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Research article

Environment- and system-specific interactions between population and trait dynamics

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Understanding population dynamics across environmental contexts is essential to predict ecosystem stability. Functional traits influence population growth, which can in turn influence the traits and thus create feedbacks between population and trait dynamics. Here, by augmenting models of population and trait change with trait and population information, respectively, we demonstrate that such a feedback occurred in an autotrophic but not in a heterotrophic microbial system. Furthermore, exposure to a pollutant disrupted this feedback: trait change and population growth ceased to interact in either system. Finally, when the models augmented with trait/population information were superior, the improvement was substantial, showing that density–trait feedbacks are potentially large, even though they are system- and environment-specific.

Keywords: density dependence, feedbacks, functional traits, global change ecology, microbial ecology, population growth

Introduction

Forecasting ecological change requires an understanding of how population density changes over time. These changes typically depend on population density itself, a process referred to as density-dependent population growth. This density-dependence is typically negative, meaning that growth is maximal at low density, and lower at high density. Since the classic experiments by Gause (1934) and Gill (1972), there has been abundant evidence of negative density-dependence across biological systems (Sibly et al. 2005, Hodgson et al. 2017, Barraquand et al. 2018, Broekman et al. 2019).

Beyond density, functional traits have also been proposed as essential predictors of population growth (Violle et al. 2007, Litchman and Klausmeier 2008, Ozgul et al. 2012, Edwards et al. 2013, Pérez-Ramos et al. 2019). One challenge when using traits to predict population dynamics is that traits themselves change over time. Rapid trait change is widespread (Ellner et al. 2011) and, while trait change caused by environmental change is arguably studied more often (Grainger and Levine 2021), traits can also change as a result of population density (Gibert et al. 2022). This can happen

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when population density is strongly-connected to demographic descriptors (e.g. size structure, Gillooly et al. 2001, Brown et al. 2004, DeLong et al. 2015, Wieczynski et al. 2021). In addition, just as density determines density change (i.e. population growth), the trait value itself can determine trait change. This becomes clear when considering body size, often used as a master trait predicting population dynamics (Litchman and Klausmeier 2008). Energetic and physiological costs associated with body size limit an individual's growth in much the same way as population size limits population growth (Haldane 1926, Schmidt-Nielsen 1984, Frank 2009). Two candidate predictors of trait change therefore stand out: population density and the trait value itself. Both population growth and trait change therefore represent a dynamical system of coupled variables. This coupling can create feedbacks, which are therefore important to identify if we are to predict the fate of populations subject to perturbations.

One way to formalize this interdependence of population and trait dynamics is as follows (Patel et al. 2018):

$$\begin{aligned} \frac{\mathrm{d}N}{N\mathrm{d}t} &= f\left(N,T\right), \\ \frac{\mathrm{d}T}{\mathrm{d}t} &= g\left(N,T\right), \end{aligned} \tag{1}$$

where N and T are the population density and mean trait value across individuals in a population, and f and g are functions describing the effects of these two predictors on the dynamics of population density and traits. Note that this framework is general; the functions f and g could capture a variety of biological mechanisms, including resource competition, and behavioural, epigenetic or genetic change. In the context of Eq. 1, the feedback between population and trait dynamics is captured by the dependence of f on T and of g on N. If either dependence is zero, feedback is lost.

Environmental conditions can affect both population growth and functional traits. For example, in phytoplankton, modest temperature shifts increase growth (Gillooly et al. 2001, Brown et al. 2004, Kremer et al. 2017) while also favouring smaller cell size (Fernández-González and Marañón 2021). Furthermore, interactions between growth and traits can also be environment-dependent, as environmental factors such as temperature have been shown to modulate how traits affect growth (Gillooly et al. 2001, Brown et al. 2004, Kremer et al. 2017). One may therefore expect that feedbacks will be environment-dependent.

Additionally, the existence and strengths of trait–growth relationships are also expected to depend on the model system and on the traits considered. In systems where the observed traits have an unequivocal contribution to energy or resource acquisition (i.e. performance traits, Violle et al. 2007), these relationships are expected to be stronger. Prime examples of such systems are leaf architecture or pigmentation in primary producer systems, as these traits have a direct link to light and carbon acquisition and therefore likely affect population growth (Chin et al. 2023). In such systems, trait information may be essential to correctly predict population dynamics (Stomp et al. 2004) and it is likely that larger changes to the environment will only increase the importance of trait information.

Here, we investigate the reciprocal links between population and trait dynamics in both a heterotrophic (six ciliate strains) and an autotrophic microbial system (four cyanobacteria strains) across four environmental conditions. To this end, we performed microcosm experiments where we monitored population densities and trait values over time. Given these data, we first asked whether augmenting a model of density-dependence with traits improved predictions of population growth and, similarly, whether augmenting a model of trait-dependence with population density improved predictions of trait change. Finally, we asked whether the contributions of traits and density to population and trait dynamics, respectively, depend on the environmental context or differ between/within the two model systems.

Augmenting growth models with trait data, and trait change models with density data, improved model performance for cyanobacteria but less so for ciliates. These improvements were most prominent in unpolluted media and, in cases when augmenting the models increased performance, the increase in prediction accuracy was substantial. Overall, our results suggest that the feedbacks between growth and trait changes are not a general feature but are system and environment-specific.

