

Range of trait variation in prey determines evolutionary contributions to predator growth rates

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Abstract

Evolutionary and ecological dynamics can occur on similar timescales and thus influence each other. While it has been shown that the relative contribution of ecological and evolutionary change to population dynamics can vary, it still remains unknown what influences these differences. Here, we test whether prey populations with increased variation in their defence and competitiveness traits will have a stronger impact on evolution for predator growth rates. We controlled trait variation by pairing distinct clonal lineages of the green alga *Chlamydomonas reinhardtii* with known traits as prey with the rotifer *Brachionus calyciflorus* as predator and compared those results with a mechanistic model matching the empirical system. We measured the impact of evolution (shift in prey clonal frequency) and ecology (shift in prey population density) for predator growth rate and its dependency on trait variation using an approach based on a 2-way ANOVA. Our experimental results indicated that higher trait variation, i.e., a greater distance in trait space, increased the relative contribution of prey evolution to predator growth rate over 3–4 predator generations, which was also observed in model simulations spanning longer time periods. In our model, we also observed clone-specific results, where a more competitive undefended prey resulted in a higher evolutionary contribution, independent of the trait distance. Our results suggest that trait combinations and total prey trait variation combine to influence the contribution of evolution to predator population dynamics, and that trait variation can be used to identify and better predict the role of eco-evolutionary dynamics in predator–prey systems.

Keywords: trade-offs, predator–prey interaction, population dynamics, experimental evolution, microbes

Introduction

There is increasing evidence that evolutionary change can influence population dynamics on contemporary timescales as much, if not more, than ecological changes (Coulson et al., 2005; Ellner et al., 2011; Hairston et al., 2005; Hiltunen & Becks, 2014; Post & Palkovacs, 2009). These evolutionary changes, including de novo mutations followed by selection (Bell & Gonzalez, 2009, 2011; Ramsayer et al., 2013) or selection on existing genotypes (Becks et al., 2010; Coulson et al., 2005; Hermann & Becks, 2022; Kasada et al., 2014; Turcotte et al., 2013), result in shifts of trait distributions within a population, thereby impacting its interaction with the environment. Evolution on contemporary timescales that affects population dynamics has been observed in life-history traits such as growth and survival rate (Bruijning et al., 2019; Ozgul et al., 2010; Williams et al., 2015), and traits involved in trophic interactions, such as competition (Bernhardt et al., 2020; Sakarchi & Germain, 2023) and anti-predator defences (Boyd et al., 2018; Griffiths et al., 2018; Kasada et al., 2014; Yoshida et al., 2007; Zamorano et al., 2023). However, while a growing number of studies demonstrate that contemporary evolutionary changes impact population dynamics, it is not clearly understood what mechanism determines the magnitude of these impacts, nor how to predict when they occur.

Some previous studies have quantified the relative contribution of evolutionary and ecological changes to changes in

some ecological properties of the system (often on population dynamics; Bruijning et al., 2019; Coutinho et al., 2016; Hairston et al., 2005; Ozgul et al., 2010; but see terHorst et al., 2014; Pantel et al., 2015 for examples in community properties). These studies have indicated that properties such as evolutionary history (Hiltunen & Becks, 2014), environmental conditions (del Arco et al., 2023; Pelletier et al., 2007), or food web structure (Frickel et al., 2017; Friman & Buckling, 2013) can determine when evolution is needed to understand the underlying processes driving ecological change (see van Benthem et al., 2017 for a review of methods applied to understand relative importance of contributing processes). However, they could not determine the cause of when evolution will be a strong or weak determinant, and few studies have directly addressed this question. One possibility is when large trait variation within populations exists, i.e., a larger trait difference along a trait axis or a larger separation in trait space, which causes larger fitness differences between genotypes, and thus results in rapid evolution that can impact ecological change on the same timescale (see Govaert et al., 2021 for a study indicating such a mechanism). The process of evolutionary rescue provides indirect evidence for this, as a species is more likely to avert population collapse after environmental deterioration through adaptive evolution when more genetic variation is available (Agashe et al., 2011; Gomulkiewicz & Holt, 1995; Lachapelle & Bell, 2012;

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Orr & Unckless, 2014). While there is evidence that rapid evolution contributes to ecological change, the evolutionary change is often slower than the ecological changes (DeLong et al., 2016) and it is currently unclear how trait variation can drive the relative importance and speed of evolution for population dynamics.

Rapid evolution associated with increased trait variation can also impact species interactions and consequent community dynamics. For example, large variation in anti-predator defence trait within a prey population (Becks et al., 2010; Ehrlich et al., 2017; Yoshida et al., 2007) and consequent trade-offs between predator defence and competitive ability (Kasada et al., 2014) facilitate rapid evolution, increasing the overlap of ecological and evolutionary timescales. But when the trait variation between prey genotypes is small, prey diversity can be lost and evolution thus does not contribute to population dynamics (Jones & Ellner, 2007). This suggests that prey trait variation should impact predator population dynamics and the importance of evolution, but this has not been empirically tested (but see Govaert et al., 2021 for a potential example of trait distance impacting the importance of evolution for groups of competing species).

We hypothesize that a larger distance between traits in one population (i.e., prey) should lead to larger relative contributions of evolution to the growth of an interacting population (i.e., predator). For example, a larger distance in traits that impact prey competition should produce a faster prey evolutionary response at low predation pressure. This would select prey with stronger competitive traits, and the large trait variation would cause faster shifts in prey genotype frequencies. When predation pressure is high, prey populations with large differences in predator defence traits should have stronger evolutionary responses to selection by predation, as frequency shifts should have a greater impact on predator fitness. For both types of traits, the relative contribution of prey evolutionary (i.e., shift in population mean traits) and ecological (i.e., shift in population abundance) change for predator population growth would thus depend on the distance in trait space for defence and competitiveness. As prey mean trait and frequency are dynamic properties, the relative contributions of evolution and ecology should change over time (see Becks et al., 2012 for an example of this), and should depend on the current selection pressure (e.g., high or low predation), ecological dynamics (e.g., prey density), and the prey trait distribution (i.e., inclusive of prey genotype frequencies).

