labelled 564 'specific morphometric traits') exhibited unexpectedly, lower effect sizes (fig. 5).

565 Our results at the intraspecific level are contrasting with the strong reliance on morphological 566 traits in TBE (Dawson et al. 2021). This popularity for morphology may hold into that those 567 traits are easily measured on immobilized or dead animals. Another reason for the popularity 568 of morphology could be its low flexibility (i.e., low intra-individual variation) and high 569 heritability compared to physiology and behavior (Mousseau and Roff 1987). Although 570 morphological traits do not maintain the strongest ecological relationships in average (this 571 meta-analysis), since they are less labile and more heritable in comparison to physiological or 572 behavioral traits, they could maintain more persistent eco-evolutionary dynamics than 573 physiology and behavior. This idea would need to be investigated. However, the lability of 574 physiological and behavioral traits does not mean randomness, as it should not prevent their use 575 in TBE. Those trait types show moderate to high repeatability among individuals (Bell et al. 576 2009), and in some cases, large heritabilities as well (Dochtermann et al. 2014). Moreover, 577 recent advances show that the residual intra-individual variation for those traits can be 578 structured, with predictable vs. unpredictable individuals (Stamps et al. 2012). Finally, if we 579 aim at quantifying the propensity of traits to be involved in eco-evolutionary dynamics, it would 580 be promising to compare the evolvabilities (Hansen et al. 2011) of those trait types with metrics 581 expressing their propensity to alter ecological dynamics.

582 General formulations have been suggested to explore theoretically the links between traits, 583 abundances, and ecosystem functions (Violle et al. 2007). Our trait functionality estimates can 584 help to parametrize eco-evolutionary or trait-based models intended to assess how shifts in trait 585 distributions through evolution, selection, patch dynamics, etc. can affect various ecological 586 responses from ecological performances to ecosystem functioning (Govaert et al. 2019). 587 Therefore, we invite to investigate how changes in the moments of traits distribution (mean, 588 variance, skewness and kurtosis), for instance under selection (Kingsolver et al. 2012) and 589 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).

596

Concluding Remarks

597 Ideal traits to move forward TBE of animals should meet two criteria: (i) link to a vast range of 598 ecological functions operating at different levels, and (ii) be 'universal', i.e., can be measured 599 across intra- and interspecific levels of various animal taxonomic groups (Carmona et al. 2016). 600 Here, several continuous traits showed relatively strong links with ecological responses, as they 601 can meet the second criterion (e.g., hormone levels, activity, metabolism, boldness, 602 stoichiometry, excretion, sociability, body condition, and cognitive abilities; fig. 5). 603 Technological developments should facilitate the measurement of such traits at the individual 604 level, allowing multi-trait approaches. Telemetry and camera traps, coupled with artificial 605 intelligence (AI) algorithms, are improving the study of movements, activity and stereotypic 606 behaviors of vertebrates in the field (Suraci et al. 2017; Salama AbdELminaam et al. 2020). 607 Flow cytometry, (-thermal) imagery, and respiration chambers are facilitating the measurement 608 of shape and size, metabolism, and behavior on aquatic invertebrates (Réveillon and Becks 609 2022). In a similar way, the continuous miniaturization of telemetry allows collecting 610 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 614 a better appraisal of the implications of biodiversity changes at the levels of individuals, 615 populations, species, communities and ecosystems. To unravel the ecological implications of 616 animal intraspecific diversity, we encourage ecologists not to neglect physiological and 617 behavioral traits. Future studies at the intraspecific level will gain in predictive abilities by 618 addressing simultaneously all the facets of a phenotype and their covariations. Multiple 619 morphological, physiological, and behavioral traits are integrated into one phenotype, and 620 acknowledging this would inform about ecological and fitness trade-offs (Arnold 1983; Violle 621 et al. 2007). Such an approach at the individual level will improve our integration of biological 622 scales, evolutionary and ecological processes, as well as predictions of the effects of global 623 changes on ecosystems.

624

Acknowledgements

We are grateful to the researchers who contributed to initial stages of the present work, especially J. Cucherousset and L. Závorka. We thank B. Corbara for the discussion about our results. We also thank A. Bruder, R. Oester, A. M. Roth, L. Govaert, S. J. Brandl, and J. O'Brien for their help in improving the manuscript before its submission to the journal. This work was funded by a French National Research grant called 'RESILIENCE' [ANR-18-CE02-0015], and a Swiss National Foundation for Science grant called 'MULTIBEF' [315230_204998].

631

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.

638	Data accessibility
639	The data and R code supporting the results and their reproducibility can be accessed through a
640	public repository (Figshare) [https://doi.org/10.6084/m9.figshare.27377529.v1].
641	Conflicts of interest
642	The authors have no conflict of interest to declare.
643	Literature Cited
644 645	Albert, C. H. 2015. Intraspecific trait variability matters. Journal of Vegetation Science 26:7–8.
646 647 648	Alberti, M., C. Correa, J. M. Marzluff, A. P. Hendry, E. P. Palkovacs, K. M. Gotanda, V. M. Hunt, et al. 2017. Global urban signatures of phenotypic change in animal and plant populations. Proceedings of the National Academy of Sciences 114:8951–8956.
649 650 651	Angelier, F., J. C. Wingfield, H. Weimerskirch, and O. Chastel. 2010. Hormonal correlates of individual quality in a long-lived bird: a test of the 'corticosterone–fitness hypothesis.' Biology Letters 6:846–849.
652	Arnold, S. J. 1983. Morphology, Performance and Fitness. American Zoologist 23:347–361.
653 654 655 656	Bailey, J. K., J. A. Schweitzer, F. Ubeda, J. Koricheva, C. J. LeRoy, M. D. Madritch, B. J. Rehill, et al. 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1607–1616.
657 658 659	Barabás, G., C. Parent, A. Kraemer, F. Van de Perre, and F. De Laender. 2022. The evolution of trait variance creates a tension between species diversity and functional diversity. Nature Communications 13:2521.
660 661	Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta- analysis. Animal Behaviour 77:771–783.
662 663 664	Bertossa, R. C. 2011. Morphology and behaviour: functional links in development and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2056–2068.
665 666	Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology & Evolution 23:361–368.
667 668 669	Blanchet, S., J. G. Prunier, I. Paz-Vinas, K. Saint-Pé, O. Rey, A. Raffard, E. Mathieu-Bégné, et al. 2020. A river runs through it: The causes, consequences, and management of intraspecific diversity in river networks. Evolutionary Applications 13:1195–1213.

- 670 Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W.
- Rudolf, et al. 2011. Why intraspecific trait variation matters in community ecology. Trends in
- 672 Ecology & Evolution 26:183–192.
- Brandl, S. J., J. S. Lefcheck, A. E. Bates, D. B. Rasher, and T. Norin. 2022. Can metabolic traits
 explain animal community assembly and functioning? Biological Reviews.12892.
- Bump, J., T. Gable, S. Johnson-Bice, A. Homkes, D. Freund, S. Windels, and S. Chakrabarti.
- 676 2022. Predator personalities alter ecosystem services. Frontiers in Ecology and the Environment
- 677 20:275–277.
- 678 Careau, V., and T. Garland. 2012. Performance, Personality, and Energetics: Correlation,
 679 Causation, and Mechanism. Physiological and Biochemical Zoology 85:543–571.
- Careau, V., D. Thomas, M. M. Humphries, and D. Réale. 2008. Energy metabolism and animal
 personality. Oikos 117:641–653.
- Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits Without Borders:
 Integrating Functional Diversity Across Scales. Trends in Ecology & Evolution 31:382–394.
- Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth
 mass extinction signaled by vertebrate population losses and declines. Proceedings of the
 National Academy of Sciences 114.
- 687 Chacón-Labella, J., C. Hinojo-Hinojo, T. Bohner, M. Castorena, C. Violle, V. Vandvik, and B.
 688 J. Enquist. 2022. How to improve scaling from traits to ecosystem processes. Trends in Ecology
- 689 & Evolution S0169534722002749.
- 690 Cianciaruso, M. V., M. A. Batalha, K. J. Gaston, and O. L. Petchey. 2009. Including
 691 intraspecific variability in functional diversity. Ecology 90:81–89.
- Darwin, C., and A. Wallace. 1858. On the Tendency of Species to form Varieties; and on the
 Perpetuation of Varieties and Species by Natural Means of Selection. Journal of the Proceedings
 of the Linnean Society of London. Zoology 3:45–62.
- Dawson, S. K., C. P. Carmona, M. González-Suárez, M. Jönsson, F. Chichorro, M. MallenCooper, Y. Melero, et al. 2021. The traits of "trait ecologists": An analysis of the use of trait
 and functional trait terminology. Ecology and Evolution 11:16434–16445.
- de Bello, F., Z. Botta-Dukát, J. Lepš, and P. Fibich. 2021. Towards a more balanced
 combination of multiple traits when computing functional differences between species.
 Methods in Ecology and Evolution 12:443–448.
- Des Roches, S., L. H. Pendleton, B. Shapiro, and E. P. Palkovacs. 2021. Conserving
 intraspecific variation for nature's contributions to people. Nature Ecology & Evolution 5:574–
 582.
- 704 Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A.
- 705 Schweitzer, et al. 2018. The ecological importance of intraspecific variation. Nature Ecology
- 706 & Evolution 2:57–64.