Material and methods

Study systems

We aimed to evaluate our research question at three levels of biological organisation – system, subsystem and strain – and test whether our findings were general or subject/context dependent. To this end, we used both ciliates and cyanobacteria as model organisms. Both study systems harbour considerable diversity, as ciliates span several taxonomic orders and the polyphyletic *Synechoccocus* has a similar order-level diversity, while, however, being less well-defined phylogenetically due to the frequency of horizontal gene transfer events (Zhaxybayeva et al. 2006, Dvořák et al. 2015, Salazar et al. 2020). These two systems were further divided into subsystems: *Synechoccocus* strains were selected from two different clades that characterise their pigmentation and biogeography (Stomp et al. 2007, Sohm et al. 2016, Grébert et al. 2018) and the ciliate strains were selected from three genera. Finally, within each subsystem, we used two different clonally-reproducing strains.

We used unicellular, clonally-reproducing strains from the two microbial model systems: six strains from four ciliate genera and four strains from two clades of the picocyanobacteria genus *Synechococcus* (Farrant et al. 2016, Sohm et al. 2016, Grébert et al. 2018). The ciliate genera used are globally-distributed freshwater mixotrophs and represent an important ecological link between primary producers and higher

trophic levels (Lu et al. 2021, Weisse and Montagnes 2022). The selected ciliate strains are diverse in their functional traits and demography – e.g. *Spirostomum* is a large, elongate, and slow-growing while *Tetrahymena* is small, more rounded and faster-growing. *Synechococcus* makes up a substantial proportion of global phytoplankton biomass and photosynthesis (Dvořák et al. 2015). The marine *Synechococcus* strains used were purchased from the Roscoff Culture Collection (Supporting information), while the ciliate strains were isolated from cultures from several collections and institutions (Supporting information).

We also grew all strains under a range of environmental conditions, represented here by temperature and a pollutant – both commonly-encountered environmental pressures in natural systems. Specifically, we consider an 'altered' environment to have increased temperature, increased concentration of a pollutant, or both. Temperature change is ubiquitously-relevant as anthropogenically-driven climate change continues to intensify. For the pollutant, we used atrazine, which is present in many aquatic ecosystems via agricultural runoff. Atrazine represents a broad class of herbicides that act via the inhibition of photosynthesis, and also induces oxidative stress in heterotrophic organisms (e.g. ciliates), reducing their fitness (Shim et al. 2022). Control conditions are hereafter indicated by 'C', temperature changes by 'T', atrazine changes by 'A', and the combined atrazine and temperature changes by 'AT'.

We grew the strains in monoculture until the population growth stabilised, and calculated growth and trait change through time by measuring the population densities and trait values at frequent intervals (Table 1, Supporting information).

Experimental setup

For the ciliate system, the microcosms consisted of 250 ml square bottles with vented caps (DURAN) containing 100 ml nutrient medium, inoculated with enough cells to initiate population growth. We obtained the required cell density by injecting a species-specific volume of 1-week old preculture into new medium (0.1, 5 and 10 ml for *Tetrahymena thermophila*, *Loxocephalus* sp. and *Spirostomum teres*, respectively). The different inoculation densities were necessary because growth dynamics vary greatly among the ciliate strains used the different starting densities enabled us to avoid extended lag phases for the slower-growing strains (e.g. *Spirostomum*) while still observing most of the population growth curves. The microcosms were kept in an incubator with a 10:14 h light/dark cycle and the nutrient medium consisted of Chalkey's solution supplemented with crushed protist pellets (Carolina biological supply; 0.55 g $^{l-1}$), filtered through a 0.22 µm filter system (BT50 500 ml) to remove all particulate matter and consecutively bacterized with *Bacillus brevis*, *Brevibacillus subtilis* and *Serratia fonticola*. Following bacterization, the medium was incubated for two days at 20°C on a shaker to allow the bacteria to grow before ciliates were added. During the experiment, we replaced 20% of the medium every third day by replacing 4 ml of the culture with 4 ml of 5× concentrated unbacterised nutrient medium with the appropriate atrazine concentration for the culture.

Table 1. Experimental design of the two model systems, indicating the experiment duration, the number of strains used, the temperature of the warming treatments in degrees Celsius, and the concentration of the pollutant (atrazine). All combinations of pollution and temperature were included in the experiment design. Treatments in bold indicate the reference conditions.

Model system	Exp. duration (days)	No. of strains	Temperature (°C)	Atrazine (mg l^{-1})
Ciliates	37	6	**22**, 24	**0**, 20
Cyanobacteria	10	4	**22**, 24	**0**, 0.1

For the cyanobacteria system, the microcosms consisted of 6 ml six-well plates (Sarstedt standard flat six well plate, 83.3920) of PCRS-11 Red Sea medium (Rippka et al. 2000), inoculated at 5000 cells ml^{-1} (the lowest feasible inoculation density while avoiding stochastic population crashes when the cultures were first added to the microcosms) inside temperature-controlled incubators (Lovibond Thermostatic Cabinet). They were cultured in white light (6500K LedAquaristik Sky Bar) in a 12:12 h light/dark cycle. The six-well plates were constantly mixed 150 RPM with a VWR mini shaker.