In this study, we combine laboratory experiments and simulations from a mechanistic model to test how the distance in trait space in prey populations influences the relative contribution of evolutionary (shift in prey clonal frequency) and ecological change (shift in prey population density) to predator growth rate over time and thus to predator–prey dynamics in an algae–rotifer system. Previous studies in this system have shown that algal prey defence can have a strong effect on predator growth rate (Bernardes et al., 2021; Huang et al., 2017; Réveillon & Becks, 2023) and that predator–prey dynamics can be altered by the trade-off cost for defence (Kasada et al., 2014) and large differences in defence and competitiveness traits within the prey population (Becks et al., 2010, 2012). We conducted short-term experiments using the rotifer *Brachionus calyciflorus* as predator and four different clonal lineages of the green algae *Chlamydomonas reinhardtii* as prey. The clonal lineages were previously isolated from a selection experiment (Bernardes et al., 2021) and were chosen

for their differences in defence and competitiveness traits and in the trade-off between these two traits (Réveillon & Becks, 2023). Two of the clonal lineages had a higher level of defence against rotifer predation (hereafter: defended clones), due to a heritable trait for growth in large multi-cell colonies (instead of as single cells) that led to a lower rotifer attack rate and higher handling time by the rotifer, and the other two lineages had a lower level of this defence trait (hereafter: undefended clones) (Bernardes et al., 2021; Réveillon & Becks, 2023). This defence trait shows a trade-off with competitive ability, as the defended clonal lineages had lower growth rates (Réveillon & Becks, 2023).

To examine the effect of trait distance in the prey population, we combined each undefended clonal lineage with each defended clonal lineage to create different distances in trait space for the prey population (four pairwise combinations of clones in total). While the distance in trait space between the defended and undefended clonal lineages was large, the distances between each clonal pairing were small as the defended and undefended clonal lineages occupied a similar position in trait space. To test whether the initial frequencies of the two clonal lineages influenced the contribution of ecological and evolutionary change, we also varied the initial frequency of the undefended clonal lineages, as previous studies suggested that initial trait distributions can impact population growth (Hermann & Becks, 2022; Orr & Unckless, 2014). We ran the experiments for 8 days to reduce the possibility of de novo mutations in the prey and predator populations that could affect the trait distance in our experiment. Finally, we compared the experimental results with a mechanistic model (Becks et al., 2010), using simulations for two undefended prey clones, each paired with a range of increasingly more defended prey clones with a trade-off in lower competitiveness (and thus a higher distance in trait space). For each pairing, we also varied the starting frequencies of the undefended prey clones. We tracked, for both the experiment and simulations, the population densities and frequencies of prey clonal lineages over time and used a 2-way ANOVA approach (Hairston et al., 2005) to quantify the effects of evolution (shifts in prey clonal frequency) and ecology (shift in prey population density) on predator growth over time.

We were able to show that the increase in distance between traits of two clonal lineages within the prey population led to an increase in the relative contribution of evolution on predator growth rate. The same pattern was observed in the model simulations. Simulation results also revealed that increases in the frequency and trait of the more competitive undefended prey led to increases in the importance of evolution, independent of the trait distance.

Material and methods

Experimental cultures

We used the rotifer *Brachionus calyciflorus* as the predator, which was cultured with the green algae *Scenedesmus sp.* as its food source prior to the experiments. The rotifer culture consisted of an obligate asexually reproducing clone (Fussmann et al., 2003), with a generation time of 1.5–2 days (Becks et al., 2010). Prior to the experiments rotifers were filtered with a 40 µm cell strainer and starved for 4 hr and then filtered again, to ensure that none of the food source algae *Scenedesmus sp.* were transferred into the experiments. The four different clonal lineages of the green algae *C. reinhardtii*,

used in our experiments as prey, have been isolated from a selection experiment in which they evolved with (defended clonal lineages) or without (undefended clonal lineages) predation by the rotifer over 6 months (Bernardes et al., 2021). Their heritable traits in defense and competition have previously been determined (Réveillon & Becks, 2023): clonal lineages CR1 and CR2 are more defended against predation by the rotifer with a trade-off in competitiveness, and the clonal lineages CR6 and CR7 are less defended against predation but more competitive. Here, we use the maximum predator ingestion rate as a measure for prey defence, and the maximum algal growth rate under nutrient-replete conditions and without predators as a measure for prey competitiveness (Figure 1). These traits were shown to be heritable and consistent over generations and are correlated to other defence (e.g., attack rate and handling time of the predator, size and stoichiometry of the prey) and competitive (e.g., nutrient affinity and half-saturation constants) traits as well as to prey and predator fitness (Becks et al., 2012; Réveillon & Becks, 2023). All stocks of the clonal lineages were kept on agar plates prior to the experiments to ensure that the traits were held constant over time. Three weeks before the experiment, we picked individual colonies from the agar plates and transferred these to nitrogen-rich medium (800 $\mu\text{M NO}_3^-$; Barreiro & Hairston, 2013) to grow to high densities under continuous light (200 $\mu\text{mol photon m}^{-2} \text{sec}^{-1}$) and shaking (120 rpm) at $20 \pm 1^\circ\text{C}$. The day before the experiments, the cultures were centrifuged at 2000 XG for 10 min and the pellet re-suspended in the growth medium used for the experiment (200 $\mu\text{M NO}_3^-$).

