Rapid plastic shifts in body size precede and determine population growth

Jean P. Gibert[1*], Ze-Yi Han[1], Daniel J. Wieczynski[1], Andrea Yammine[1]

[1]Department of Biology, Duke University, Durham NC, USA

*Corresponding author: jean.gibert@duke.edu

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CONFLICTS OF INTERESTS

None

AUTHOR CONTRIBUTIONS

JPG conceived the study and designed the experimental work with AY. AY collected the experimental data. JPG analyzed the data with inputs from ZYH and DJW. JPG wrote the first version of the manuscript and all authors contributed to subsequent versions. All authors approved the final version for submission and agree to be held accountable for all information within.

DATA AVAILABILITY

All data and code is already available at https://github.com/JPGibert/Tetra_Rapid_BodySize_Shifts and will be archived in Zenodo and/or Dryad upon publication.

ABSTRACT

1. Body size is a fundamental trait linked to many ecological processes—from individuals to ecosystems. Although the effects of body size on metabolism are well-known, how body size influences, and is influenced by, population growth and density is less clear. Specifically, 1) whether body size, or population dynamics, more strongly influences the other, and, 2) whether observed changes in body size are due to plasticity or rapid evolutionary change, are not well understood.
2. Here, we address these two issues by experimentally tracking population density and mean body size in the protist *Tetrahymena pyriformis* as it grows from low density to carrying capacity. We then use state-of-the-art time series analyses to infer the direction, magnitude, and causality of the link between body size and ecological dynamics. Last, we fit two alternative dynamical models to our empirical time series to assess whether plasticity or rapid evolution better explains changes in mean body size.
3. Our results clearly indicate that changes in body size precede and determine changes in population density, not the other way around. We also show that a model assuming that size changes via plasticity more parsimoniously explains these observed coupled phenotypic and ecological dynamics than one that assumes rapid evolution drives changes in size.
4. Together these results suggest that rapid, plastic phenotypic change not only occurs well within ecological timescales but may even precede—and causally influence—ecological dynamics. Furthermore, large individuals may be favored and fuel high population growth rates when population density is low, but smaller individuals may be favored once populations reach carrying capacity and resources become scarcer. Thus, rapid plastic changes in functional traits may play a fundamental and currently unrecognized role in familiar ecological processes like logistic population growth.

Key Words: Eco-evolutionary Dynamics, Traits, Phenotypes, Phenotypic change, Ecological dynamics

INTRODUCTION

Because of its myriad ecological consequences—from individuals (e.g., (Glasheen & McMahon 1996; Hurlbert, Ballantyne IV & Powell 2008; Pavković-Lučić & Kekić 2013)) to ecosystems (e.g., (Brown *et al.* 2004; Riede *et al.* 2011; Trebilco *et al.* 2013))—body size is one of the most important functional traits. Body size controls energetic demands (Gillooly *et al.* 2001; Brown *et al.* 2004), diet breadth (Wasserman & Mitter 1978; Gravel *et al.* 2013), the strength of ecological interactions (Berlow *et al.* 2009), trophic cascades (DeLong *et al.* 2015), and food web structure (Brose *et al.* 2006; Riede *et al.* 2011; Gravel *et al.* 2013; Gibert & DeLong 2014), all of which have ecosystem-level consequences (Anderson-Teixeira, Vitousek & Brown 2008; Trebilco *et al.* 2013). Body size can fuel or limit population growth through well-known relationships with demographic parameters like carrying capacity (K) and the intrinsic growth rate (r) (Damuth 1981; Savage *et al.* 2004; DeLong *et al.* 2015). For example, smaller organisms typically reproduce faster and can reach higher carrying capacities than larger ones, but also have higher mortality rates, which leads to faster population turnover (e.g., (Huryn & Benke 2007)). As a consequence, body size often determines how populations grow, and hence, ecological dynamics.