The growth media of each microcosm was adjusted to include the appropriate amount of atrazine and microcosms were kept at a constant temperature throughout (Table 1). All sampling was undertaken in sterile environments to prevent contamination.

Experimental sampling procedure

Population densities and traits were monitored using procedures specifically designed for each system.

Ciliate microcosms were sampled by digital dark-field imaging using an updated version of the method described by Pennekamp and Schtickzelle (2013). For each microcosm, at each sample time, we took a series of pictures of an 810 µl sub-sample using a Sony A9 camera equipped with an FE 90 mm F2.8 Macro G OSS lens and a dark-field approach (indirect light and black background). Each series consisted of 10 second burst shots at 10 fps in grey scale (other settings: 1/160s, F11, ISO 6400), resulting in 100 pictures per sample. We then proceeded with automated image analysis using Fiji (Schindelin et al. 2012, Van Rossum 2022) to count, track, and characterize the traits of all moving particles i.e. cell size (area), cell shape (aspect ratio), movement speed, and movement linearity in the sample (Pennekamp et al. 2014). The traits were population averages of cell size, cell aspect ratio, linearity of the cell's movement, and movement speed. Cell morphology influences the maintenance requirement and resource uptake rates while the motility traits affect the encounter rate of ciliates for their bacterial resources (Kiørboe 2011, Kempes et al. 2017).

Cyanobacteria microcosms were sampled using a flow cytometer (Guava easyCyte 12HT) that measures cell densities and trait values using several channels, which correspond to specific excitation and fluorescence combinations by lasers and detectors. The flow cytometer channels correspond

approximately to cell size and amount of three photosynthetic pigments present in *Synechococcus*: chlorophyll-a, phycocyanin and phycoerythrin. At each sampling time, 57 µl of distilled water was added to counteract evaporation. Then, 200 µl of the 6 ml microcosm was removed and replaced with 200 µl of fresh medium. This 200 µl sample of the culture was diluted with distilled water to be between 50 and 500 cells μl^{-1}, the density range for which the flow cytometer gives accurate measurements, and 200 µl of the appropriately-diluted sample was put into a 96-well plate and processed by the flow cytometer. The flow cytometer then measures 1000 cells from each well to determine the cell density and measure the trait values. The traits were population averages of several flow cytometer channels, indicative of cell size and amounts of chlorophyll-a, phycocyanin and phycoerythrin. Cell size again influences resource uptake and maintenance and the photosynthetic pigments influence the light absorption (Stomp et al. 2007, Marañón 2015). Sampled debris, dead cells, and doublets were removed from the analysed data using the 'CyanoFilter' and 'PeacoQC' packages in R ver. 2.3.1 (Olusoji et al. 2021, Emmaneel et al. 2022, www.r-project.org).

Analyses

The objectives of our analyses were to investigate if a model using both density and trait data predicted population per capita growth rate (hereafter 'growth', γ) better than a model using density data only. Similarly, we tested if a model using trait and density data predicted trait change (hereafter τ) better than a model using only trait data.

Since there were multiple correlated traits, we first summarised the traits into a single aggregate trait (hereafter 'trait') using a principal component analysis, PCA, per strain and treatment. This eliminated the impact of trait covariance and collinearity, and ensured that trait information was represented by a single variable, as was population density. We used only the first component of this PCA to represent the traits, which always contains the largest amount of explained variance. We performed identical supplementary analyses using only cell size to confirm whether the results were consistent without aggregating all the traits (Supporting information).

We calculated, for all combinations of strains and environmental conditions, the growth rate at each time point, $\gamma_t = \Delta^{-1}\log(N_{t+\Delta}/N_t)$, where N_t is population density at time t and Δ is the time between consecutive sampling times. We then fitted two linear models, for all combinations of strains and environmental conditions, of γ_t against N_t:

$$\gamma_t = \beta_0 + \beta_1 N_t, \tag{2}$$

$$\gamma_t = \beta_0 + \beta_1 N_t + \beta_2 T_t, \tag{3}$$

where N_t (density, continuous) and T_t (trait value, continuous) are predictors, and the β_i are regression coefficients. The first model, Eq. 2, is the standard model of linear, density-dependent growth. The second model, Eq. 3, is the model augmented with trait data.

Similarly, for all combinations of strains and environmental conditions, we calculated the trait change at each time point τ_t, as $\tau_t = \Delta^{-1}(T_{t+\Delta} - T_t)$, where T_t is the trait value, and Δ is again the time between consecutive sampling times. We again fitted two models, but now using trait change as the response variable:

$$\tau_t = \beta_0 + \beta_1 T_t, \tag{4}$$

$$\tau_t = \beta_0 + \beta_1 T_t + \beta_2 N_t, \tag{5}$$

where N_t (density, continuous) and T_t (trait value, continuous) are predictors, and the β_i are regression coefficients. Again, Eq. 5 is the augmented version of Eq. 4.

With these models, we evaluated the augmented models in terms of their parsimoniousness, prediction accuracy and likelihood. Firstly, we compared the Akaike weights computed from AICc (Akaike information criterion corrected for small sample size, Burnham and Anderson 2004) of the fitted models to determine how relatively parsimonious the augmented model was (Burnham and Anderson 2004, Wagenmakers and Farrell 2004). Secondly, we compared the change in the total prediction error of the augmented model relative to the single model. Lastly, because the growth (trait change) is calculated using the density (trait value), there is a possibility that state-dependence is induced erroneously, as the response and predictor are not independent (Dennis and Taper 1994, Corani and Gatto 2007, Detto et al. 2019). To overcome this, we performed a parametric bootstrap likelihood ratio (PBLR) test with 5000 simulations for each augmented model (i.e. for every strain, treatment and response variable combination) to calculate the probability that the augmented model was superior to both the single-predictor model as well as a null model without any state-dependence (i.e. constant growth/trait change).