Prey trait distance

We used the previously measured trait estimates of rotifer maximum ingestion rate and algal maximum growth rate (Réveillon & Becks, 2023) to calculate the Euclidean distance between the traits in a defense-competition trait space after normalizing each trait value with the following equation:

$$(x_i - \min(x)) / (\max(x) - \min(x))$$

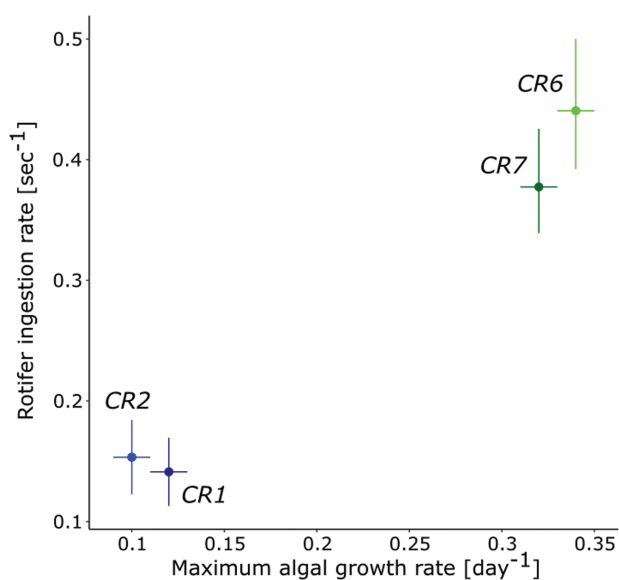


Figure 1. Defense-competitiveness trait space of the undefended, CR6 and CR7, and the defended clones, CR1 and CR2 used in this study. Shown is the position in the trait space (dots) with standard deviation for both traits (as horizontal and vertical bars).

where x_i is a specific trait value of clonal lineage i for trait x . This bounds each trait value between 0 and 1.

Experimental setup

The experiment was set up in tissue culture flasks (TC T-25 standard surface filter cap, Sarstedt) with 21 ml of growth medium containing 200 $\mu\text{M NO}_3^-$. Experimental flasks were inoculated with a starting density of four rotifers ml^{-1} and 3.85×10^5 algal cells ml^{-1} . Algal populations were combined in pairs of one undefended clonal lineage (CR6 or CR7) and one defended clonal lineage (CR1 or CR2) resulting in four distinct combinations of clonal lineages. Cultures with only one clonal lineage served as controls to test for the effects of the different algal lineages on the rotifer fitness under the experimental conditions (Supplementary Figure S1). For each combination, we used four different initial frequencies of the undefended clonal lineages (0.4, 0.3, 0.2, and 0.1). For each treatment (four combinations \times four initial frequencies of the undefended clonal lineage = 16 treatments) and control, we started with 10 replicates, but data from some replicates were excluded due to contaminations or rotifer extinction (see Supplementary Table S1 for details). The flasks were kept at continuous light (200 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) and shaking (120 rpm) at $20 \pm 1^\circ\text{C}$. Our experiments lasted for 8 days, during which we replaced a third of the volume (7 ml) with fresh growth medium every day before randomly placing the flasks back on the orbital shaker. We used the replaced volume for daily monitoring of rotifer (5 ml was used for counting the rotifers alive) and algal densities and frequencies of clonal lineages (1 ml was fixed with a solution of paraformaldehyde 0.01% and glutaraldehyde 0.1% final concentration).

To determine the algal density and frequencies of the clonal lineages when combined, we used previously established methods. Fixed samples were counted using a high-content imaging microscope (ImageXpress Micro 4; Molecular Devices), which measures the auto-fluorescence of chlorophyll a with a CY5 filter (see Hermann & Becks, 2022 for details). For assessing the frequencies of clonal lineages, we acquired single-cell images using a imaging flow cytometer (Imagestream Mk II; Luminex) and applied a neural network model that distinguished the different clonal lineages (see Hermann & Becks, 2024 for details).

Statistical analysis

All analyses were done in the R environment (R Core Team, 2023; version 4.3.0) and graphics were made using the “ggplot2” R package (Wickham, 2009; version: 3.4.3). The effect of the combination of clonal lineages (CR6 & CR1, CR6 & CR2, CR7 & CR1, and CR7 & CR2) and initial frequency (0.4, 0.3, 0.2, and 0.1) on the algal density each day of the experiment (days 0–8) was analyzed using a generalized linear mixed-effects model (GLMM), with the “lme4” R package (Bates et al., 2015; version 1.1.34) with day (numerical), initial frequency (categorical), and clonal combination (categorical) and their interactions as fixed effects, using a gamma distribution with a log link function to model for algal density. Rotifer densities were log-transformed before being analyzed using a linear mixed model (LMM) with initial frequency (categorical) and clonal combination (categorical) as interacting and day (numerical) as an additive fixed effect. The interaction effect was dropped, as the maximum likelihood ratio test showed no significance when excluding it. To detect if the different treatments had an effect on final rotifer densities, we

compared the rotifer densities on day 8 across clonal combination using a Kruskal–Wallis test. Undefended algal frequencies were logit transformed and analyzed using an LMM with clonal combination (categorical), initial frequency (categorical), and day (categorical) as interacting fixed effects. For all three mixed-effect models, replicates were added as random effects to account for potential random variation deriving from repeated measurements over time. For each analysis, the best-fitting model was estimated using model comparison and maximum likelihood ratio tests. Afterwards, the significance of all fixed effects was tested using the analysis of deviance with the type II Wald chi-square test.

To quantify the effects of evolution (change in undefended prey frequency from one day to the next) and ecology (change in total prey density from one day to the next) on predator growth rate, we applied a two-way ANOVA to estimate how changes in the ecological and evolutionary predictor variable contribute to changes in the response variable, predator growth rate (e.g., calculating the average change in the response variable when one of the predictors was allowed to change while the other was held constant; following Ellner et al., 2011; Hairston et al., 2005). We used this approach based on the criteria provided by van Benthem et al. (2017) and the observation that the traits considered here are heritable within the time frame of the experiment and the effects of phenotypic plasticity can be neglected. To apply this method, we used the linear model for predator growth rate as a function of X where $X_t = F_t * D_t$. We then used the model coefficients (intercept α and slope β) to calculate the average effect sizes:

$$a = (\alpha + \beta F_{t+1} D_t) - (\alpha + \beta F_t D_t)$$

$$b = (\alpha + \beta F_{t+1} D_{t+1}) - (\alpha + \beta F_t D_{t+1})$$

$$Evolution_{t+1} = \frac{a + b}{2},$$

where F_t is the frequency of the undefended clonal lineage at time point t and D_t is the density of the total algae population at time point t . The estimates a and b thus show how much a shift in the frequency from t to $t + 1$ contributed to a change in the predator growth rate, while the population density was held constant at t (fraction a) or $t + 1$ (fraction b). As these estimates are still partially influenced by the constant of population density at different time points, they are added together and divided by two. This averages out the influence of a shift in frequency while minimizing the ecological impact and gives an estimate of the contribution of evolution on changes in predator growth rate. The same fractions are afterwards calculated for changes in population density, while keeping the frequency constant, thus averaging out the effect of changes in prey population on changes in predator growth rate (see [Supplementary Information](#) for a detailed explanation).