- Dochtermann, N. A., T. Schwab, and A. Sih. 2014. The contribution of additive genetic
 variation to personality variation: heritability of personality. Proceedings of the Royal Society
 B: Biological Sciences 282:20142201–20142201.
- Ellison, A. M. 2019. Foundation Species, Non-trophic Interactions, and the Value of BeingCommon. iScience 13:254–268.
- Elser, J. j., R. w. Sterner, E. Gorokhova, W. f. Fagan, T. a. Markow, J. b. Cotner, J. f. Harrison,
 et al. 2000. Biological stoichiometry from genes to ecosystems. Ecology Letters 3:540–550.
- Elton, C. S. 1927. Animal ecology, by Charles Elton; with an introduction by Julian S. Huxley.
 Macmillan Co., New York,.
- Find Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, et al.
 2015. Scaling from Traits to Ecosystems. Pages 249–318 *in*Advances in Ecological Research
 (Vol. 52). Elsevier.
- Exposito-Alonso, M., T. R. Booker, L. Czech, L. Gillespie, S. Hateley, C. C. Kyriazis, P. L. M.
 Lang, et al. 2022. Genetic diversity loss in the Anthropocene. Science 377:1431–1435.
- 721 Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C.
- 722 Laughlin, et al. 2017. Revisiting the Holy Grail: using plant functional traits to understand
- ecological processes. Biological Reviews 92:1156–1173.
- Gable, T. D., S. M. Johnson-Bice, A. T. Homkes, S. K. Windels, and J. K. Bump. 2020.
 Outsized effect of predation: Wolves alter wetland creation and recolonization by killing
 ecosystem engineers. Science Advances 6:eabc5439.
- Gibert, J. P., A. I. Dell, J. P. DeLong, and S. Pawar. 2015. Scaling-up Trait Variation from
 Individuals to Ecosystems. Pages 1–17 *in*Advances in Ecological Research (Vol. 52). Elsevier.
- Gordon, D. M. 2011. The fusion of behavioral ecology and ecology. Behavioral Ecology 22:225–230.
- Govaert, L., E. A. Fronhofer, S. Lion, C. Eizaguirre, D. Bonte, M. Egas, A. P. Hendry, et al.
 2019. Eco-evolutionary feedbacks—Theoretical models and perspectives. Functional Ecology
 33:13–30.
- Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Societyof London. B, Biological Sciences 326:119–157.
- Green, S. J., C. B. Brookson, N. A. Hardy, and L. B. Crowder. 2022. Trait-based approaches to
 global change ecology: moving from description to prediction. Proceedings of the Royal
 Society B: Biological Sciences 289:20220071.
- Hagen, M., M. Wikelski, and W. D. Kissling. 2011. Space Use of Bumblebees (Bombus spp.)
 Revealed by Radio-Tracking. PLoS ONE 6:e19997.
- Haller, B. C., and A. P. Hendry. 2014. Solving the paradox of stasis: squashed stabilizing
- selection and the limits of detection: selection and the limits of detection. Evolution 68:483–500.

- Hansen, T. F., C. Pélabon, and D. Houle. 2011. Heritability is not Evolvability. EvolutionaryBiology 38:258–277.
- Harmon, L. J., B. Matthews, S. Des Roches, J. M. Chase, J. B. Shurin, and D. Schluter. 2009.
- Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458:1167–
 1170.
- Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affects
 species coexistence. Ecology Letters 19:825–838.
- 751 Hendry, A. P. 2017. Eco-evolutionary dynamics. Princeton University Press, Princeton.
- 752 ——. 2019. A critique for eco-evolutionary dynamics. Functional Ecology 33:84–94.
- Hinchliff, C. E., S. A. Smith, J. F. Allman, J. G. Burleigh, R. Chaudhary, L. M. Coghill, K. A.
- 754 Crandall, et al. 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life.
- 755 Proceedings of the National Academy of Sciences 112:12764–12769.
- Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative
 Biology 22:415–427.
- 758 Kingsolver, J. G., S. E. Diamond, A. M. Siepielski, and S. M. Carlson. 2012. Synthetic analyses
- of phenotypic selection in natural populations: lessons, limitations and future directions.
- 760 Evolutionary Ecology 26:1101–1118.
- 761 Kleiber, M. 1932. Body size and metabolism. Hilgardia 6:315–353.
- Laland, K. N., F. J. Odling-Smee, and M. W. Feldman. 1999. Evolutionary consequences of
 niche construction and their implications for ecology. Proceedings of the National Academy of
 Sciences 96:10242–10247.
- Lawton, J. H. 1994. What Do Species Do in Ecosystems? Oikos 71:367.
- Lecerf, A., and E. Chauvet. 2008. Intraspecific variability in leaf traits strongly affects alderleaf decomposition in a stream. Basic and Applied Ecology 9:598–605.
- Lefcheck, J. S., V. A. G. Bastazini, and J. N. Griffin. 2015. Choosing and using multiple traits
 in functional diversity research. Environmental Conservation 42:104–107.
- Macarthur, R., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of
 Coexisting Species. The American Naturalist 101:377–385.
- McGhee, K. E., L. M. Pintor, and A. M. Bell. 2013. Reciprocal Behavioral Plasticity and
 Behavioral Types during Predator-Prey Interactions. The American Naturalist 182:704–717.
- McGill, B., B. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology
 from functional traits. Trends in Ecology & Evolution 21:178–185.
- Merilä, J., and B. C. Sheldon. 2000. Lifetime Reproductive Success and Heritability in Nature.
 The American Naturalist 155:301–310.

- 778 Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological
- scales? A case for trait-based ecology: How do traits vary across ecological scales? Ecology
- 780 Letters 13:838–848.
- Michonneau, F., J. W. Brown, and D. J. Winter. 2016. rotl: an R package to interact with the
 Open Tree of Life data. Methods in Ecology and Evolution 7:1476–1481.
- Mlambo, M. C. 2014. Not all traits are 'functional': insights from taxonomy and biodiversity ecosystem functioning research. Biodiversity and Conservation 23:781–790.
- Møller, A., and M. D. Jennions. 2002. How much variance can be explained by ecologists and
 evolutionary biologists? Oecologia 132:492–500.
- Moran, N. P., A. Sánchez-Tójar, H. Schielzeth, and K. Reinhold. 2021. Poor nutritional
 condition promotes high-risk behaviours: a systematic review and meta-analysis. Biological
 Reviews 96:269–288.
- Moran, N. P., B. B. M. Wong, and R. M. Thompson. 2017. Weaving animal temperament into
 food webs: implications for biodiversity. Oikos 126:917–930.
- Morrissey, M. B. 2016. Meta-analysis of magnitudes, differences and variation in evolutionary
 parameters. Journal of Evolutionary Biology 29:1882–1904.
- Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.
- Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical
 significance: a practical guide for biologists. Biological Reviews 82:591–605.
- Nakagawa, S., M. Lagisz, M. D. Jennions, J. Koricheva, D. W. A. Noble, T. H. Parker, A.
 Sánchez-Tójar, et al. 2022. Methods for testing publication bias in ecological and evolutionary
 meta-analyses. Methods in Ecology and Evolution 13:4–21.
- Nakagawa, S., M. Lagisz, R. E. O'Dea, P. Pottier, J. Rutkowska, A. M. Senior, Y. Yang, et al.
 2023. orchaRd 2.0: An R package for visualising meta-analyses with orchard plots. Methods in
 Ecology and Evolution 14:2003–2010.
- Noble, D. W. A., M. Lagisz, R. E. O'dea, and S. Nakagawa. 2017. Nonindependence and
 sensitivity analyses in ecological and evolutionary meta-analyses. Molecular Ecology 26:2410–
 2425.
- Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic
 diversity and ecosystem functioning in changing environments: A theoretical framework.
 Proceedings of the National Academy of Sciences 98:11376–11381.
- 810 O'Dea, R. E., M. Lagisz, M. D. Jennions, J. Koricheva, D. W. A. Noble, T. H. Parker, J.
- 811 Gurevitch, et al. 2021. Preferred reporting items for systematic reviews and meta-analyses in 812 ecology and evolutionary biology: a PRISMA extension. Biological Reviews 96:1695–1722.
- Paine, R. T. 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure.
 The Journal of Animal Ecology 49:666.

- Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and
 evolutionary analyses in R. Bioinformatics 35:526–528.
- Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. Philosophical
 Transactions of the Royal Society B: Biological Sciences 364:1483–1489.
- Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward.
 Ecology Letters 9:741–758.
- 821 Peters, R. H. 1993. The ecological implications of body size. Univ. Press, Cambridge [u.a.]
- 822 Pianka, E. R. 1970. On r- and K-Selection. The American Naturalist 104:592–597.
- Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific variation in
 a predator affects community structure and cascading trophic interactions. Ecology 89:2019–
 2032.
- Raffard, A., A. Lecerf, J. Cote, M. Buoro, R. Lassus, and J. Cucherousset. 2017. The functional
 syndrome: linking individual trait variability to ecosystem functioning. Proceedings of the
 Royal Society B: Biological Sciences 284:20171893.
- Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019. The community and ecosystem
 consequences of intraspecific diversity: a meta-analysis: The ecological effects of intraspecific
 diversity. Biological Reviews.
- Réveillon, T., and L. Becks. 2022. Consistency in defence and competitiveness trade-off in a
 planktonic predator-prey system (preprint). Ecology.
- Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology
 & Evolution 17:462–468.
- 836 Romero, G. Q., T. Gonçalves-Souza, C. Vieira, and J. Koricheva. 2015. Ecosystem engineering
- effects on species diversity across ecosystems: a meta-analysis: Ecosystem engineering effects
 across ecosystems. Biological Reviews 90:877–890.
- Rota, T., J. Jabiol, E. Chauvet, and A. Lecerf. 2018. Phenotypic determinants of inter-individual
 variability of litter consumption rate in a detritivore population. Oikos.
- Rota, T., J. Jabiol, S. Lamothe, D. Lambrigot, É. Chauvet, and A. Lecerf. 2024. Phenotypes of
 predator individuals underpin contrasting ecosystem effects. Freshwater Biology.14242.
- Rota, T., A. Lecerf, É. Chauvet, and B. Pey. 2022. The importance of intraspecific variation in
 litter consumption rate of aquatic and terrestrial macro-detritivores. Basic and Applied Ecology
 63:175–185.
- Salama AbdELminaam, D., A. M. Almansori, M. Taha, and E. Badr. 2020. A deep facial
 recognition system using computational intelligent algorithms. PLOS ONE 15:e0242269.
- 848 Sanderson, S., D. I. Bolnick, M. T. Kinnison, R. E. O'Dea, L. D. Gorné, A. P. Hendry, and K.
- 849 M. Gotanda. 2023. Contemporary changes in phenotypic variation, and the potential 850 consequences for eco-evolutionary dynamics. Ecology Letters 26.

- Schleuning, M., D. García, and J. A. Tobias. 2023. Animal functional traits: Towards a traitbased ecology for whole ecosystems. Functional Ecology 37:4–12.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated
 indirect interactions: Primacy of trait-mediated indirect interactions. Ecology Letters 7:153–
- 855 163.
- 856 Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen,
- et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant
- 858 communities. Ecology Letters 18:1406–1419.
- Sobral, M. 2021. All Traits Are Functional: An Evolutionary Viewpoint. Trends in Plant
 Science 26:674–676.
- Stamps, J. A., M. Briffa, and P. A. Biro. 2012. Unpredictable animals: individual differences in
 intraindividual variability (IIV). Animal Behaviour 83:1325–1334.
- Suraci, J. P., M. Clinchy, B. Mugerwa, M. Delsey, D. W. Macdonald, J. A. Smith, C. C.
 Wilmers, et al. 2017. A new Automated Behavioural Response system to integrate playback
 experiments into camera trap studies. Methods in Ecology and Evolution 8:957–964.
- Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. Personality, foraging
 behavior and specialization: integrating behavioral and food web ecology at the individual
 level. Oecologia 182:55–69.
- Toscano, B. J., and B. D. Griffen. 2014. Trait-mediated functional responses: predator
 behavioural type mediates prey consumption. Journal of Animal Ecology 83:1469–1477.
- Van Valen, L. 1965. Morphological Variation and Width of Ecological Niche. The American
 Naturalist 99:377–390.
- Viechtbauer, W. 2010. Conducting Meta-Analyses in *R* with the **metafor** Package. Journal ofStatistical Software 36.
- 875 Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, et al. 2012.
- 876 The return of the variance: intraspecific variability in community ecology. Trends in Ecology
 877 & Evolution 27:244–252.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007.
 Let the concept of trait be functional! Oikos 116:882–892.
- Wainwright, P. C., and S. M. Reilly, eds. 1994. Ecological morphology: integrative organismal
 biology. University of Chicago Press, Chicago.
- Wheelwright, N. T., L. F. Keller, and E. Postma. 2014. The effect of trait type and strength of selection on heritability and evolvability in an island bird population. Evolution 68:3325–3336.
- 884 Wong, M. K. L., and C. P. Carmona. 2021. Including intraspecific trait variability to avoid
- distortion of functional diversity and ecological inference: Lessons from natural assemblages.
 Methods in Ecology and Evolution.

- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. CavenderBares, et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.
- 889 Wright, J., G. H. Bolstad, Y. G. Araya-Ajoy, and N. J. Dingemanse. 2019. Life-history
- evolution under fluctuating density-dependent selection and the adaptive alignment of pace-oflife syndromes: Pace-of-life syndromes. Biological Reviews 94:230–247.
- Yang, Y., M. Lagisz, C. Williams, D. W. A. Noble, J. Pan, and S. Nakagawa. 2024*a*. Robust
 point and variance estimation for meta-analyses with selective reporting and dependent effect
 sizes. Methods in Ecology and Evolution 15:1593–1610.
- Yang, Y., D. W. A. Noble, A. M. Senior, M. Lagisz, and S. Nakagawa. 2024b. Interpreting
 prediction intervals and distributions for decoding biological generality in meta-analyses.
- 897 (Preprint)

898 Literature Cited in The Meta-Analysis (*)

- *ADAMS, C.E. & HUNTINGFORD, F.A. (2002) The functional significance of inherited
 differences in feeding morphology in a sympatric polymorphic population of Arctic charr. *Evolutionary Ecology* 16, 15–25.
- *AKÇAY, Ç., CAMPBELL, S.E. & BEECHER, M.D. (2015) The fitness consequences of honesty:
 Under-signalers have a survival advantage in song sparrows. *Evolution* 69, 3186–3193.
- *ALLGEIER, J.E., CLINE, T.J., WALSWORTH, T.E., WATHEN, G., LAYMAN, C.A. & SCHINDLER,
 D.E. (2020) Individual behavior drives ecosystem function and the impacts of harvest. *Science Advances* 6, eaax8329.
- *ÁLVAREZ, D. & NICIEZA, A.G. (2005) Is metabolic rate a reliable predictor of growth and
 survival of brown trout (*Salmo trutta*) in the wild? *Canadian Journal of Fisheries and Aquatic Sciences* 62, 643–649.
- *ANGELIER, F., WINGFIELD, J.C., WEIMERSKIRCH, H. & CHASTEL, O. (2010) Hormonal
 correlates of individual quality in a long-lived bird: a test of the 'corticosterone-fitness
- 912 hypothesis'. *Biology Letters* **6**, 846–849.
- *ARMITAGE, K.B. (1986) Individuality, Social Behavior, and Reproductive Success in YellowBellied Marmots. *Ecology* 67, 1186–1193.
- *ARMITAGE, K.B. & VAN VUREN, D.H. (2003) Individual differences and reproductive success
 in yellow-bellied marmots. *Ethology Ecology & Evolution* 15, 207–233.
- 917 *AUER, S.K., SALIN, K., RUDOLF, A.M., ANDERSON, G.J. & METCALFE, N.B. (2015a) The
- 918 optimal combination of standard metabolic rate and aerobic scope for somatic growth depends
- 919 on food availability. *Functional Ecology* **29**, 479–486.
- *AUER, S.K., SALIN, K., RUDOLF, A.M., ANDERSON, G.J. & METCALFE, N.B. (2015b)
 Flexibility in metabolic rate confers a growth advantage under changing food availability. *Journal of Animal Ecology* 84, 1405–1411.
- 923 *BAKER, J.A., CRESKO, W.A., FOSTER, S.A. & HEINS, D.C. (2005) Life-history differentiation
- 924 of benthic and limnetic ecotypes in a polytypic population of threespine stickleback
- 925 (Gasterosteus aculeatus). *Evolutionary Ecology Research* 7, 121–131.
- 926 *BANKS, P.B., NORRDAHL, K. & KORPIMÄKI, E. (2002) Mobility decisions and the predation
- 927 risks of reintroduction. *Biological Conservation* **103**, 133–138.
- 928 *BEAUCHAMP, G. (2006) Phenotypic Correlates of Scrounging Behavior in Zebra Finches: Role
- 929 of Foraging Efficiency and Dominance. *Ethology* **112**, 873–878.