The data was analysed and figures produced using the 'tidyverse', 'Hmisc', 'ggpubr', and 'ggh4x' packages in R ver. 2.3.1 (Wickham et al. 2019, Harrell and Harrell 2019, Kassambara 2023, Van Den Brand 2023, www.r-project.org).

Results

Population growth and trait change

Augmenting the growth models with trait data (Eq. 3) did not generally improve predictions in either system (Fig. 1a–d). Augmenting the trait change models with density data (Eq. 5), however, did improve predictions specifically for many of the cyanobacterial strains (Fig. 1e–h).

Models of per capita growth as a function of density only (Eq. 2) demonstrated mostly negative density-dependence in both systems (Supporting information), except in some of the polluted cyanobacteria cultures, where growth was very

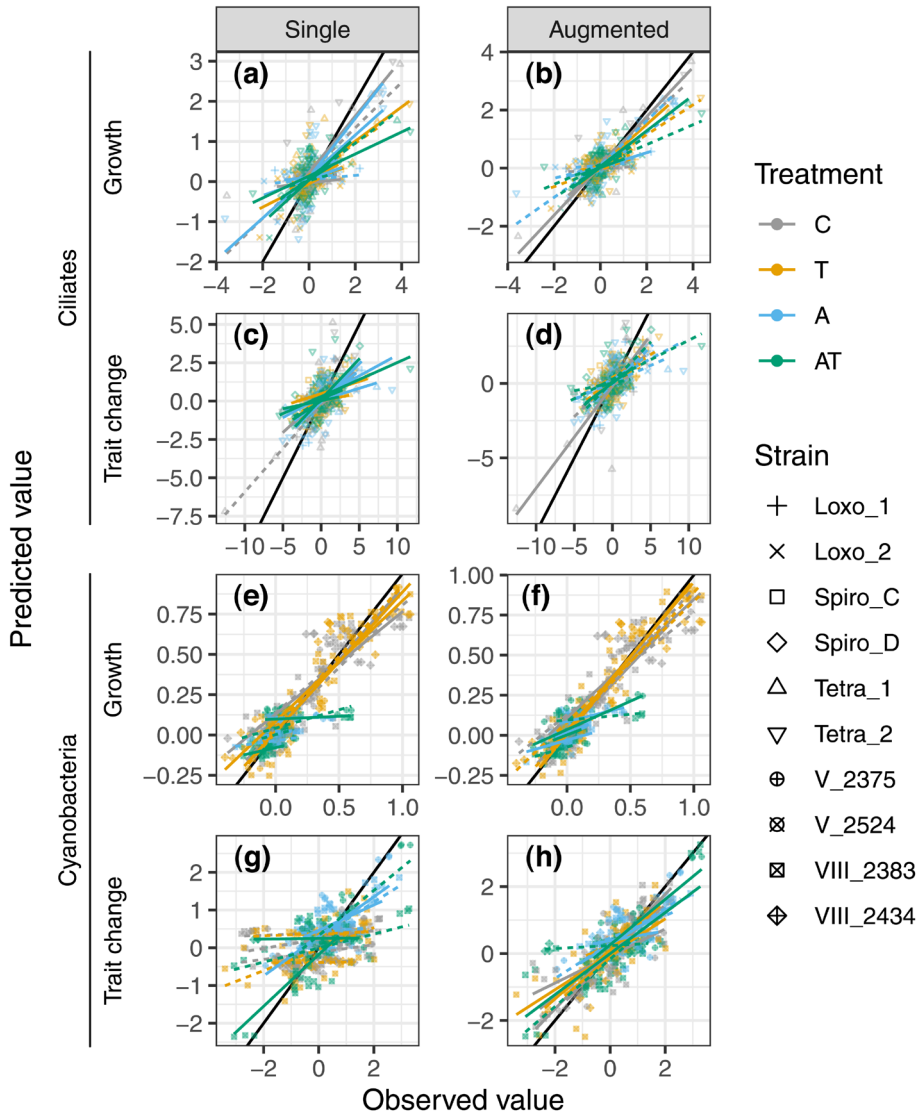

Figure 1. Including trait data did not generally improve predictions of population growth (a, b, e, f), while including density data did improve predictions of trait change in cyanobacteria (c, d, g, h). Observed (x-axis) and predicted (y-axis) population growth and trait change, including either one (left column) or both predictors (right column), for various strains (point types) of ciliates (a–d) and cyanobacteria (e–h) and across environmental conditions (colours). Dashed and solid lines indicate that the regression was more supported on the basis of AICc (i.e. if a line is solid for in the augmented panel, then, for that strain and condition, the augmented model was more supported than the single model, and vice versa).

low and unrelated to density. Models of trait change as a function of traits only (Eq. 4) showed that trait change was trait-dependent in both systems (Supporting information). Trait dependence was consistently negative in ciliates and the magnitude of trait dependence varied little across treatments: traits had the tendency to increase less when at a larger value. In cyanobacteria, the trait change depended less consistently on the trait value itself. The trait-dependence of trait change was more evident in the ciliate system.