The relative contributions of evolution and ecology per day of the experiment are here reported as the log-transformed absolute values of the ratio *Evolution/Ecology*, where *Evolution* and *Ecology* were calculated using the method described above. Positive values represent time points where evolution was contributing relatively more than ecology to predator growth rate, and negative values when ecology contributed more than evolution. To evaluate changes in the $\log(|Evolution/Ecology|)$ values over time, these values were analyzed using an LMM with the clonal combination

(categorical) and day (categorical) as interacting and starting frequency (categorical) as an additive fixed effect and replicates as random effect. Initial frequency was dropped as a predictor, as the maximum likelihood ratio test showed no significance when excluding it. We applied a Tukey post-hoc test for pairwise comparisons between combinations of clonal lineages on each day and predicted the mean $\log(|Evolution/Ecology|)$ value for each day and combination of clonal lineages (hereafter: estimated marginal means) with the “emmenas” R package (Lenth, 2024; version: 1.8.8). To analyze the correlation between the average contributions of evolution and ecology against the distance in trait space for each clonal combination, we applied a non-parametric Spearman’s correlation test.

Because the algal counts led to an unexpected high increase in the density of the algal population on days 1 and 2, we ran an additional analysis, in which these unexpectedly high data points were omitted and afterwards predicted from a statistical model. The data with these predicted values were then re-analyzed. The analyses showed a very similar result and we continued with analyses including the data points (results are summarized in the [Supplementary Information](#), in Analysis with predicted values, including [Supplementary Tables S2 and S3](#) and [Supplementary Figures S2 and S3](#)).

Model simulations

We ran simulations with the model from Becks et al. (2010), which is based on the rotifer–algal system depicting a single predator with two different prey clones in chemostats. The predator population consists of a single genotype with fixed traits, yet is divided into two life stages, where reproducing predators (B) age at rate λ and become non-reproducing (S). The two prey clones compete over the limiting resource (N) and differ in their investment into the functional traits of the half-saturation constant ($K_{C,i}$), describing their competitiveness and palatability (p_i ; probability of consumption), which depicts their defence. The undefended clone, thereafter C_1 is described by a higher palatability than the defended clone, C_2 . Following previous work with this model, the trade-off of competitiveness and defence was depicted with differences in the half-saturation constant. Therefore, C_1 has a higher nutrient uptake at low concentration than C_2 , while being consumed at a higher rate by the predator (Becks et al., 2010; Yoshida et al., 2003). The model is given by the following equations:

$$(1) \quad \frac{dN}{dt} = \delta (N_I - N) - \frac{\rho C_1 N}{K_{C,1} + N} - \frac{\rho C_2 N}{K_{C,2} + N}$$

$$(2) \quad \frac{dC_i}{dt} = C_i \left[\frac{X_C \rho N}{K_{C,i} + N} - \frac{p_i G (B + S)}{K_B + Q} - \delta \right] \quad i = 1, 2$$

$$(3) \quad \frac{dB}{dt} = B \left[\frac{X_B G Q}{K_B + Q} - (\delta + m + \lambda) \right]$$

$$(4) \quad \frac{dS}{dt} = \lambda B - (\delta + m) S$$

The prey consumption of the limiting resource nitrogen (N) and growth rate is modelled by a Monod equation. Both clones have the same conversion efficiency X_C and maximum per capita recruitment β_C which are included by the parameters $\rho = \beta_C X_C$. The limiting resource is renewed at

the concentration N_i with the constant inflow of the dilution rate δ . Predator consumption of the prey is given by the Monod equation and influenced by the clones' palatability. β_B describes the predator conversion efficiency and the predator half-saturation constant K_B is introduced by $G = \beta_B/K_B$. Therefore, the predator growth rate is a function of the total algal density and frequency of each clone $Q = p_1 C_1 + p_2 C_2$. Reproducing and non-reproducing predators die at the same constant mortality rate m (see [Supplementary Table S4](#) for all parameters and values).

We ran two sets of simulations each with fixed traits for the undefended clone C_1 , $p_1 = 0.8$ with $K_{C,1} = 2$ for the first set and $p_1 = 0.9$ with $K_{C,1} = 1$ for the second set of simulations. In both simulation sets, we changed the traits of the defended clone C_2 from $p_2 = 0.2$ with $K_{C,2} = 8$ to $p_2 = 0.79$ with $K_{C,2} = 2.1$ in the first set and to $p_2 = 0.89$ with $K_{C,2} = 1.1$ in the second set in 100 steps. For each combination of traits of C_1 and C_2 , we had four different starting frequencies of $C_2 = 0.6, 0.7, 0.8,$ and 0.9 and ran the simulation for 100 model time steps, equaling to a total of 800 simulations (100 for each set of traits of C_1 and starting frequency of C_2). The results were then analyzed with the same methods as the experimental results to determine if the influence of evolution (change in undefended prey frequency) had a relatively greater impact than ecology (change in total prey density) on predator growth rate.

Results

The pairs of undefended and defended clonal lineages differed in their trait distance ([Figure 1](#)), with the smallest distance for the pairs of CR7 & CR1 and CR7 & CR2 (1.15 and 1.18, respectively) and the largest distance for the pairs of CR6 & CR1 and CR6 & CR2 (1.36 and 1.39, respectively). The combination of clonal lineages significantly affected rotifer densities over time ([Figure 2A–D](#), LMM with Wald chi-square test: combination: $\chi^2 = 9.82$, $df = 3$, $p = 0.02$; initial frequency: $\chi^2 = 1.57$, $df = 3$, $p = 0.67$; day: $\chi^2 = 512.41$, $df = 1$, $p < 2.20 * 10^{-16}$; interaction of combination and initial frequency: $\chi^2 = 31.07$, $df = 9$, $p = 3 * 10^{-4}$; interaction effect of day: $\chi^2 = 5.43$, $df = 15$, $p = 0.99$) with highest rotifer densities for the combination of CR1 & CR6 and the lowest for CR2 & CR7. The initial frequency had overall no significant effect on the rotifer density. The significant interaction between combination and initial frequency indicates that initial frequencies had a different impact on rotifer density for different combinations of clonal lineages (e.g., clonal combination of CR1 & CR7, in which rotifer density was lower when CR1 had an initial frequency of 0.9; [Figure 2C](#)). While the rotifer population dynamics differed over the 8 days, their final density showed no difference between the clonal combinations (Kruskal–Wallis test: $\chi^2 = 0.96$, $df = 3$, $p = 0.81$).