However, ecological dynamics can themselves influence body size, although these effects are less well understood. For example, individual size is under physiological regulatory control (Davidowitz, Roff & Nijhout 2005; Chelini, Delong & Hebets 2019) and therefore responds to changes in resource levels (Marañón *et al.* 2013). While resource levels can vary independently of population abundance (Holt 2008; Fey, Gibert & Siepielski 2019; Nguyen, Lara-Gutiérrez & Stocker 2020), high abundance leads to crowding and increasing intra-specific competition (Gavina *et al.* 2018). Stronger competition in turn effectively reduces resource availability at the

individual level, which often results in stunted growth and smaller body sizes (e.g., (Vanni *et al.* 2009)). Consequently, while body size can, and often does, influence ecological dynamics, ecological dynamics can also influence body size. Which one more strongly influences the other, however, is not known.

Body size can change over time through multiple mechanisms, both plastic (David, Legout & Moreteau 2006; Ghosh, Testa & Shingleton 2013) and evolutionary (Hairston *et al.* 2005; DeLong *et al.* 2016), and body size is well-known to be under both natural and sexual selection (Preziosi & Fairbairn 2000; Chelini, Delong & Hebets 2019). For example, predation selects for smaller but faster growing prey in pitcher plant inquiline communities (terHorst, Miller & Levitan 2010) and for shorter developmental times that result in smaller individuals in mayflies (Peckarsky *et al.* 2001). Selection can act on traits rather quickly (Thompson 1998; Hairston *et al.* 2005), and rapid evolutionary change has been shown to influence ecological dynamics as they unfold (e.g., (Becks *et al.* 2012; Rudman *et al.* 2018; Schaffner *et al.* 2019)). However, ecological dynamics in turn influence the pace and direction of evolutionary change (e.g., (Cortez 2016; DeLong & Gibert 2016; Frickel, Sieber & Becks 2016; Gibert & Yeakel 2019)). In such eco-evolutionary feedback loops, selection imposed by ecological dynamics may influence body size, whose rapid change can in turn alter ecological dynamics. However, studying rapid evolutionary change in body size in unfeasible for most organisms and it is therefore unclear how pervasive these processes are in nature.

While body size can change through evolution, rapid or otherwise, it also can change within generations through plasticity (Lafuente, Duneau & Beldade 2018; Cameron *et al.* 2020). For example, organisms grow in size throughout ontogeny and the environment often influences ontogenetic trajectories, leading to variation in body size (Chelini, Delong & Hebets 2019),

while epigenetic DNA modifications can result in rapid phenotypic change from one generation to the next in response to shifts in biotic or abiotic conditions (e.g., maternal effects, (Roach & Wulff 1987; Galloway & Etterson 2007; Barbour & Gibert 2021)). Whether plastic change or rapid evolutionary responses more strongly contribute to observed changes in body size over short periods of time, however, is not well understood (e.g., (DeLong, Hanley & Vasseur 2014)). Among other reasons, this is because teasing apart plastic and evolutionary change can be challenging even when sufficiently long time series exist (Ellner, Geber & Hairston 2011). However, because body size mediates ecological interactions and processes, and can change on ecological timescales, it is important to understand, track, and predict such change.

Here, we address these gaps by answering the following questions: 1) do rapid changes in body size more strongly influence (and precede) population growth, or instead, does population growth more strongly influence (and precede) changes in body size?, and, 2) are observed changes in body size more consistent with a model of plasticity or rapid evolution? To address the first question, we track changes in the density and body size of multiple experimental populations of the protist *Tetrahymena pyriformis*, then use state-of-the art time series analysis to assess causality. In protists, we expect changes in body size to be at least partly caused by plasticity because reproduction (cell division) is tightly linked to ontogenetic changes in body size (cells grow then divide when a critical size is attained). However, *T. pyriformis* also reproduces extremely fast (4+ generations per day) and exhibits wide standing variation in body size (Wieczynski *et al.* 2021), so rapid evolutionary change is also possible. Therefore, to address our second question, we compare two alternative mathematical models: one that assumes only plasticity drives change in body size (plasticity model), and one that assumes only rapid evolution drives change in body size (eco-evolutionary model). We then fit the proposed models