- *BERCHTOLD, A.E., COLBORNE, S.F., LONGSTAFFE, F.J. & NEFF, B.D. (2015)
 Ecomorphological patterns linking morphology and diet across three populations of
 pumpkinseed sunfish (*Lepomis gibbosus*). *Canadian Journal of Zoology* 93, 289–297.
- 933 *BLACKMER, A.L., MAUCK, R.A., ACKERMAN, J.T., HUNTINGTON, C.E., NEVITT, G.A. &
- WILLIAMS, J.B. (2005) Exploring individual quality: basal metabolic rate and reproductive
 performance in storm-petrels. *Behavioral Ecology* 16, 906–913.
- 936 *BLAKE, C.A. & GABOR, C.R. (2014) Effect of prey personality depends on predator species.
- 937 *Behavioral Ecology* **25**, 871–877.
- *BLANCKENHORN, W.U. (1991a) Fitness consequences of food-based territoriality in water
 striders, *Gerris remigis. Animal Behaviour* 42, 147–149.
- 940 *BLANCKENHORN, W.V. (1991b) Fitness consequences of foraging success in water striders
 941 (*Gerris remigis*; Heteroptera: Gerridae). *Behavioral Ecology* 2, 46–55.
- 942 *BLIGHT, O., VILLALTA, I., CERDÁ, X. & BOULAY, R. (2016) Personality traits are associated
- with colony productivity in the gypsy ant *Aphaenogaster senilis*. *Behavioral Ecology and Sociobiology* **70**, 2203–2209.
- *BOLNICK, D.I. & ARAÚJO, M.S. (2011) Partitioning the relative fitness effects of diet and
 trophic morphology in the threespine stickleback. *Evolutionary Ecology Research* 13, 439–459.
- *BOLNICK, D.I. & PAULL, J.S. (2009) Morphological and dietary differences between
 individuals are weakly but positively correlated within a population of threespine stickleback. *Evolutionary Ecology Research* 11, 1217–1233.
- 950 *BOON, A.K., RÉALE, D. & BOUTIN, S. (2008) Personality, habitat use, and their consequences
- 951 for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* **117**, 1321–1328.
- *BORATYŃSKI, Z., KOSKELA, E., MAPPES, T. & SCHRODERUS, E. (2013) Quantitative genetics
 and fitness effects of basal metabolism. *Evolutionary Ecology* 27, 301–314.
- *BORATYŃSKI, Z. & KOTEJA, P. (2010) Sexual and natural selection on body mass and
 metabolic rates in free-living bank voles: Selection on metabolic rate. *Functional Ecology* 24,
 1252–1261.
- *BOTH, C., DINGEMANSE, N.J., DRENT, P.J. & TINBERGEN, J.M. (2005) Pairs of extreme avian
 personalities have highest reproductive success. *Journal of Animal Ecology* 74, 667–674.
- *BOULTON, K., WALLING, C.A., GRIMMER, A.J., ROSENTHAL, G.G. & WILSON, A.J. (2018)
 Phenotypic and genetic integration of personality and growth under competition in the
 sheepshead swordtail, *Xiphophorus birchmanni. Evolution* **72**, 187–201.
- 962 *BREMNER-HARRISON, S., PRODOHL, P.A. & ELWOOD, R.W. (2004) Behavioural trait
- assessment as a release criterion: boldness predicts early death in a reintroduction programme
 of captive-bred swift fox (*Vulpes velox*). *Animal Conservation* 7, 313–320.
- *BRODIN, T. & JOHANSSON, F. (2004) Conflicting selection pressures on the growth/predationrisk trade-off in a damselfly. *Ecology* 85, 2927–2932.
- *CALSBEEK, R. (2009) Sex-specific adult dispersal and its selective consequences in the brown
 anole, *Anolis sagrei. Journal of Animal Ecology* 78, 617–624.
- 969 *CARLSTEAD, K., MELLEN, J. & KLEIMAN, D.G. (1999) Black rhinoceros (Diceros bicornis) in
- 970 U.S. zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology*971 18, 17–34.
- 972 *CARTER, A.J., GOLDIZEN, A.W. & TROMP, S.A. (2010) Agamas exhibit behavioral syndromes:
- bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology* 21, 655–
- 974 661.

- *CHISM, J. & ROGERS, W. (2010) Male Competition, Mating Success and Female Choice in a
 Seasonally Breeding Primate (*Erythrocebus patas*). *Ethology* 103, 109–126.
- 977 *CLOBERT, J., OPPLIGER, A., SORCI, G., ERNANDE, B., SWALLOW, J.G. & GARLAND, T. (2000)
- 978 Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and
- 979 susceptibility to parasitism in a lizard, *Lacerta vivipara*: *Trade-offs in phenotypic traits*.
 980 *Functional Ecology* 14, 675–684.
- *COLE, E.F. & QUINN, J.L. (2012) Personality and problem-solving performance explain
 competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences* 279,
- 982 competitive ability in the wild. *Proceedings of the Royal Soci*983 1168–1175.
- *CORNWELL, T.O., MCCARTHY, I.D. & BIRO, P.A. (2020) Integration of physiology, behaviour
 and life history traits: personality and pace of life in a marine gastropod. *Animal Behaviour* 163,
- 985 and me history traits, personanty and pace of me in a marine gastropod. Animal Benaviour
 986 155–162.
- *COTE, J., DREISS, A. & CLOBERT, J. (2008) Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences* 275, 2851–2858.
- 989 *CUCHEROUSSET, J., ACOU, A., BLANCHET, S., BRITTON, J.R., BEAUMONT, W.R.C. & GOZLAN,
- R.E. (2011) Fitness consequences of individual specialisation in resource use and trophic
 morphology in European eels. *Oecologia* 167, 75–84.
- 992 *CUTTS, C.J., ADAMS, C.E. & CAMPBELL, A. (2001) Stability of physiological and behavioural
- determinants of performance in Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 58, 961–968.
- *DAVID, M., AUCLAIR, Y. & CÉZILLY, F. (2011) Personality predicts social dominance in
 female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour* 81, 219–
 224.
- 998 *DAVID, M., AUCLAIR, Y., GIRALDEAU, L.-A. & CÉZILLY, F. (2012) Personality and body
- 999 condition have additive effects on motivation to feed in Zebra Finches *Taeniopygia guttata*:
 1000 Personality and feeding motivation. *Ibis* 154, 372–378.
- *DAY, T. & MCPHAIL, J.D. (1996) The effect of behavioural and morphological plasticity on
 foraging efficiency in the threespine stickleback (*Gasterosteus sp.*). *Oecologia* 108, 380–388.
- *DENOEL, M. (2004) Feeding Performance in Heterochronic Alpine Newts is Consistent with
 Trophic Niche and Maintenance of Polymorphism. *Ethology* **110**, 127–136.
- 1005 *DERTING, T.L. & MCCLURE, P.A. (1989) Intraspecific Variation in Metabolic Rate and Its
- 1006 Relationship with Productivity in the Cotton Rat, Sigmodon hispidus. Journal of Mammalogy
- 1007 **70**, 520–531.
- 1008 *DES ROCHES, S., SHURIN, J.B., SCHLUTER, D. & HARMON, L.J. (2013) Ecological and 1009 Evolutionary Effects of Stickleback on Community Structure. *PLoS ONE* **8**, e59644.
- *DEWSBURY, D.A. (1984) Aggression, Copulation, and Differential Reproduction of Deer Mice
 (*Peromyscus Maniculatus*) in a Semi-Natural Enclosure. *Behaviour* 91, 1–23.
- 1012 *DIAZ PAULI, B., EDELINE, E. & EVANGELISTA, C. (2020) Ecosystem consequences of multi-
- 1013 trait response to environmental changes in Japanese medaka, Oryzias latipes. Conservation
- 1014 *Physiology* **8**, coaa011.
- 1015 *DINGEMANSE, N.J., BOTH, C., DRENT, P.J. & TINBERGEN, J.M. (2004) Fitness consequences
- 1016 of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London*.
- 1017 *Series B: Biological Sciences* **271**, 847–852.
- *DUGATKIN, L.A. (1992) Tendency to inspect predators predicts mortality risk in the guppy
 (*Poecilia reticulata*). *Behavioral Ecology* 3, 124–127.
- 1020 *EHLINGER, T.J. & WILSON, D.S. (1988) Complex foraging polymorphism in bluegill sunfish.
- 1021 *Proceedings of the National Academy of Sciences* **85**, 1878–1882.

- *EINUM, S., FOSSEN, E.I.F., PARRY, V. & PÉLABON, C. (2019) Genetic Variation in Metabolic
 Rate and Correlations with Other Energy Budget Components and Life History in Daphnia
- 1023 Rate and Correlations with Other Energy Bud 1024 magna. *Evolutionary Biology* **46**, 170–178.
- 1025 *FERNÁNDEZ-REIRIZ, M.J., IRISARRI, J. & LABARTA, U. (2016) Flexibility of Physiological

1026 Traits Underlying Inter-Individual Growth Differences in Intertidal and Subtidal Mussels 1027 Mytilusgalloprovincialis. *PLOS ONE* **11**, e0148245.