We found that algal density differed significantly as a function of combination of clonal lineages and the initial frequency of the undefended clonal lineage, and changed over time as a function of the combinations of lineages ([Figure 2E–H](#), GLMM with Wald chi-square test: combination: $\chi^2 = 55.76$, $df = 3$, $p = 4.73 * 10^{-12}$; initial frequency: $\chi^2 = 18.26$, $df = 3$, $p = 4 * 10^{-4}$; day: $\chi^2 = 189.52$, $df = 1$, $p < 2.20 * 10^{-16}$; interaction of combination and day: $\chi^2 = 14,493$, $df = 3$, $p = 2 * 10^{-3}$) with algal densities being highest for the combinations CR1 & CR6 and CR1 & CR7 compared to the combinations of CR2 & CR6 and CR2 & CR7.

Evolutionary dynamics, here shifts in frequencies of the two clonal lineages in the prey population, also differed over time depending on the combination of clonal lineages and changed depending on the initial frequency of the undefended clonal lineage ([Figure 2I–L](#), LMM with Wald chi-square test: combination: $\chi^2 = 111.217$, $df = 3$, $p = 2.20 * 10^{-16}$; initial frequency: $\chi^2 = 41.64$, $df = 3$, $p = 5 * 10^{-9}$; day: $\chi^2 = 217.90$, $df = 8$, $p = 2.20 * 10^{-16}$; interaction of combination and day: $\chi^2 = 217.98$, $df = 24$, $p = 2.20 * 10^{-16}$; interaction of initial frequency and day: $\chi^2 = 50.17$, $df = 24$, $p = 1 * 10^{-3}$; interaction of combination and starting frequency: $\chi^2 = 21.38$, $df = 9$, $p = 1 * 10^{-2}$). We observed the highest frequencies of the undefended clonal lineage, in the first half of the experiment, for the combination of CR1 & CR6 which is one of the combinations with the highest trait distance. The frequency of the undefended clonal lineage was highest in the middle of the experiment, for the combination CR1 & CR7 which had a lower trait distance.

Evolutionary and ecological contribution

We estimated the relative contributions of evolutionary (frequency of undefended clonal lineage) and ecological (prey density) changes on changes in predator growth rate over time ([Supplementary Figure S4](#)), expressed here as the log ratio of the contribution of ecology over evolution ($\log(\text{Evolution}/\text{Ecology})$) (see [Supplementary Figure S5](#) for their separate impacts). Overall, we found a higher contribution of evolution to predator growth rate (mean ratio 0.563) over the 8 days of the experiment and that combination of clonal lineages, time, and their interaction had a significant effect on the ratio, while the initial frequencies showed no significant influence ([Figure 2M–P](#); LMM with Wald chi-square test: combination, $\chi^2 = 29.69$, $df = 3$, $p = 2 * 10^{-6}$; day, $\chi^2 = 68.61$, $df = 7$, $p = 3 * 10^{-12}$; starting frequency, $\chi^2 = 8.84$, $df = 37$, $p = 3 * 10^{-2}$; interaction combination and day $\chi^2 = 31.82$, $df = 21$, $p = 6 * 10^{-2}$). We found that the contribution of evolution was highest for the first part of the experiment (days 0–4) when starting with a larger trait distance (CR6 & CR1, CR6 & CR2) ([Figure 2M–P](#), [Supplementary Figure S6](#)). In contrast, when starting with a smaller trait distance (CR7 & CR1, CR7 & CR2) the relative contribution of evolutionary change was smaller during the first part of the experiment ([Figure 2M–P](#), [Supplementary Figure S6](#)). Overall, the contributions changed over time, with time points when evolution and when ecology contributed more (see [Supplementary Table S5](#) for details). In all cases, the contribution of evolution and ecology became more similar in all clonal combination towards the end of the experiments but shifted again on the final day ([Figure 2M–P](#), [Supplementary Figure S6](#)). The contribution of evolutionary change to rotifer growth rate correlated positively with trait distance when averaged over all replicates, initial frequencies, and time points, indicating a greater relative contribution of evolution with greater trait distance ([Figure 3A](#); Spearman's rank correlation, $S = 0$, $\rho = 1$, $p = 0.08$).

The same correlations were found in the simulations, where an increase in the trait distance between both prey clones present led to an increase in the relative contribution of evolution ([Figure 3B](#)). A lower starting frequency of the undefended clone led to a lower relative contribution of evolution, when it was lower in its trait values ($p_1 = 0.8$ and $K_{C,1} = 2$). Generally, the simulation runs with the undefended clone with higher trait values ($p_1 = 0.9$ and $K_{C,1} = 1$), had a higher