139 to abundance and body size time series from our experiment and use model comparison to infer
140 what mechanism—plasticity or rapid evolution—most likely explains our data. Our results show
141 that rapid plastic changes in body size precede and determine changes in population density over
142 time, thus suggesting that plastic phenotypic change may be integral to ecological dynamics.
143
144 METHODS
145 *Microcosm experiments*
146 We tracked changes in abundance and body size in the protist *Tetrahymena pyriformis* for 14
147 days. To do so, we set up 6 experimental microcosms in 250 mL autoclaved borosilicate jars
148 filled with 200 mL of Carolina protist pellet media (1L of autoclaved DI water per pellet)
149 inoculated with pond bacteria from Duke Forest (Gate 9/Wilbur pond, Lat=36.02°, Long=-
150 78.99°, Durham, NC, Fig 1). Microcosms were initialized at densities of 10 ind/mL and were
151 incubated in temperature (22°C) and humidity-controlled (65% humidity) growth chambers
152 (Percival AL-22L2, Percival Scientific, Perry, Iowa) on a 12hr night/day cycle. Densities
153 (ind/mL) and trait dynamics were tracked daily through fluid imaging of 1 mL subsamples of
154 each microcosm through fluid imaging (Fig 1, FlowCam, Fluid Imaging Technologies,
155 Scarborough, ME, USA). In doing so, we imaged over 150k individual cells, thus giving our
156 experiment unparalleled insight into how density and body size changed together over the course
157 of this experiment. Last, neither water nor nutrients were replaced throughout the course of this
158 experiment.
159
160 *Time-series analysis*

To assess whether change in body size more strongly influenced changes in density, or vice versa, we used *Convergent Cross Mapping* (or CCM, (Sugihara *et al.* 2012; Rogers *et al.* 2020)) on the density and body size time series. CCM quantifies the degree to which one time series causally influences another one by estimating how much information of the one is contained in the other (Sugihara *et al.* 2012): if a variable X causally influences another variable Y, but Y does not influence X, we should expect Y to contain information about X, but not the other way around. CCM assesses this by quantifying whether variable X at time t can be used to predict variable Y at time t+1 for subsets of the time series of increasing length (the length of these subsets is called the 'library size'). If X more strongly influences changes in Y than the other way around, it also means Y responds to X more strongly than X responds to Y. If the effect of X on Y is causal, as opposed there being simple correlation, the ability to predict Y from X should increase with library size, while the error associated with that prediction should decline. If predictability that does not change with library size, there is correlation but not causation. If X causes Y, it also implies that change in X precedes change in Y, to which Y responds to. The analysis produces an estimate of how well one time series predicts the other (i.e., the *predictability* coefficient): the larger this value, the stronger the link—causal or correlative—between one time series and the other (Sugihara *et al.* 2012). To perform the analysis, we used R package multispatialCCM v1.0 (Clark *et al.* 2015), which allowed us to use replicated time series to increase power. Previous studies have shown that CCM allows for the inference of causation in different ecological systems and environmental conditions for which long enough time series exist (Sugihara *et al.* 2012; Clark *et al.* 2015; Karakoç, Clark & Chatzinotas 2020; Kondoh *et al.* 2020; Rogers *et al.* 2020).

184 *Mathematical models*

185 To assess whether observed changes in body size were more likely due to plasticity or rapid
186 evolution, we fitted two possible models that track change in the abundance and average body
187 size of a population, *N*, as it grows logistically towards a carrying capacity *K* with intrinsic
188 growth rate *r*. Following previous work (Abrams 1977; Abreu *et al.* 2019; Lax, Abreu & Gore
189 2020; Wieczynski *et al.* 2021), we included an additional mortality term in the ecological
190 dynamics, mN, to account for regular loss of individuals from the population (through
191 sampling). This additional mortality term has been shown to better describe the ecological
192 dynamics of a microbial microcosm with frequent sampling, like ours (Abreu *et al.* 2019; Lax,
193 Abreu & Gore 2020). Furthermore, we assumed that the intrinsic growth rate and the carrying
194 capacity were functions of body size, M, of the forms $r = aM^{\alpha}$ and $K = bM^{\gamma}$, following well-
195 known allometric relationships (Damuth 1981; Savage *et al.* 2004). Taken together, the
196 ecological baseline model was thus written as:

197 $$\frac{dN}{dt} = aM^{\alpha}\left(1 - \frac{N}{bM^{\gamma}}\right) - mN. \qquad \text{eq [1]}$$

198 To incorporate the coupling between changes in N and changes in M, we used two
199 alternative model formulations to track changes in M: the first assumed that only plastic change
200 in M could occur (plasticity model), the second assumed that only rapid evolutionary change in
201 M could occur (eco-evolutionary model). The plasticity model modifies the existing Supply-
202 Demand model for body size dynamics (DeLong 2012; DeLong & Walsh 2015) and assumes
203 that the rate of change in body size, $\frac{dM}{dt}$, increases with energy intake (supply), and decreases
204 with energy loss (demand). Following a recent study (DeLong 2020), we assumed that the supply
205 in a species growing logistically depends on the ratio of the carrying capacity, K, and the
206 abundance of the species, N, times a conversion rate constant *e*, that converts the supply to units

of M. When the population is small, the supply approaches infinity, and it approaches e when N grows to K. Following previous studies (DeLong, Hanley & Vasseur 2014), we also assumed that the demand was the metabolic cost of the organism, which is known to increase allometrically with body size, as cM^{δ}. Taken together, the equation controlling changes in body size M was:

$$\frac{dM}{dt} = \frac{eK}{N} - cM^{\delta}. \qquad \text{eq [2]}$$

For the evolutionary model, we followed previous studies on eco-evolutionary dynamics (e.g., (Abrams, Harada & Matsuda 1993; Abrams & Matsuda 1997; Jones *et al.* 2009; Ellner & Becks 2010; Jones & Gomulkiewicz 2012; Cortez 2016; Cortez 2018)) to incorporate evolution in M at a rate that equals the product of the total amount of additive heritable variation in body size (*i.e.*, the product of the total phenotypic variance, σ^2, and the narrow sense heritability, h^2), and the selection gradient (*i.e.,* the change in fitness, *F*, with respect to a change in *M*, which represents the strength of selection acting on *M*). Taken together, the equation controlling the change in M over time under these assumptions was:

$$\frac{dM}{dt} = \sigma^2 h^2 \frac{\partial F(M)}{\partial M}, \qquad \text{eq [3]}$$

were $F(M) = \frac{1}{N}\frac{dN}{dt}$ (Lande 1976; Schreiber, Bürger & Bolnick 2011).

Model fitting, parameter uncertainty, and model selection

To assess how well the models in Eqs 1-3 reproduced empirical body size and density dynamics from experimental microcosms, we fitted the models to the *T. pyriformis* time series using R package FME v1.3.6.1 (Soetaert & Petzoldt 2010). The allometric parameters a and b for r and K respectively, should not differ between the two models, so they were optimized during preliminary model fitting, then set constant for both models during final model fitting and

230 estimation of parameter uncertainty (Table 1). We assumed that the scaling parameter of the
231 metabolic cost, δ, equaled 1, as has been shown to be the case for protists (DeLong *et al.* 2010),
232 despite it being closer to ¾ for metazoans (Gillooly *et al.* 2001; Brown *et al.* 2004; DeLong *et al.*
233 2010). Fitting of ordinary differential equations using package FME relies on the Levenberg-
234 Marquardt algorithm for parameter estimation, and a Metropolis-Hastings MCMC procedure for
235 estimation of parameter uncertainty (Soetaert & Petzoldt 2010). Model comparison was done
236 using Akaike Information Criterion (Burnham & Anderson 2002) as:

237 $$AIC_i = 2k_i + n_N \ln(SSE_{i,N}) + n_M \ln(SSE_{i,M}) \quad , \qquad \text{eq[4]}$$