1028 *FISHER, D.N., JAMES, A., RODRÍGUEZ-MUÑOZ, R. & TREGENZA, T. (2015) Behaviour in 1029 captivity predicts some aspects of natural behaviour, but not others, in a wild cricket population.

- 1030 Proceedings of the Royal Society B: Biological Sciences 282, 20150708.
- *FOOTE, A.D., NEWTON, J., PIERTNEY, S.B., WILLERSLEV, E. & GILBERT, M.T.P. (2009)
 Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale
 populations. *Molecular Ecology* 18, 5207–5217.
- 1034 *FORMICA, V.A., WOOD, C.W., LARSEN, W.B., BUTTERFIELD, R.E., AUGAT, M.E., HOUGEN,
- 1035 H.Y. & BRODIE, E.D. (2012) Fitness consequences of social network position in a wild
- 1036 population of forked fungus beetles (Bolitotherus cornutus). Journal of Evolutionary Biology
- 1037 **25**, 130–137.
- 1038 *FOSTER, W.C., ARMSTRONG, C.M., CHISM, G.T. & PRUITT, J.N. (2017) Smaller and bolder
- prey snails have higher survival in staged encounters with the sea star *Pisaster giganteus*.
 Current Zoology, zow116.
- 1041 *GAGNON, M.-C. & TURGEON, J. (2011) Sexual conflict in Gerris gillettei (Insecta: Hemiptera):
- 1042 intraspecific intersexual correlated morphology and experimental assessment of behaviour and
- 1043 fitness: Sexual conflict in *G. gillettei* populations. *Journal of Evolutionary Biology* 24, 1505–
 1044 1516.
- 1045 *GALEOTTI, P., SACCHI, R., PELLITTERI-ROSA, D., BELLATI, A., COCCA, W., GENTILLI, A.,
- 1046 SCALI, S. & FASOLA, M. (2013) Colour polymorphism and alternative breeding strategies:
- 1047 effects of parent's colour morph on fitness traits in the common wall lizard. *Evolutionary*
- 1048 Biology 40, 385–394.
- 1049 *GANGLOFF, E.J., VLECK, D. & BRONIKOWSKI, A.M. (2015) Developmental and Immediate
- 1050 Thermal Environments Shape Energetic Trade-Offs, Growth Efficiency, and Metabolic Rate in
- 1051 Divergent Life-History Ecotypes of the Garter Snake *Thamnophis elegans*. *Physiological and* 1052 *Biochemical Zoology* 88, 550–563.
- *GIFFORD, M.E., CLAY, T.A. & CAREAU, V. (2014) Individual (Co)variation in Standard
 Metabolic Rate, Feeding Rate, and Exploratory Behavior in Wild-Caught Semiaquatic
 Salamanders Physiological and Biochemical Zoology 87, 384, 396
- 1055 Salamanders. *Physiological and Biochemical Zoology* **87**, 384–396.
- *GIMÉNEZ, J.O. (2015) Determinants of phenotypic variation in the iberian wall lizard species
 complex (*Podarcis hispanicus*). Master thesis.
- *GLON, M.G., LARSON, E.R. & PANGLE, K.L. (2016) Connecting laboratory behavior to field
 function through stable isotope analysis. *PeerJ* 4, e1918.
- *GRIFFEN, B.D. & MOSBLACK, H. (2011) Predicting diet and consumption rate differences
 between and within species using gut ecomorphology: Predicting diet and consumption rate
 differences. *Journal of Animal Ecology* 80, 854–863.
- 1063 *HROMADA, M., KUCZYŃSKI, L., KRIŠTÍN, A. & TRYJANOWSKI, P. (2003) Animals of different
- 1064 phenotype differentially utilise dietary niche The case of the Great Grey Shrike *Lanius* 1065 *excubitor. Ornis Fennica* **80**, 71–78.
- 1066 *HSU, Y.-C., SHANER, P.-J., CHANG, C.-I., KE, L. & KAO, S.-J. (2014) Trophic niche width
- 1067 increases with bill-size variation in a generalist passerine: a test of niche variation hypothesis.
- 1068 Journal of Animal Ecology 83, 450–459.

- 1069 *HULTHÉN, K., CHAPMAN, B.B., NILSSON, P.A., HANSSON, L.-A., SKOV, C., BRODERSEN, J.,
- 1070 VINTERSTARE, J. & BRÖNMARK, C. (2017) A predation cost to bold fish in the wild. *Scientific* 1071 *Reports* **7**, 1239.
- 1072 *INGRAM, T., SVANBÄCK, R., KRAFT, N.J.B., KRATINA, P., SOUTHCOTT, L. & SCHLUTER, D.
- 1073 (2012) Intraguild predation drives evolutionary niche shift in threespine stickleback: 1074 evolutionary response to intraguild predation. *Evolution* **66**, 1819–1832.
- *IOANNOU, C.C., PAYNE, M. & KRAUSE, J. (2008) Ecological consequences of the bold–shy
 continuum: the effect of predator boldness on prey risk. *Oecologia* 157, 177.
- 1077 *JABLONSZKY, M., SZÁSZ, E., KRENHARDT, K., MARKÓ, G., HEGYI, G., HERÉNYI, M., LACZI,
- 1078 M., NAGY, G., ROSIVALL, B., SZÖLLŐSI, E., TÖRÖK, J. & GARAMSZEGI, L.Z. (2018) Unravelling 1079 the relationships between life history, behaviour and condition under the pace-of-life
- 1080 syndromes hypothesis using long-term data from a wild bird. *Behavioral Ecology and* 1081 *Sociobiology* **72**, 52.
- *JOHNSON, J.C. & SIH, A. (2005) Precopulatory sexual cannibalism in fishing spiders
 (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology* 58, 390–396.
- 1085 *JOLLES, J.W., MANICA, A. & BOOGERT, N.J. (2016) Food intake rates of inactive fish are
- 1086 positively linked to boldness in three-spined sticklebacks Gasterosteus aculeatus. Journal of
- 1087 Fish Biology 88, 1661–1668.
- *KAIN, M.P. & MCCOY, M.W. (2016) Anti-predator behavioral variation among *Physa acuta*in response to temporally fluctuating predation risk by Procambarus. *Behavioural Processes* **133**, 15–23.
- 1091 *KARPESTAM, E. & FORSMAN, A. (2011) Dietary differences among colour morphs of pygmy
- 1092 grasshoppers revealed by behavioural experiments and stable isotopes. *Evolutionary Ecology* 1093 *Research* 13, 461–477.
- *KATANO, O. (2011) Effects of individual differences in foraging of pale chub on algal biomass
 through trophic cascades. *Environmental Biology of Fishes* 92, 101–112.
- 1096 *KAUSE, A., OSSIPOV, V., HAUKIOJA, E., LEMPA, K., HANHIMÄKI, S. & OSSIPOVA, S. (1999)
- Multiplicity of biochemical factors determining quality of growing birch leaves. *Oecologia* 120, 102–112.
- 1099 *KEISER, C.N., INGLEY, S.J., TOSCANO, B.J., SCHARF, I. & PRUITT, J.N. (2018) Habitat 1100 complexity dampens selection on prey activity level. *Ethology* **124**, 25–32.
- 1101 *KEISER, C.N., SLYDER, J.B., CARSON, W.P. & PRUITT, J.N. (2015) Individual differences in
- 1102 predators but not producers mediate the magnitude of a trophic cascade. Arthropod-Plant
- 1103 Interactions 9, 225–232.
- *KERR, N.R. (2017) Links between personality and individual niche in the freshwater fish
 Gobiomorphus cotidianus. In pp. 1–76. Master Thesis, Otago, New Zealand.
- 1106 *KHELIFA, R., ZEBSA, R., AMARI, H., MELLAL, M.K. & MAHDJOUB, H. (2019) Field estimates
- 1107 of fitness costs of the pace-of-life in an endangered damselfly. Journal of Evolutionary Biology
- **32**, 943–954.
- 1109 *KOBLER, A., KLEFOTH, T., MEHNER, T. & ARLINGHAUS, R. (2009) Coexistence of behavioural
- 1110 types in an aquatic top predator: a response to resource limitation? *Oecologia* **161**, 837–847.
- 1111 *KORHONEN, H., NIEMELÄ, P. & SIIRILÄ, P. (2001) Temperament and reproductive 1112 performance in farmed sable. *Agricultural Food Science Finland* **10**, 91–98.
- 1113 *KORHONEN, H.T., JAUHIAINEN, L. & REKIL&AUML, T. (2002) Effect of temperament and
- 1114 behavioural reactions to the presence of a human during the pre-mating period on reproductive