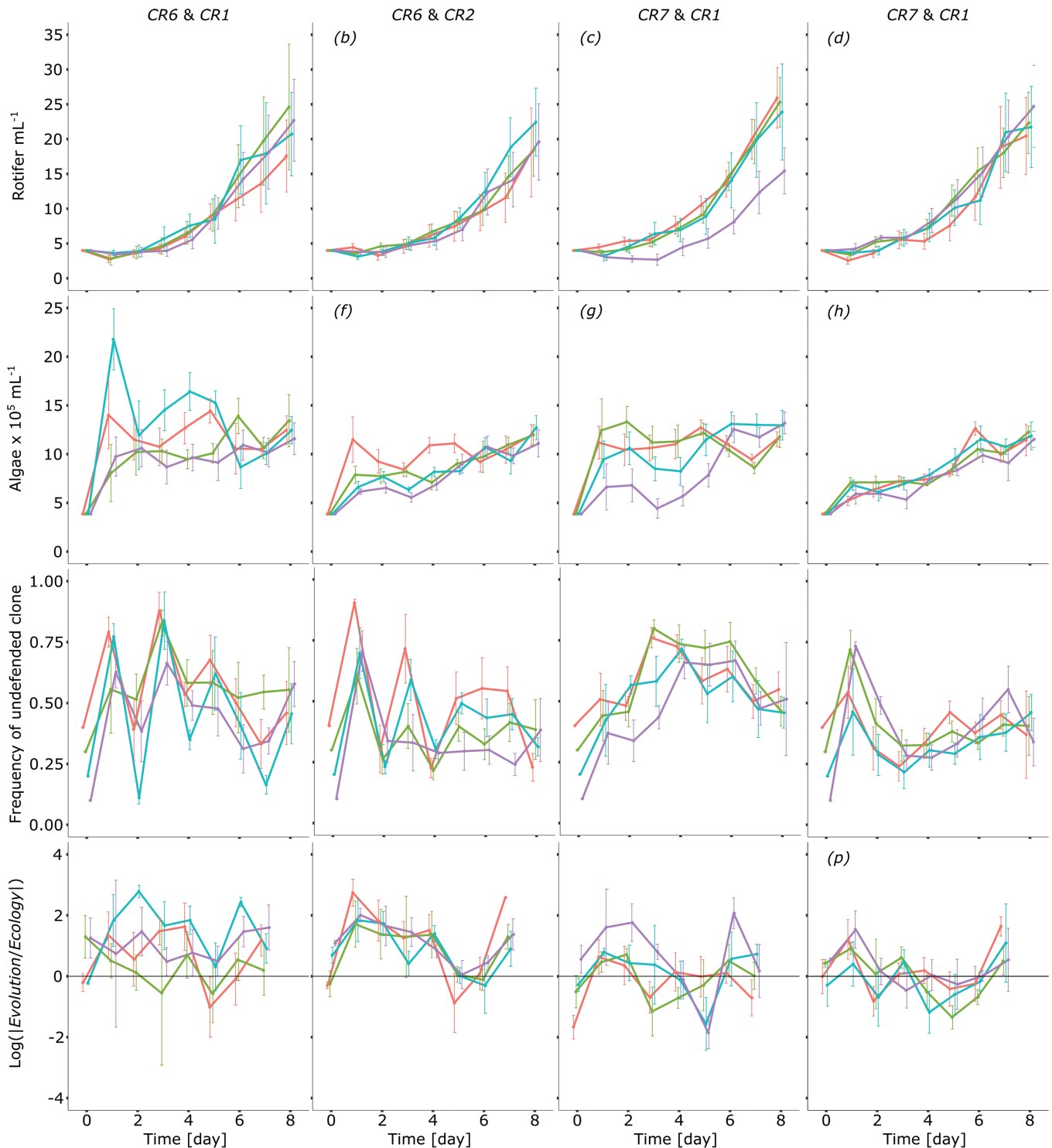


Figure 2. Effect of trait distance in prey population on rotifer and algae population dynamics, frequencies of undefended algal clonal lineage within prey population, and the contribution ecology and evolution to rotifer growth rate over time. (A)–(D) Rotifer population dynamics (*B. calyciflorus*). (E)–(H) Algae population dynamics (*C. reinhardtii*). (I)–(L) Frequency of the undefended clonal lineage within algal populations over time. (M)–(P) Relative importance of *Evolution* and *Ecology* on rotifer growth rate shown as the log of the ratio of evolutionary to ecological contribution. The horizontal black line of 0 represents the level when evolution and ecology are equally important. Shown are averages (lines, dots) for replicates (mean \pm SE, $n = 5$ –10); colors indicate different initial frequency of the undefended clonal lineages: 0.4 (red), 0.3 (green), 0.2 (blue), and 0.1 (purple).

contribution of evolution at the same distance in the trait space (Figure 3B).

Discussion

Contemporary evolution can affect ecological dynamics, such as changes in population size, when ecological and

evolutionary timescales overlap (Ezard et al., 2009; Lion, 2018; Strauss et al., 2008; Thompson, 1998). An increasing number of studies provide examples of this, but it remains largely unclear what conditions favour this overlap. Building from indications of existing theory (Fronhofer et al., 2023; Lande, 1976; Orr & Unckless, 2008), we predicted that the trait variation within a population would determine the