Trait aggregation

We created the aggregate trait by using only the first component of a principal component analysis (PCA) fitted on the trait data. This captured the majority of the trait information for both the ciliates and the cyanobacteria (Fig. 2a–b). Trait aggregation was more consistent for the cyanobacteria strains, with the majority of strain–treatment combinations being loaded in the same direction (Fig. 2c–d). The traits of the ciliate strains were more frequently loaded in opposite directions, meaning that an increase in the aggregate trait indicates that some traits are increasing while others decrease.

Model parsimony and prediction accuracy

In the ciliate system, using the augmented models generally did not improve predictions of growth/trait change (Fig. 3a, c). For predictions of growth, the augmented model was only

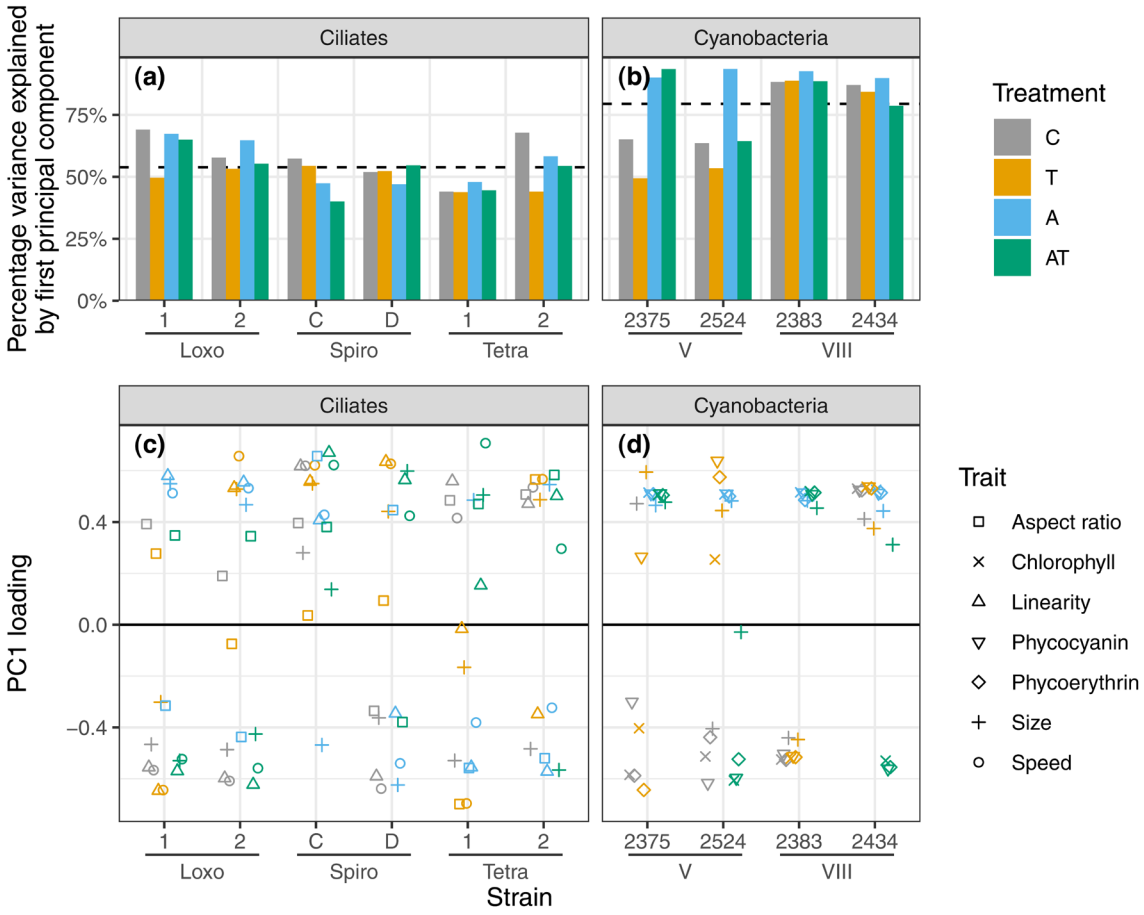

Figure 2. Amount of variance explained (a–b) and individual trait loadings (c–d) of the first principal component (aggregate trait) by treatment (colour) and strain (x-axis). In (a) and (b), the horizontal dashed lines indicate the mean value within the system. In (c) and (d), for a given strain and treatment, if individual traits (point shapes) are loaded in the same direction (positive or negative), then changes in the aggregate trait indicate that the individual traits are changing in the same direction. The absolute direction that individual traits are loaded on is not meaningful.

more likely in a few cases (particularly *Tetrahymena* strains and *Loxocephalus 1*). Predictions of trait change with the augmented model were even less likely to outperform the trait-only model.

In the cyanobacteria system, for treatments without atrazine, the augmented models were generally better at predicting both population growth and trait change (Fig. 2b, d). For predictions of population growth, the augmented model was generally likely to best describe the data, with some exceptions in which the added trait data provided no benefit to predictions. For predictions of trait change, the augmented model was more likely to be better, with only some cases in the treatments with atrazine where it failed to improve the predictive ability. Notably, in the cases where the augmented models fitted the cyanobacteria data less well, the models using a single predictor were similarly poorly-fitting (Supporting information).