- performance in farmed mink (*Mustela vison*). Canadian Journal of Animal Science 82, 275–
 282.
- *KRALJ-FIŠER, S., HEBETS, E.A. & KUNTNER, M. (2017) Different patterns of behavioral
 variation across and within species of spiders with differing degrees of urbanization. *Behavioral Ecology and Sociobiology* **71**, 125.
- 1120 *KRUUK, L.E.B., CLUTTON-BROCK, T.H., SLATE, J., PEMBERTON, J.M., BROTHERSTONE, S. &
- 1121 GUINNESS, F.E. (2000) Heritability of fitness in a wild mammal population. *Proceedings of the* 1122 National Academy of Sciences **97**, 698, 703
- 1122 National Academy of Sciences **97**, 698–703.
- 1123 *LANG, I., PAZ-VINAS, I., CUCHEROUSSET, J. & LOOT, G. (2021) Patterns and determinants of
- phenotypic variability within two invasive crayfish species. *Freshwater Biology* 66, 1782–
 1798.
- *LAPIEDRA, O., SCHOENER, T.W., LEAL, M., LOSOS, J.B. & KOLBE, J.J. (2018) Predator-driven
 natural selection on risk-taking behavior in anole lizards. *Science* 360, 1017–1020.
- 1128 *LARIVEE, M. (2010) The fitness consequences of variation in resting metabolic rate in juvenile
- 1129 North American red squirrels (*Tamiasciurus hudsonicus*). University of Alberta Libraries.
- *LATTANZIO, M.S. & MILES, D.B. (2016) Trophic niche divergence among colour morphs that
 exhibit alternative mating tactics. *Royal Society Open Science* 3, 150531.
- 1132 *LAURILA, A. & KUJASALO, J. (1999) Habitat duration, predation risk and phenotypic plasticity
- 1133 in common frog (*Rana temporaria*) tadpoles. *Journal of Animal Ecology* **68**, 1123–1132.
- 1134 *LAVIN, P.A. & MCPHAIL, J.D. (1986) Adaptive Divergence of Trophic Phenotype among
- 1135 Freshwater Populations of the Threespine Stickleback (Gasterosteus aculeatus). Canadian
- 1136 Journal of Fisheries and Aquatic Sciences 43, 2455–2463.
- 1137 *LEPETZ, V., MASSOT, M., CHAINE, A.S. & CLOBERT, J. (2009) Climate warming and the 1138 evolution of morphotypes in a reptile. *Global Change Biology* **15**, 454–466.
- 1139 *Luiz, O.J., Crook, D.A., Kennard, M.J., Olden, J.D., Saunders, T.M., Douglas, M.M.,
- 1140 WEDD, D. & KING, A.J. (2019) Does a bigger mouth make you fatter? Linking intraspecific
- 1141 gape variability to body condition of a tropical predatory fish. *Oecologia* **191**, 579–585.
- 1142 *MALDONADO, K., PABLO, S., PIRIZ, G., BOGDANOVICH, J.M., NESPOLO, R.F. & BOZINOVIC, F.
- (2016) Is maximum food intake in endotherms constrained by net or factorial aerobic scope?lessons from the leaf-eared mouse. *Frontiers in physiology* 7.
- 1145 *MARSHALL, H.H., SANDERSON, J.L., MWANGHUYA, F., BUSINGE, R., KYABULIMA, S., HARES,
- 1146 M.C., INZANI, E., KALEMA-ZIKUSOKA, G., MWESIGE, K., THOMPSON, F.J., VITIKAINEN, E.I.K.
- 1147 & CANT, M.A. (2016) Variable ecological conditions promote male helping by changing
- banded mongoose group composition. *Behavioral Ecology* **27**, 978–987.
- 1149 *MASKREY, D.K., WHITE, S.J., WILSON, A.J. & HOUSLAY, T.M. (2018) Who dares does not 1150 always win: risk-averse rockpool prawns are better at controlling a limited food resource.
- 1151 Animal Behaviour **140**, 187–197.
- 1152 *MATTHEWS, B., AEBISCHER, T., SULLAM, K.E., LUNDSGAARD-HANSEN, B. & SEEHAUSEN, O.
- (2016) Experimental evidence of an eco-evolutionary feedback during adaptive divergence.
 Current Biology 26, 483–489.
- 1155 *MATTHEWS, B., MARCHINKO, K.B., BOLNICK, D.I. & MAZUMDER, A. (2010) Specialization of
- 1156 trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology* **91**, 1025–
- 1157 1034.
- 1158 *MCCOLLUM, S.A. & VAN BUSKIRK, J. (1996) Costs and benefits of a predator-induced
- 1159 polyphenism in the gray treefrog *Hyla chrysoscelis*. *Evolution* **50**, 583–593.

- 1160 *MCPHEE, M.V. & QUINN, T.P. (1998) Factors affecting the duration of nest defense and
- 1161 reproductive lifespan of female sockeye salmon, Oncorhynchus nerka. Environmental Biology
- 1162 of Fishes 51, 369–375.
- *METCALFE, N.B., TAYLOR, A.C. & THORPE, J.E. (1995) Metabolic rate, social status and life-1163 1164 history strategies in Atlantic salmon. Animal Behaviour 49, 431–436.
- *MØLLER, A.P. (2010) Brain size, head size and behaviour of a passerine bird. Journal of 1165 1166 Evolutionary Biology 23, 625–635.
- 1167 *MONCEAU, K., DECHAUME-MONCHARMONT, F.-X., MOREAU, J., LUCAS, C., CAPODURO, R.,
- 1168 MOTREUIL, S. & MORET, Y. (2017) Personality, immune response and reproductive success: an 1169 appraisal of the pace-of-life syndrome hypothesis. Journal of Animal Ecology 86, 932–942.
- *MONTIGLIO, P., WEY, T.W., CHANG, A.T., FOGARTY, S. & SIH, A. (2017) Correlational 1170 1171 selection on personality and social plasticity: morphology and social context determine 1172 behavioural effects on mating success. Journal of Animal Ecology 86, 213–226.
- 1173 *MORALES, J.A., CARDOSO, D.G., DELLA LUCIA, T.M.C. & GUEDES, R.N.C. (2013) Weevil x
- 1174 Insecticide: Does 'Personality' Matter? PLoS ONE 8, e67283.
- 1175 *NAKAYAMA, S., RAPP, T. & ARLINGHAUS, R. (2016) Fast-slow life history is correlated with
- 1176 individual differences in movements and prey selection in an aquatic predator in the wild.
- 1177 Journal of Animal Ecology.
- 1178 *NANNINI, M.A., PARKOS, J. & WAHL, D.H. (2012) Do behavioral syndromes affect foraging
- 1179 strategy and risk-taking in a juvenile fish predator? Transactions of the American Fisheries 1180 *Society* **141**, 26–33.
- 1181 *NIEMELÄ, P.T., LATTENKAMP, E.Z. & DINGEMANSE, N.J. (2015) Personality-related survival 1182 and sampling bias in wild cricket nymphs. *Behavioral Ecology* 26, 936–946.
- *NIEMELÄ, P.T., NIEHOFF, P.P., GASPARINI, C., DINGEMANSE, N.J. & TUNI, C. (2019) Crickets 1183
- 1184 become behaviourally more stable when raised under higher temperatures. *Behavioral Ecology* 1185 and Sociobiology 73, 81.
- 1186 *NOBLE, D.W.A., WECHMANN, K., KEOGH, J.S. & WHITING, M.J. (2013) Behavioral and 1187 Morphological Traits Interact to Promote the Evolution of Alternative Reproductive Tactics in
- 1188 a Lizard. The American Naturalist 182, 726–742.
- 1189 *NYQVIST, M.J., CUCHEROUSSET, J., GOZLAN, R.E. & BRITTON, J.R. (2018) Relationships
- 1190 between individual movement, trophic position and growth of juvenile pike (*Esox lucius*). 1191 Ecology of Freshwater Fish 27, 398–407.
- 1192 *OUYANG, J.Q., SHARP, P.J., DAWSON, A., QUETTING, M. & HAU, M. (2011) Hormone levels
- 1193 predict individual differences in reproductive success in a passerine bird. Proceedings of the
- 1194 Royal Society B: Biological Sciences 278, 2537–2545.
- *VAN OVERVELD, T., ADRIAENSEN, F. & MATTHYSEN, E. (2015) No evidence for correlational 1195 1196 selection on exploratory behaviour and natal dispersal in the great tit. *Evolutionary Ecology* **29**, 1197 137–156.
- 1198 *PALKOVACS, E.P. & POST, D.M. (2009) Experimental evidence that phenotypic divergence in 1199
- predators drives community divergence in prey. *Ecology* **90**, 300–305.
- 1200 *PALKOVACS, E.P., WASSERMAN, B.A. & KINNISON, M.T. (2011) Eco-evolutionary trophic 1201 dynamics: Loss of top predators drives trophic evolution and ecology of prey. PLoS ONE 6, 1202 e18879.
- 1203 *PARSONS, K.J. & ROBINSON, B.W. (2007) Foraging performance of diet-induced morphotypes
- 1204 in pumpkinseed sunfish (Lepomis gibbosus) favours resource polymorphism. Journal of 1205 Evolutionary Biology 20, 673–684.