238 Where k_i is the number of parameters of model i, n_N is the number of datapoints considered in
239 the density time series, n_M the number of datapoints considered in the body size time series,
240 $SSE_{i,N}$ the sum of squared errors of model i with respect to the density time series, and $SSE_{i,M}$ is
241 the sum of squared errors of model i with respect to the body size time series. All data and code
242 are available at https://github.com/JPGibert/Tetra_Rapid_BodySize_Shifts.
243

244 RESULTS

245 Tetrahymena abundances increased to carrying capacity roughly 4 days after microcosms where
246 initialized (Fig 2a). Body size increased over the first day, then decreased continuously for 12-13
247 days (Fig 2b). Results from CCM analysis showed large predictability values for densities using
248 changes in body size as a predictor, but smaller predictability values for body size using densities
249 as the predictor (Fig 2c). Moreover, the stronger effect of body size on densities was found to be
250 causal (sharp increase in predictability with library size and decrease in standard deviation, Fig
251 2c), but that of densities on body size is either not, or only weakly causal (slow convergence of
252 predictability and little change in standard deviation, Fig 2c). This indicates that changes in body

size influence density changes over time more strongly than density influences body size, and because size predicts density but not the other way around, it also indicates that changes in body size precede changes in population density.

Both models (plasticity and eco-evolutionary) fit the empirical data remarkably well (Fig 3a-d, Table 1). MCMC chains converged for all fitted parameters (Appendix Fig S1, S2) and model parameters were identifiable and free of correlations for all but three parameter pairs across the two models (α and *m,* and c and e in the plasticity model, and γ and m in the eco-evo model, Fig S3, S4). The plasticity model did a slightly better job at fitting the abundance data than the eco-evolutionary model (notice departures of eco-evo model during initial dynamics, Fig 3e), and both did a good job at fitting the body size data (Fig 3f). Both models arrived at very similar fitted values for the three model parameters they had in common (Table 1), indicating good agreement between the two. Consistent with existing literature, both models identified the scaling of K and M (γ), as a negative number close to -¾ (Table 1). However, both models predicted the scaling between r and M (α) as positive and close to 1 (Table 1) while the literature pins that value—across species—to -¼ (Savage *et al.* 2004). Last, model selection through AIC indicated that the plasticity model was the most parsimonious of the two (Table 1), likely indicating that observed coupled density and body size dynamics were mostly driven by plasticity.

DISCUSSION

Because of the myriad ecological consequences of body size (e.g. (Gillooly *et al.* 2001; Brown *et al.* 2004; DeLong *et al.* 2010)), it is important to understand how changes in body size—plastic or evolutionary—may influence or be influenced by ecological dynamics. We show

that changes in body size more strongly influence changes in densities than the other way around (Fig 2), and that a model that accounts for rapid plastic change in body size provides the most parsimonious explanation for the observed paired ecological and body size dynamics (Fig 3, Table 1). While previous studies found that phenotypic change often lags behind ecological rates of change (e.g., (DeLong *et al.* 2016)), our results clearly show that phenotypic change not only occurs well within ecological timescales, but may even precede—and causally influence—those dynamics (Fig 2c). Our results thus emphasize the need to further study and understand the ecological consequences of rapid plastic phenotypic change (Yamamichi, Yoshida & Sasaki 2011; Tariel, Plénet & Luquet 2020), as plasticity may play a crucial role in determining the fate of networks of species interactions in a warming world (Barbour & Gibert 2021; Jacob & Legrand 2021).

Cells can enter and leave the cell division cycle depending on cell size and nutrient availability (Baserga 1968; Fukada *et al.* 2007). As the *T. pyriformis* population reaches carrying capacity, low resource levels likely cue cells into existing the cell division cycle, in turn resulting in stunted growth (cells grow to reproduce (Baserga 1968)) and reduced average body sizes. Observed total standing phenotypic variation is thus likely largely non-heritable, as also suggested in a recent study (Jacob & Legrand 2021). Surprisingly, the eco-evolutionary model itself supports this idea, as it indicates that the total amount of standing heritable variation in body size is rather small ($\sigma^2 h^2 = 0.992$, Table 1). For comparison, the total amount of phenotypic variation (heritable or not) in our initial population was 94 (units of μm^3 squared), so the heritable portion of that total phenotypic variation would be of the order of ~1%, in agreement with our model selection results. Shifts in *T. pyriformis* phenotype have also been