For both systems, the probability that the augmented model fitted best substantially improved the prediction accuracy (Fig. 3). Thus, cases in which the augmented model was much better fitting (e.g. predictions of growth in *Tetrahymena 1* in control conditions, or in cyanobacteria strains in control or heated conditions), predictions of growth/trait change were much more accurate. Model parsimony and accuracy were similar for both the cyanobacteria and ciliate systems when using only size, rather than the aggregated trait (Supporting information).

PBLR of augmented model

The PBLR test computes the probability that the augmented model better describes the data than both the single-predictor models and null models which assume a constant rate of change of the state variable. The augmented model almost always outperformed the null model for both systems (Fig. 4a, d) and produced similar results to the AICc comparison for when contrasted with the single-predictor models (Fig. 4b, c, e, f). Note that modelling population growth using only trait information and vice versa was seldom successful (Fig. 4c, e). As before, the same test applied to the only the size trait resulted in similar performance for both systems (Supporting information).

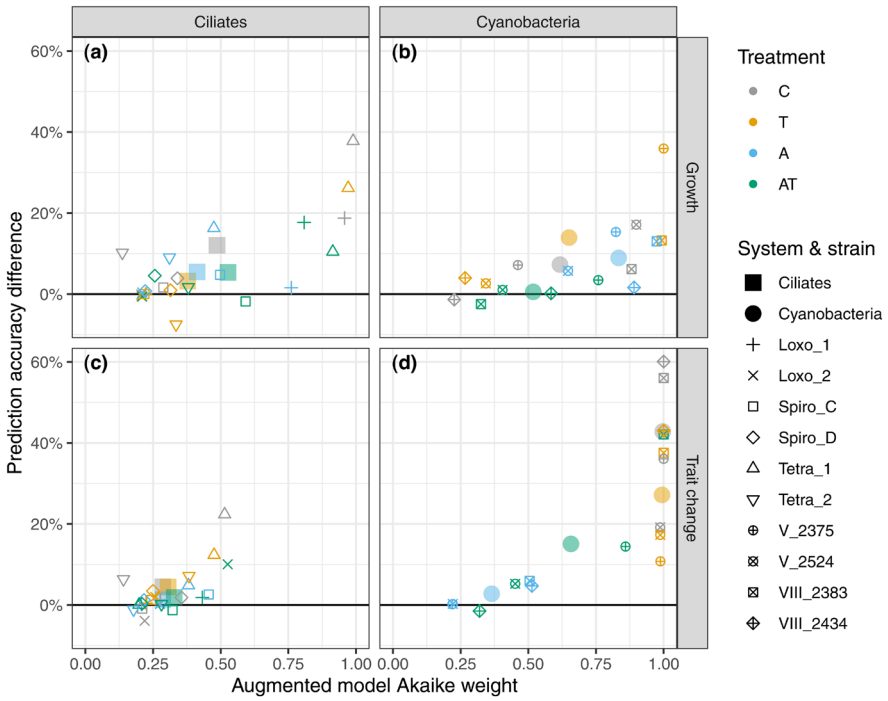

Figure 3. Improvements in predictive accuracy as a function of the probability of the augmented model being the best model on the basis of AICc. Model error was calculated as the absolute sum of the residuals and the prediction accuracy difference was calculated as $(\text{error}_{\text{single}} - \text{error}_{\text{augmented}})/\text{error}_{\text{single}}$.

Summary

Broadly, predictions of growth and especially trait change in the cyanobacteria system were more improved by using the augmented model than the cilia system. However, differences in model performance due to changes in environmental conditions were often even greater than differences between the two study systems. Furthermore, both the subsystems (ciliate genera and cyanobacteria clades) and the individual strains within these subsystems were varied in their augmented model performance.

Discussion

We have analysed population and trait dynamics in two microbial systems and across four environmental conditions. Our results do not support a general reciprocal relationship between population and trait dynamics across both systems and environmental conditions. We do observe that population growth and trait change of cyanobacteria were better predicted when considering traits and population density, respectively, but only in absence of the pollutant.

Our results therefore suggest that the relationship between population and trait dynamics is highly context-dependent (Wieczynski et al. 2021, Gibert et al. 2022).

Traits as intermediaries

Traits are often considered as intermediaries between environmental change and effects on population growth. This intermediary role can happen through two proposed mechanisms. A first and long-standing proposed mechanism is that environmental factors first affect traits, which would then cascade to affect population growth (Smith et al. 2009, Strock and Menden-Deuer 2021). The observations that the time scales at which trait shifts occur can be similar to the ones of population growth has prompted including trait dynamics into this mechanism (Kremer et al. 2018, Fey et al. 2021, Layden et al. 2022). Our results illustrate that trait dynamics are trait-dependent, but can also be affected by population density in certain conditions (Brass et al. 2021). In other words, there may exist an optimum trait value for growth in a given abiotic environment (treatment), but which is modulated by the dynamic biotic environment (density). Thus, while this first mechanism is key to understanding population response to environmental change, it most likely does not capture the full extent of these responses.