- *PATRICK, S.C. & WEIMERSKIRCH, H. (2014) Personality, Foraging and Fitness Consequences
 in a Long Lived Seabird. *PLoS ONE* 9, e87269.
- 1208 *PEIMAN, K.S., BIRNIE-GAUVIN, K., LARSEN, M.H., COLBORNE, S.F., GILMOUR, K.M.,
- 1209 AARESTRUP, K., WILLMORE, W.G. & COOKE, S.J. (2017) Morphological, physiological and
- 1210 dietary covariation in migratory and resident adult brown trout (*Salmo trutta*). Zoology **123**, 1211 79–90.
- 1212 *Petitjean, Q., Jean, S., Côte, J., Lamarins, A., Lefranc, M., Santos, R., Perrault, A.,
- 1213 LAFFAILLE, P. & JACQUIN, L. (2020) Combined effects of temperature increase and immune
- 1214 challenge in two wild gudgeon populations. *Fish Physiology and Biochemistry* **46**, 157–176.
- 1215 *PINTOR, L.M., MCGHEE, K.E., ROCHE, D.P. & BELL, A.M. (2014) Individual variation in
- foraging behavior reveals a trade-off between flexibility and performance of a top predator. *Behavioral Ecology and Sociobiology* 68, 1711–1722.
- *PINTOR, L.M., SIH, A. & BAUER, M.L. (2008) Differences in aggression, activity and boldness
 between native and introduced populations of an invasive cravitish. *Oikos* 117, 1629–1636.
- 1220 *PINTOR, L.M., SIH, A. & KERBY, J.L. (2009) Behavioral correlations provide a mechanism for
- 1221 explaining high invader densities and increased impacts on native prey. *Ecology* **90**, 581–587.
- 1222 *PIOUET, J.C., LÓPEZ-DARIAS, M., VAN DER MAREL, A., NOGALES, M. & WATERMAN, J. (2018)
- 1223 Unraveling behavioral and pace-of-life syndromes in a reduced parasite and predation pressure
- 1224 context: personality and survival of the Barbary ground squirrel. *Behavioral Ecology and* 1225 *Sociobiology* **72**, 147.
- *POST, D.M., PALKOVACS, E.P., SCHIELKE, E.G. & DODSON, S.I. (2008) Intraspecific variation
 in a predator affects community structure and cascading trophic interactions. *Ecology* 89, 2019–
 2032.
- *POWERS, D.R. & NAGY, K.A. (1988) Field Metabolic Rate and Food Consumption by FreeLiving Anna's Hummingbirds (*Calypte anna*). *Physiological Zoology* 61, 500–506.
- 1231 *PRUITT, J.N., KEISER, C.N., BANKA, B.T., LIEDLE, J.S., BROOKS, A.J., SCHMITT, R.J. &
- HOLBROOK, S.J. (2018) Collective aggressiveness of an ecosystem engineer is associated with coral recovery. *Behavioral Ecology*.
- *PRUITT, J.N., RIECHERT, S.E. & JONES, T.C. (2008) Behavioural syndromes and their fitness
 consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour* 76,
 871–879.
- *QUEVEDO, M., SVANBÄCK, R. & EKLÖV, P. (2009) Intrapopulation niche partitioning in a
 generalist predator limits food web connectivity. *Ecology* **90**, 2263–2274.
- 1239 *QUINN, J.L., PATRICK, S.C., BOUWHUIS, S., WILKIN, T.A. & SHELDON, B.C. (2009) 1240 Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of* 1241 Animal Exclame **78**, 1202, 1215
- 1241 Animal Ecology **78**, 1203–1215.
- 1242 *RAFFARD, A., CUCHEROUSSET, J., MONTOYA, J.M., RICHARD, M., ACOCA-PIDOLLE, S., POÉSY,
- 1243 C., GARREAU, A., SANTOUL, F. & BLANCHET, S. (2021) Intraspecific diversity loss in a predator
- species alters prey community structure and ecosystem functions. *PLOS Biology* **19**, e3001145.
- *RAFFARD, A., CUCHEROUSSET, J., SANTOUL, F., DI GESU, L. & BLANCHET, S. (2023) Climate
 and intraspecific variation in a consumer species drive ecosystem multifunctionality. *Oikos*.
- 1247 *RAFFARD, A., LECERF, A., COTE, J., BUORO, M., LASSUS, R. & CUCHEROUSSET, J. (2017) The
- 1248 functional syndrome: linking individual trait variability to ecosystem functioning. *Proceedings*
- 1249 of the Royal Society B: Biological Sciences 284, 20171893.
- 1250 *RAFFARD, A., SANTOUL, F., BLANCHET, S. & CUCHEROUSSET, J. (2020) Linking intraspecific
- 1251 variability in trophic and functional niches along an environmental gradient. Freshwater
- 1252 *Biology* **65**, 1401–1411.

- *RAINE, N.E. & CHITTKA, L. (2005) Colour preferences in relation to the foraging performance
 and fitness of the bumblebee *Bombus Terrestris*. *Uludag Bee Journal* 5, 145–150.
- *RÉALE, D. & FESTA-BIANCHET, M. (2003) Predator-induced natural selection on temperament
 in bighorn ewes. *Animal Behaviour* 65, 463–470.
- 1257 *RÉALE, D., GALLANT, B.Y., LEBLANC, M. & FESTA-BIANCHET, M. (2000) Consistency of
- temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*60, 589–597.
- *REID, D., ARMSTRONG, J.D. & METCALFE, N.B. (2011) Estimated standard metabolic rate
 interacts with territory quality and density to determine the growth rates of juvenile Atlantic
 salmon: SMR, density, territory and growth. *Functional Ecology* 25, 1360–1367.
- *REID, D., ARMSTRONG, J.D. & METCALFE, N.B. (2012) The performance advantage of a high
 resting metabolic rate in juvenile salmon is habitat dependent: RMR, dominance, habitat and
 growth in salmon. *Journal of Animal Ecology* 81, 868–875.
- *ROBINSON, B.W. (2000) Trade offs in Habitat-Specific Foraging Efficiency and the Nascent
 Adaptive Divergence of Sticklebacks in Lakes. Behaviour. *Behaviour* 137, 865–888.
- 1268 *ROTA, T., JABIOL, J., CHAUVET, E. & LECERF, A. (2018) Phenotypic determinants of inter-
- individual variability of litter consumption rate in a detritivore population. *Oikos* 127, 1670–1678.
- *ROTA, T., JABIOL, J., LAMOTHE, S., LAMBRIGOT, D., CHAUVET, É. & LECERF, A. (2024)
 Phenotypes of predator individuals underpin contrasting ecosystem effects. *Freshwater Biology*. https://doi.org/10.1111/fwb.14242.
- 1274 *RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., STIER, A., SATO, T., HEAVYSIDE, J., EL-SABAAWI,
- 1275 R.W. & CRUTSINGER, G.M. (2015) Adaptive genetic variation mediates bottom-up and top-
- down control in an aquatic ecosystem. *Proceedings of the Royal Society B: Biological Sciences*282, 20151234.
- *RUDMAN, S.M. & SCHLUTER, D. (2016) Ecological Impacts of Reverse Speciation in
 Threespine Stickleback. *Current Biology* 26, 490–495.
- *SAMPAIO, A.L.A., PAGOTTO, J.P.A. & GOULART, E. (2013) Relationships between
 morphology, diet and spatial distribution: testing the effects of intra and interspecific
 morphological variations on the patterns of resource use in two Neotropical Cichlids. *Neotropical Ichthyology* 11, 351–360.
- *SANTICCHIA, F., DANTZER, B., VAN KESTEREN, F., PALME, R., MARTINOLI, A., FERRARI, N. &
 WAUTERS, L.A. (2018) Stress in biological invasions: Introduced invasive grey squirrels
 increase physiological stress in native Eurasian red squirrels. *Journal of Animal Ecology* 87, 1342–1352.
- 1288 *SANTOSTEFANO, F., WILSON, A.J., NIEMELÄ, P.T. & DINGEMANSE, N.J. (2017) Indirect genetic 1289 effects: a key component of the genetic architecture of behaviour. *Scientific Reports* **7**, 10235.
- *SARNO, R.J. & FRANKLIN, W.L. (1999) Maternal expenditure in the polygynous and
 monomorphic guanaco: suckling behavior, reproductive effort, yearly variation, and influence
 on juvenile survival. *Behavioral Ecology* 10, 41–47.
- 1293 *SCHAACK, S. & CHAPMAN, L.J. (2003) Interdemic variation in the African cyprinid Barbus
- *neumayeri* : correlations among hypoxia, morphology, and feeding performance. *Canadian Journal of Zoology* **81**, 430–440.
- 1296 *Schuett, W., Dall, S.R.X., Kloesener, M.H., Baeumer, J., Beinlich, F. & Eggers, T.
- 1297 (2015) Life-history trade-offs mediate 'personality' variation in two colour morphs of the pea 1298 aphid, *Acyrthosiphon pisum. Journal of Animal Ecology* **84**, 90–101.