298 shown to occur differentially across environmental conditions (DeLong *et al.* 2017; Weber de
299 Melo *et al.* 2020), again suggesting the occurrence of plasticity.
300 While the rapid evolution model is less parsimonious, our results do not rule out the
301 possibility of rapid evolution. Indeed, plastic change often precedes evolutionary change and
302 occurs mostly along the axes of variation with the largest amount of heritable variation (the
303 classic evolutionary 'path of least resistance' (Lande 1976; Lande 1979; Lande & Arnold 1983)),
304 thus setting the stage for evolution to occur along those axes (Noble, Radersma & Uller 2019). A
305 similar process may be at play here. Indeed, despite low heritability, the less parsimonious eco-
306 evolutionary model suggests that short term selection imposed by density-dependence may be
307 strong enough to consistently shift body size over time, which in turn influences population
308 dynamics (Fig 2). Our own data indicate that *T. pyriformis* reproduces at a rate of 3.5-4 new
309 individuals per individual per day. This extremely fast population growth may eventually allow
310 for evolutionary change in body size—if selection is strong enough, as heritability is low, but not
311 nil—even if it likely lags behind plastic change (Chevin, Lande & Mace 2010; Fox *et al.* 2019).
312 Interestingly, neither water nor nutrients were replenished during our experiment; both
313 were limited and were likely consistently lost from the system over time through sampling. This
314 nutrient impoverishment should lead to a strong decline in K. However, a strong decline in K
315 was not only not observed, but the most parsimonious model suggests that such a decline either
316 does not occur, or does so only weakly (Fig 3). Because carrying capacity declines with body
317 size (Damuth 1981), a rapid decline in nutrient concentrations may thus select for smaller body
318 size (Vanni *et al.* 2009), which could in turn counter the effect of negative density-dependence
319 overall. These results suggest a way in which rapid plastic change in body size may allow

organisms to regulate population growth and density-dependent factors, even as nutrients become increasingly limited.

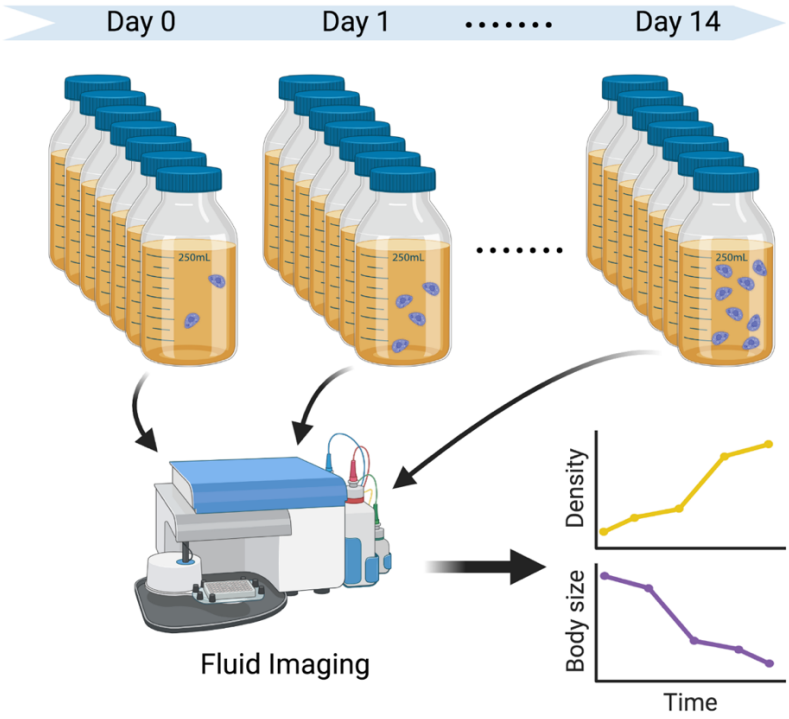
Last, both the eco-evolutionary and plasticity models predicted a positive relationship between body size and the intrinsic growth rate (Fig 4a). This result stands in contrast to empirical data across species, which show lower intrinsic growth rates for larger organisms (or $\alpha < 0$, REFS). Within species, however, larger individuals typically reproduce more and die at lower rates (Peters 1983), leading to higher *r* due to lower mortality and higher reproduction (Kingsolver & Huey 2008). This positive relationship between body size and the demographic processes that fuel intrinsic growth rates are well understood within species (Peters 1983; Kingsolver & Huey 2008), emphasizing how inter-species and intra-species body size scaling may often differ (Rall *et al.* 2012).