A second mechanism happens when traits predict population-level response to environmental change in the so-called 'response trait' framework (Suding et al. 2008, Mensens et al. 2017). Briefly, the trait value of a species (e.g. its size) may predict its response to an environmental change (e.g. a temperature increase), as has been shown for both protists (Wieczynski et al. 2021) and phytoplankton (Bestion et al. 2018). Such response traits have proven successful in predicting persistence, coexistence and community structure following environmental changes. Our findings, however, imply that this procedure can be complicated in systems where traits themselves change as a function of their own value and population density.

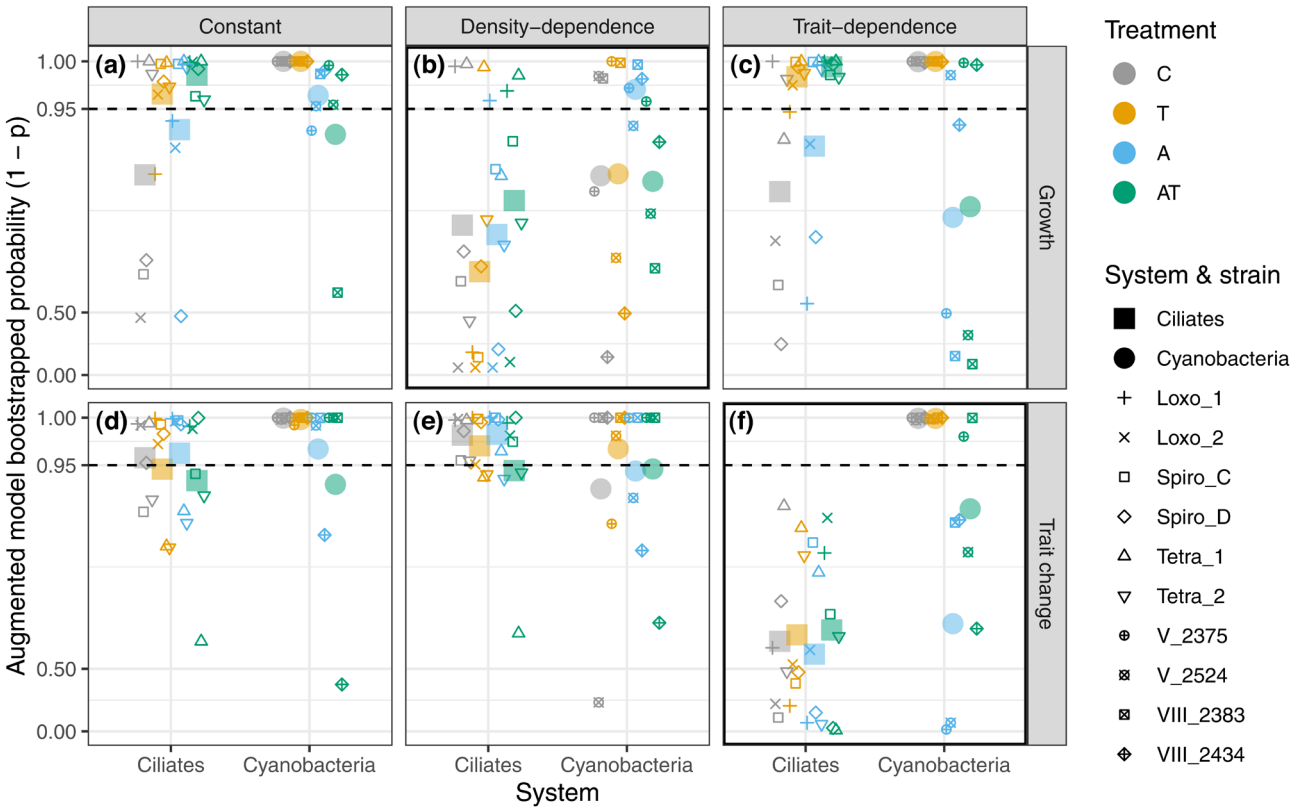

Figure 4. PBLR test showing the probability that the augmented models for growth (a–c) or trait change (d–f) better described the data than the models for constant change (a, d), density-dependent change (b, e), or trait-dependent change (c, f). The dashed horizontal line indicates a typical significance value for a one-tailed test, p = 0.95. Colours indicate treatments, point types indicate strains, and the x-axis separates the two model systems. The facets where a single state variable is being used to predict its own rate of change are shown in bold.

Trait–density feedbacks

One important implication of our results is that they suggest the absence of feedbacks between population and trait dynamics for many of the microcosms. We did find support for such feedbacks for certain cyanobacteria in unpolluted environments, as the relationships between population and trait dynamics were reciprocal and yielded substantial improvements in model prediction accuracy (Fig. 3–4). However, our results suggest that these feedbacks are mostly driven by effects of density on trait change, as augmenting trait change models with density increased predictive capacity more than augmenting growth models with traits. Theory indicates that the strength of the feedback depends on the multiplication of the two constituent effects – traits on density and density on traits (Patel et al. 2018) – implying that our finding that only one of these effects is large does not preclude a large feedback.