- *SCHULTE-HOSTEDDE, A.I. & MILLAR, J.S. (2004) Intraspecific variation of testis size and
 sperm length in the yellow-pine chipmunk (*Tamias amoenus*): implications for sperm
 competition and reproductive success. *Behavioral Ecology and Sociobiology* 55, 272–277.
- *SHACKLETON, M.A., JENNIONS, M.D. & HUNT, J. (2005) Fighting success and attractiveness
 as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the
 effectiveness of no-choice tests. *Behavioral Ecology and Sociobiology* 58, 1–8.
- *SHORT, K.H. & PETREN, K. (2008) Boldness underlies foraging success of invasive
 Lepidodactylus lugubris geckos in the human landscape. *Animal Behaviour* 76, 429–437.
- *SMITH, T.B. (1987) Bill size polymorphism and intraspecific niche utilization in an African
 finch. *Nature* 329, 717–719.
- *SNOWBERG, L.K. & BOLNICK, D.I. (2008) Assortative mating by diet in a phenotypically
 unimodal but ecologically variable population of stickleback. *The American Naturalist* 172,
 733–739.
- 1312 *SNOWBERG, L.K., HENDRIX, K.M. & BOLNICK, D.I. (2015) Covarying variances: more
- 1313 morphologically variable populations also exhibit more diet variation. *Oecologia* **178**, 89–101.
- *SOARES, A.O. & SCHANDERL, D.C.H. (2001) Fitness of two phenotypes of *Harmonia axyridis*(Coleoptera: Coccinellidae). 98, 287–293.
- *SONG, Z.-G. & WANG, D.-H. (2003) Metabolism and thermoregulation in the striped hamster
 Cricetulus barabensis. Journal of Thermal Biology 28, 509–514.
- 1318 *SPEAKMAN, J.R., KRÓL, E. & JOHNSON, M.S. (2004) The functional significance of individual 1319 variation in basal metabolic rate. *Physiological and Biochemical Zoology* **77**, 900–915.
- *SPRITZER, M.D., MEIKLE, D.B. & SOLOMON, N.G. (2005) Female choice based on male spatial
 ability and aggressiveness among meadow voles. *Animal Behaviour* 69, 1121–1130.
- *START, D. & GILBERT, B. (2017) Predator personality structures prey communities and trophic
 cascades. *Ecology Letters* 20, 366–374.
- *START, D. & GILBERT, B. (2019) Trait variation across biological scales shapes community
 structure and ecosystem function. *Ecology* 100.
- 1326 *STEINMEYER, C., MUELLER, J.C. & KEMPENAERS, B. (2013) Individual variation in sleep 1327 behaviour in blue tits *Cyanistes caeruleus* : assortative mating and associations with fitness-
- 1328 related traits. *Journal of Avian Biology* **44**, 159–168.
- *SVANBACK, R. & EKLOV, P. (2004) Morphology in perch affects habitat specific feeding
 efficiency. *Functional Ecology* 18, 503–510.
- 1331 *TOSCANO, B.J. & GRIFFEN, B.D. (2014) Trait-mediated functional responses: predator 1332 behavioural type mediates prey consumption. *Journal of Animal Ecology* **83**, 1469–1477.
- *VAN BUSKIRK, J. & MCCOLLUM, S.A. (2000) Influence of tail shape on tadpole swimming
 performance. *Journal of Experimental Biology* 203, 2149–2158.
- 1335 *VAN BUSKIRK, J., MCCOLLUM, S.A. & WERNER, E.E. (1997) Natural selection for 1336 environmentally induced phenotypes in tadpoles. *Evolution* **51**, 1983–1992.
- *VARGAS, R., MACKENZIE, S. & REY, S. (2018) 'Love at first sight': The effect of personality
 and colouration patterns in the reproductive success of zebrafish (*Danio rerio*). *PLOS ONE* 13,
 e0203320.
- 1340 *VERCKEN, E., MASSOT, M., SINERVO, B. & CLOBERT, J. (2007) Colour variation and
- 1341 alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. Journal
- 1342 *of Evolutionary Biology* **20**, 221–232.

- 1343 *WALTON, M. (1988) Relationships among Metabolic, Locomotory, and Field Measures of
- Organismal Performance in the Fowler's Toad (*Bufo woodhousei fowleri*). *Physiological Zoology* 61, 107–118.
- 1346 *WARD, A.J.W., THOMAS, P., HART, P.J.B. & KRAUSE, J. (2004) Correlates of boldness in three-
- spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* 55, 561–
 568.
- *WEBSTER, M.M., WARD, A.J.W. & HART, P.J.B. (2009) Individual boldness affects
 interspecific interactions in sticklebacks. *Behavioral Ecology and Sociobiology* 63, 511–520.
- *WELLBORN, G.A. (2000) Selection on a sexually dimorphic trait in ecotypes within the
 Hyalella azteca species complex (Amphipoda: Hyalellidae). *The American Midland Naturalist*
- 1353 **143**, 212–225.
- *WHITE, J.R., MEEKAN, M.G., MCCORMICK, M.I. & FERRARI, M.C.O. (2013) A comparison of
 measures of boldness and their relationships to survival in young fish. *PLoS ONE* 8, e68900.
- *WHITEMAN, H.H., WISSINGER, S.A. & BROWN, W.S. (1996) Growth and foraging
 consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum. Evolutionary Ecology* 10, 433–446.
- *WIELEBNOWSKI, N.C. (1999) Behavioral differences as predictors of breeding status in captive
 cheetahs. *Zoo Biology* 18, 335–349.
- *WILSON, A.D.M., GODIN, J.-G.J. & WARD, A.J.W. (2010) Boldness and reproductive fitness
 correlates in the eastern mosquitofish, *Gambusia holbrooki. Ethology* **116**, 96–104.
- *WILSON, D.S., COLEMAN, K., CLARK, A.B. & BIEDERMAN, L. (1993) Shy-bold continuum in
 pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal*of Comparative Psychology 107, 250–260.
- 1366 *WRAY, M.K., MATTILA, H.R. & SEELEY, T.D. (2011) Collective personalities in honeybee 1367 colonies are linked to colony fitness. *Animal Behaviour* **81**, 559–568.
- *YAMAMOTO, T., UEDA, H. & HIGASHI, S. (1998) Correlation among dominance status,
 metabolic rate and otolith size in masu salmon. *Journal of Fish Biology* 52, 281–290.
- 1370 *ZAVORKA, L., ALDVEN, D., NASLUND, J., HOJESJO, J. & JOHNSSON, J.I. (2015) Linking lab
- 1371 activity with growth and movement in the wild: explaining pace-of-life in a trout stream.
 1372 *Behavioral Ecology* 26, 877–884.
- 1373 *ZÁVORKA, L., KOECK, B., CUCHEROUSSET, J., BRIJS, J., NÄSLUND, J., ALDVÉN, D., HÖJESJÖ,
- 1375 ¹ZAVORKA, L., KOECK, B., CUCHEROUSSET, J., BRIJS, J., NASLUND, J., ALDVEN, D., HOJESJO, 1374 J., FLEMING, I.A. & JOHNSSON, J.I. (2017) Co-existence with non-native brook trout breaks
- down the integration of phenotypic traits in brown trout parr. *Functional Ecology* **31**, 1582–1376 1591.
- 1377 *ZENG, L.-Q., ZHANG, A.-J., KILLEN, S.S., CAO, Z.-D., WANG, Y.-X. & FU, S.-J. (2017)
- 1378 Standard metabolic rate predicts growth trajectory of juvenile crucian carp (*Carassius auratus*)
 1379 under changing food availability. *Biology Open*, bio.025452.
- *ZHAO, T., VILLÉGER, S., LEK, S. & CUCHEROUSSET, J. (2014) High intraspecific variability in
 the functional niche of a predator is associated with ontogenetic shift and individual
 specialization. *Ecology and Evolution* 4, 4649–4657.
- 1383 *ZUB, K., BOROWSKI, Z., SZAFRAŃSKA, P.A., WIECZOREK, M. & KONARZEWSKI, M. (2014)
- 1384 Lower body mass and higher metabolic rate enhance winter survival in root voles, *Microtus*
- 1385 *oeconomus. Biological Journal of the Linnean Society* **113**, 297–309.