Overall, our study shows that rapid plastic change in phenotypes more strongly influences ecological dynamics than the other way around, suggesting that rapid changes in body size are likely integral to the process of population growth itself. This study sheds light on the ecological and evolutionary constraints that regulate population growth and provides new insights about how organisms cope with the negative effects of density-dependence.

Table 1: Parameter estimates and uncertainty for both fitted models.

		r scaling with body size (α)	K scaling with body size (γ)	Mortality rate (m)	Supply-Demand conversion parameter (e)	Supply-Demand loss parameter (c)	Heritable Variation ($\sigma^2 h^2$)		Allometric Intercept for r (a)	Allometric Intercept for K (b)	**AIC (ΔAIC)**
(a) Plasticity Model	Estimate	-0.721	1.022	0.969	24.295	0.0873	—	Set value	~10^{-4}	~10^{6}	**3246.97 (0)**
	95% Credible Interval	(-0.735, -0.720)	(1.010, 1.023)	(0.770, 0.991)	(18.400, 26.714)	(0.077, 0.091)	—	Post-Optimization	$2.2*10^{-4}$	$8.2*10^{6}$	
(b) Eco-Evo Model	Estimate	-0.748	1.056	0.897	—	—	0.992	Initial value	As above	As above	**3287.66 (+40.69)**
	95% Credible Interval	(-0.753, -0.743)	(1.048, 1.064)	(0.770, 1.026)	—	—	(0.825, 1.193)	Post-Optimization	As above	As above	

346 FIGURES



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348 Fig 1: Depiction of experimental procedure: microcosms were initialized at 10ind/mL and each

349 microcosm was replicated six times. Population density and cell size were recorded daily for 14

350 days thereafter using fluid imaging.

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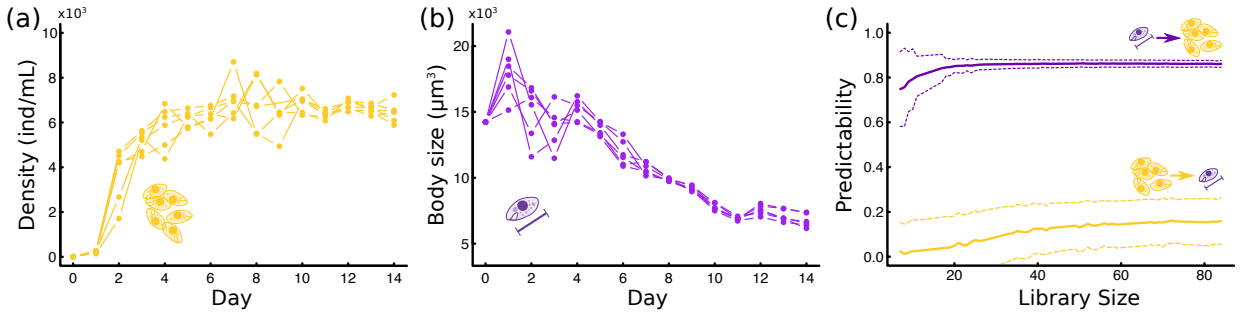

Fig 2: (a) Time series of Tetrahymena density. (b) Time series of mean Tetrahymena body size. (c) Convergent Cross Mapping predictability plot against library size (i.e., length of the time series used for analysis), using body size to predict density (purple) or density to predict body size (yellow), repeated 1000 times. Solid line indicates mean values and dashed lines indicate standard deviation of the mean.