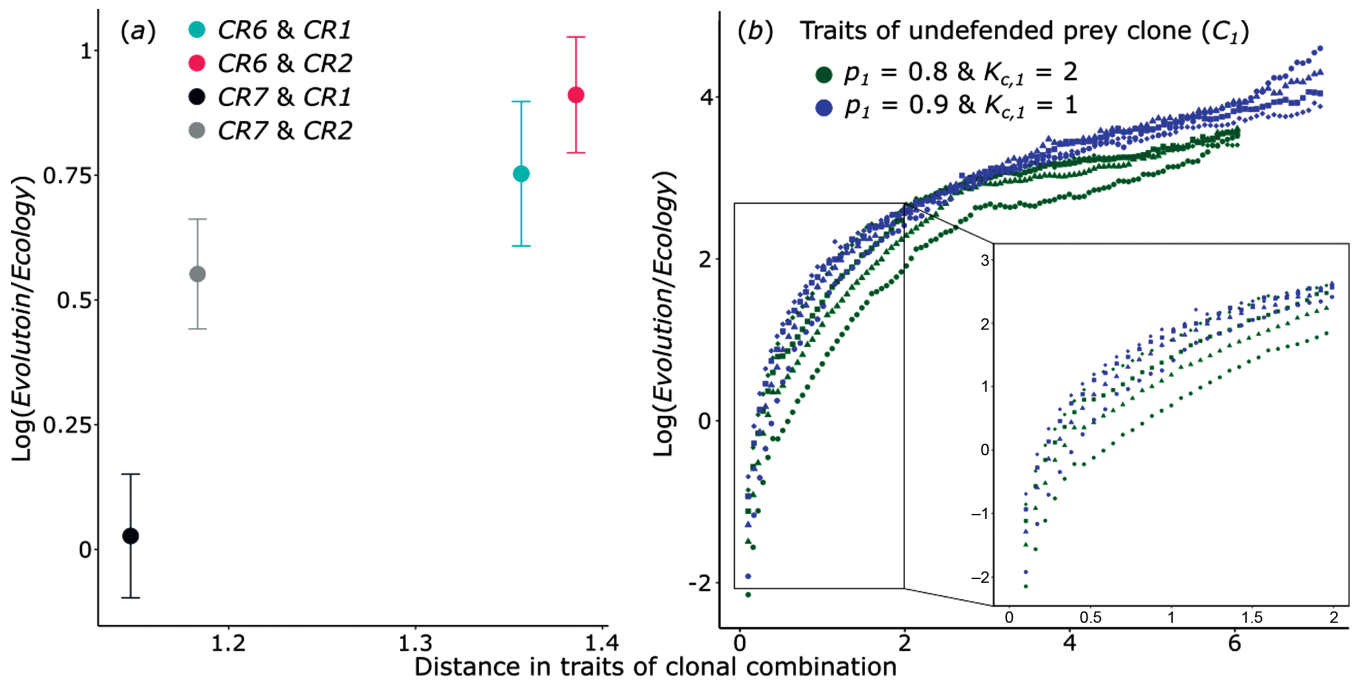


Figure 3. Relative contribution of *Evolution* and *Ecology* for the different clonal combinations. Correlation between distance in trait space and relative contribution from (A) the experimental data. Shown are averages (dots) of the mean relative contribution over all days of each replicate (mean \pm SE, $n = 5-10$); colors indicate different clonal combinations: *CR6* & *CR1* (turquoise), *CR6* & *CR2* (red), *CR7* & *CR1* (black) and *CR7* & *CR2* (grey). (B) Simulations with results of a trait distance between 0 and 2 zoomed in, green dots denote simulations with the parameters $p_1 = 0.8$ and $K_{C,1} = 2$, with p_2 changing from 0.2 to 0.79 and $K_{C,2}$ from 8 to 2.1 and blue dots with $p_1 = 0.9$ and $K_{C,1} = 1$, with p_2 from 0.2 to 0.89 and $K_{C,2}$ from 8 to 1.1. Shapes of the points of the simulation results denote the starting frequency of C_2 (circle: 0.4, triangle: 0.3, square: 0.2, and diamond: 0.1). For details see *Methods* section.

impact of evolution on ecological dynamics. Here, we first experimentally tested the relative contribution of evolutionary change in a prey population to the growth of an interacting predator population, and whether it varies with trait distance in the prey population and the initial frequencies of genotypes in the prey population. We found that the relative contribution of prey evolution to predator growth rate was greater than the relative contribution of ecological change of prey population density, and we also confirmed our prediction that the evolutionary contribution increased with greater distance in trait space. This contribution was not affected by the initial frequencies of clones in the prey population. We then explored a larger parameter space with simulations of a mechanistic model. Simulations not only confirmed the experimental results but also indicated that the particular trait values of the undefended prey impacted the contribution. The undefended prey clone that was less defended and more competitive produced a higher contribution of evolution for predator growth rate, and this effect was independent of the trait distance. While we did not anticipate this finding, it may result from the higher growth rate in a more competitive prey clone that would increase in frequency faster than a less competitive prey with the same degree of trait distance as the other clone in the population.

We were able to identify conditions that contribute to a better understanding of the conditions enabling an overlap of ecological and evolutionary timescales and eco-evolutionary dynamics, despite the short duration of the experiment (approximately 2–3 rotifer and 8–12 algal generations). Final rotifer densities (day 8) did not differ across the treatments with different combinations of clonal lineages, even though

the relative contribution of evolution to rotifer growth rate varied. This is probably because the evolutionary contributions varied in distinct ways over time for the various combinations of clonal lineages. The evolutionary contributions were different at the beginning of the experiment but became more similar towards the end. Our results indicate that the daily time series was necessary to detect the evolutionary contribution to predator growth rate and that the true effect would have been missed if only the starting and ending points were compared. This finding confirms observations in previous studies that coarse sampling might underestimate the contribution of evolution (Coulson et al., 2005; Hairston et al., 2005; Yoshida et al., 2007), and suggests that studies reporting effect sizes in pairs of time points (e.g., only starting and ending points, or any single pair of time points) may not reflect the true degree of evolutionary and ecological contributions (Hattich et al., 2021).

So why should we care about trait distance and the evolutionary contribution to predator growth, and population dynamics in general? It may help explain some results from previous studies. We found that increasing trait distance in the prey led to a greater contribution of evolutionary change to the predator growth rate. This is consistent with predictions for eco-evolutionary dynamics in predator-prey systems with prey evolution, where a stronger trade-off between defence against predation and competitiveness led to the strong and rapid release from predation (Kasada et al., 2014; van Velzen & Gaedke, 2017), resulting in antiphase cycles of predator and prey over longer timescales (Abrams & Matsuda, 1997; Yoshida et al., 2003). Previous work has also shown that trait distance in the prey population, and thus the potential

to evolve rapidly, determines the likelihood of indirect evolutionary rescue (Hermann & Becks, 2022; Yamamichi & Miner, 2015), where a non-evolving predator is rescued from extinction after environmental deterioration by the evolution of its prey. Both antiphase cycles and indirect evolutionary rescue contribute to the maintenance of heritable prey trait variation and thus could contribute to the potential for future evolutionary response to changes in selection.

We also found that the more defended clonal lineages (CR1, CR2) had similar fitness effects on predator growth (Figure 1, Réveillon & Becks, 2023), but when combined with a less defended prey clonal lineage, they impacted the relative contribution of evolution to predator growth. This result suggests that measures of trait–fitness relationships involving species interactions alone may not be sufficient for a comprehensive understanding of the underlying processes driving predator growth rate. Measurements of how trait variation translates into fitness over time are thus necessary as well (Agashe et al., 2011; Ehrlich et al., 2017; Wojcik et al., 2021).