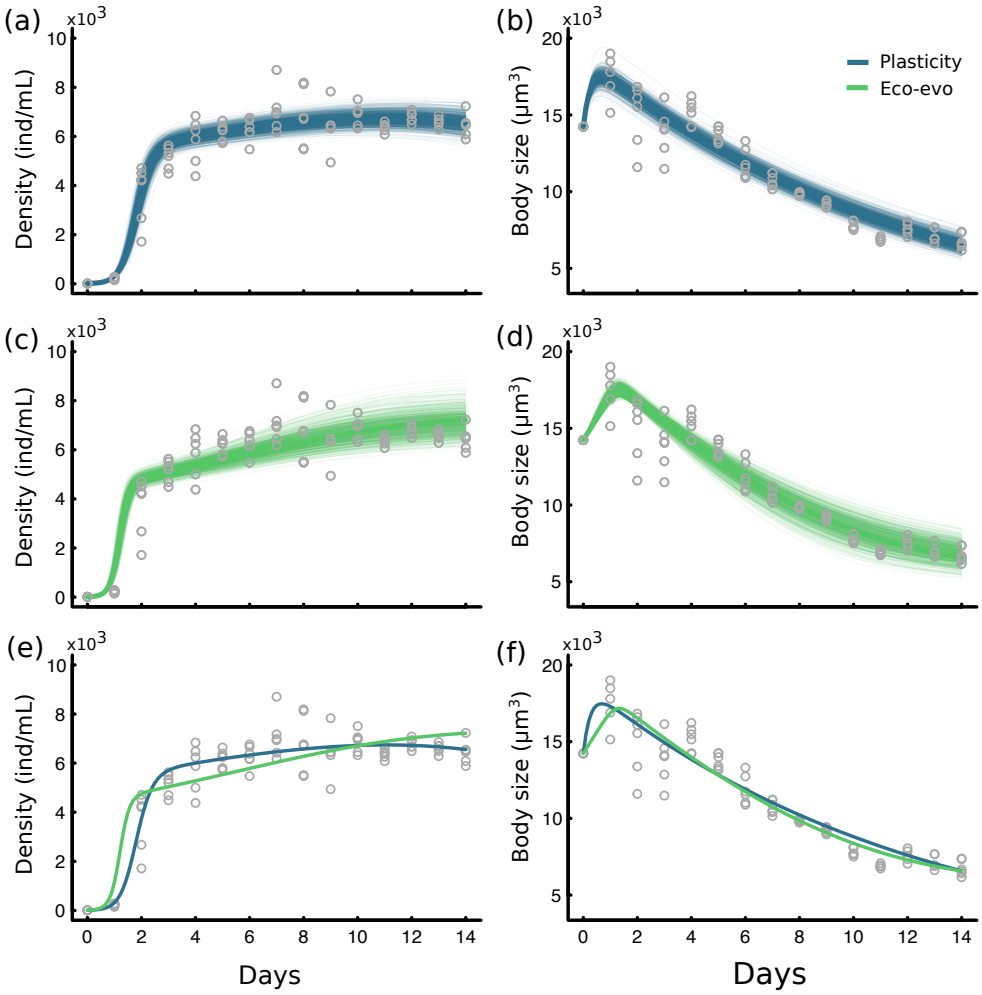

Fig 3: (a) Density data (grey points) and plasticity model fit (solid blue). Uncertainty is represented as 700 model predictions whose parameters were sampled from posterior distributions for each model parameter, estimated during model fitting (transparent blue, Table 1). (b) As in (a), but for body size data. (c–d) As in (a–b) but for the eco-evolutionary model fit. (e) Comparison of the plasticity (blue) and evo-evolutionary (green) model fits to the density data. The plasticity model fits the data slightly better, especially at the beginning of the experiment. (f) As in (e) but for body size data. The eco-evolutionary model fits the data slightly better at first, although both models fit well after day 2.

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