In our experiment, we manipulated trait distance in the prey population by combining different clonal lineages of *C. reinhardtii* with predefined traits. Trait distance was estimated from a trait space of growth rate (i.e., as a measure of competitive strength at low predator densities) and predator ingestion rate (i.e., as a measure of prey defence against predator consumption). The absolute values of the trait distance estimates will differ if alternative measures of competition and defence are used, but a previous study demonstrated that the relative position of clonal lineages in trait space is unaffected by the choice of traits to describe defense and competition (Réveillon & Becks, 2023). Other unmeasured traits may also have contributed to the evolutionary and ecological dynamics in the prey population and hence influence predator growth rate. While this may be the case here, the observed relative contributions of evolution and ecology to predator growth rate over time are consistent with predictions based on defence and competitive traits and their fitness consequences for prey and predator.

At the start of the experiment, predator densities were low, and the predation pressure was initially not strong enough to control or suppress prey population growth, as evidenced by the increase in both the predator and prey populations for the first days of the experiment. The low predation pressure favoured the more competitive and less defended prey at the beginning of the experiment, and we found shifts in the prey population towards the less defended prey (CR6 and CR7), which contributed to an increase in predator growth rate. While the model (Supplementary Figure S7) and experiments (Figure 2) show similar behaviour at the first timepoints of an increase in the frequency of undefended prey, the increase is much stronger in the experiments. Possible explanations for this discrepancy include differences in the assumed competitive traits (model: half saturation; experiment: growth rate; but see Réveillon & Becks, 2023), or other unmeasured traits (i.e., stoichiometry or behaviour; Guariento et al., 2018). Moreover, deterministic model trajectories will always be much smoother than experimental trajectories, since the latter are subject to various sources of stochasticity (demographic, genetic, and sampling/estimation error). Additionally, this model has been shown to replicate long-term dynamics community dynamics (Becks et al., 2012; Ehrlich et al., 2017), while being less comparable to short-term dynamics. Therefore, we applied the model to show the mechanism over

a longer time period, acknowledging that the model is not a direct quantitative comparison for this experimental setup. As predator density increased over time, selection caused a shift towards the more defended and less competitive prey. The relative contribution of evolution decreased on average over time but was on average still more important than the ecological contribution.

This pattern was the strongest for combinations with CR6, in which the higher trait distance led to a greater relative contribution of evolution at the start of the experiment. A potential explanation for this result comes from the mechanistic model, where the more competitive (and also less defended) clone increased in frequency faster due to its higher total growth rates. The empirical results can be explained by this pattern as well, as the clonal lineage CR6 increased in frequency faster due to its higher total growth rates compared to CR7. The fluctuations in population density (Figure 2I–L) are likely explained by a general increase in frequency in both undefended clonal lineages shortly after their introduction, followed by a short delay where rotifers may have ingested the undefended clonal lineages at a higher rate, leading to a decrease again in their frequency. At this time (days 3–4 in Figure 2I and J), the higher maximum growth rate of CR6 led to a repetition of this pattern, before the rotifer population size was finally high enough (days 5–8) to stabilize the dynamics and inhibit the fast increase in the frequency of CR6.

A few additional points should be considered to interpret the results. First, our data show the relative influence of evolutionary change on an ecological property but does not demonstrate eco-evolutionary feedback between these two properties (see Bassar et al., 2021). Second, we also observed that a greater distance in the competition trait axis (i.e., the clone combinations with CR6) led to a greater contribution of evolutionary change. We therefore emphasize that traits and trait distances should be considered in their ecological context, as ecological parameters may influence the strength of the evolutionary contribution. If the competitive prey leads to rapid frequency changes, and thus a stronger relative effect of evolution at low prey population sizes and low predation, this effect may be dampened as prey population sizes and predation increase. Finally, we found that the model and experiment show an overall higher evolutionary contribution with increasing trait difference, the magnitude of the evolutionary contribution is, however, much higher in the model than in our experiments (Figure 3). A possibility of the higher evolutionary contribution in the model is the longer time period, in which the population dynamics stabilize increasing the relative impact of frequency shifts in the prey population. The time used to estimate the contributions was much shorter in the experiment (8 days) than in the model (100 simulated days), and our model simulations showed a very strong shift in the abundance of prey species early in the simulation (Supplementary Figures S7 and S8 at time steps 10–20) that was not captured in the experiments.

Making robust predictions about when ecological and evolutionary dynamics influence each other on a time scale requires quantifying the ecological and evolutionary contributions and how they change with conditions, over time and space. Collecting such data is a considerable undertaking, especially for natural communities, but several studies have taken up the challenge (Coulson et al., 2005; Ezard et al., 2009; Govaert et al., 2021; Ozgul et al., 2010) and additional

approaches have been developed to test eco-evolutionary hypotheses when less data are available (Pantel & Becks, 2023). Laboratory studies remain an important tool for studying principles of eco-evolutionary dynamics, as they allow the direct manipulation of the ecological and/or evolutionary processes (Agashe et al., 2011; Bruijning et al., 2019; Turcotte et al., 2013) as we have done here. Such studies contribute to a mechanistic understanding of the underlying processes in eco-evolutionary dynamics by helping to determine when contemporary evolution should impact population dynamics within and among species. These approaches can be used, to predict where eco-evolutionary “hotspots” can occur in natural communities or how populations will respond to environmental changes.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

The data underlying this article are available at: <https://zenodo.org/records/11193317>.

Author contributions

Ruben Joseph Hermann (Conceptualization [equal], Data curation, Formal analysis [lead], Investigation, Methodology, Resources [equal], Visualization [lead], Writing—original draft, Writing—review & editing [equal]), Jelena Pantel (Formal analysis, Methodology [equal], Writing—original draft, Writing—review & editing [supporting]), Tom Revéillon (Formal analysis, Writing—original draft [supporting]), and Lutz Becks (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [lead], Investigation, Methodology [equal], Project administration [lead], Resources [equal], Supervision [lead], Validation [supporting], Writing—original draft, Writing—review & editing [equal])

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Conflicts of interest

There is no conflict of interest.

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