One explanation of why we found effects of population density on trait change to be more important than effects of traits on growth may be that our experimental design involved static environmental conditions. While we have tested four environmental conditions, these conditions remained constant over time. It has been shown that in temporally-changing environments, trait shifts can precede changes of population growth (Baruah et al. 2019), or that historic environmental conditions can influence population response to a novel environment (Klepsatel et al. 2020). Thus, in such variable environments, the scope for trait effects on population density is likely greater than in our experimental setup. Applying our analysis to data from temporally forced systems can be an avenue for future research.

Differences between systems

The superior performance of the augmented model in the cyanobacteria system relative to that of the ciliate system may be due to differences in the actual traits measured in each system. The ciliate traits were less congruent over time (Supporting information) and were been less well-summarised by the aggregate trait (Fig. 2). In the cyanobacteria system, the aggregate trait captured more information overall and the traits were almost always loaded in the same direction (Fig. 2), indicating that all traits were positively correlated with each other over time (Fig. 2). Therefore, as the aggregate trait value increased, so did size and amount of all photosynthetic pigments. In contrast, within the ciliate system, the loadings of the individual trait values onto the first principal component differed by strain and treatment, and any mechanistic interpretation of the aggregate trait must differ

accordingly (Fig. 2). This implies greater variation in trait responses to density and environmental conditions in the ciliate strains, which may reflect different, context-dependent resource acquisition or survival strategies. These complexities may help explain the poorer performance of the augmented model in the ciliate system (Fig. 3–4), as these individual traits may have distinct biological responses to the changes in population densities and treatments applied, which would not be captured in the aggregated trait. Indeed, by analysing size and density dynamics alone, without aggregating the different traits, the augmented model performed slightly better in some of ciliate microcosms (Supporting information). There may be important information from the other traits that is lost, however, when focusing on only a single trait which, while not always well-summarised by the aggregate trait described here, should be taken into account.

Differences within systems

In the cyanobacteria system, the two clades/ecotypes (V and VIII) were similarly affected by the augmentation of the model (). Because strains from clade V have an extra pigment (phycoerythrin), they were not as well-summarised by the aggregate trait (Fig. 2) and they also did not reach as high population densities (Supporting information). Despite this, the model performance was similar, possibly because the different cyanobacteria traits ultimately perform similar functions (i.e. light acquisition) and are therefore more directly linked to growth than the ciliate traits. Both the amount of photosynthetic pigments and the overall surface area of the cell affect incoming light absorption and therefore growth. The effectiveness of light harvesting, due to cell shading, is likely to be density-dependent, which makes the pigmentation content subject to plastic change in the time frame of our experiment (Stomp et al. 2004). Pigmentation and size in cyanobacteria therefore may effectively represent a dynamic single resource uptake trait which influences and depends on population growth, regardless of the exact pigment type of the strain (Stomp et al. 2007, Marañón 2015).

In contrast, in the ciliate system, the genera differed more greatly in their individual traits (Supporting information). These may represent differences in resource uptake strategies and may therefore not be so easily collapsed down into one single aggregate trait. To compute a more directly functional aggregate trait for each genus of the ciliate system would require a more tailored analysis, for example, by combining the movement and cell size traits into a clearance rate, which may be more strongly-linked to the growth of the heterotrophic ciliates (Kiørboe and Saiz 1995, Jacob et al. 2019). Note that we do not advocate that a PCA is necessarily the best way to aggregate multiple traits, but use it here simply to reduce the model complexity and avoid collinearity without requiring custom, highly-specific models of trait-dependent dynamics.

Furthermore, within each subsystem, there were relevant differences between strains. For example, in the ciliate system, the dynamics of *Tetrahymena* strain 1 were often better-described by the augmented model. This strain was fast-growing (Supporting information) and its traits were not well-summarised by the aggregate trait (Fig. 2). However, this contrasts with the closely-related *Tetrahymena* strain 2, which had very similar growth dynamics and trait loadings but which was not generally better-described by the augmented model (). Across both study systems, the *Tetrahymena* strains were the fastest-growing (Supporting information) and the fastest-changing in terms of their trait values (Supporting information), and so it may be that feedbacks were very rapid and easily-missed within a discrete sampling regime. This further highlights the delicate context-dependencies and system-specific requirements when attempting to forecast ecological dynamics.

Differences between environmental conditions

The effect of the treatments on density–trait feedbacks within a system were comparable in magnitude to differences between the two systems – environmental conditions may impact density–trait feedbacks just as strongly as the type of organism studied. The impacts of the environmental factors on these feedbacks may also have non-additive effects when combined. For example, in the cyanobacteria system, the performance of the augmented model in predicting growth was increased by both the treatment and atrazine treatments, but decrease*d* when both treatments were combined, once again highlighting the importance of context-dependence on these fundamental dynamics.

We notably observed that treatments involving the addition of the pollutant, atrazine, strongly disrupted the relationships between population and trait dynamics. Particularly for the cyanobacteria system, adding atrazine strongly impacted the population density and growth (Supporting information). Such environmental changes – severe enough to disrupt classic density-dependence – are prime candidates for augmenting population models with trait information. In these situations, when population growth is poorly-predicted by the population density itself (Supporting information), the trait information can be far more informative (while also outperforming the null models, Fig. 4). Monitoring traits in situations of drastic environmental degradation may therefore be vital for predicting population dynamics when those predictions matter most.

Outlook and limitations

The time series of the population microcosms used to fit the models are discrete, with intervals between sampling events. For the cyanobacteria, these sampling events were daily while for the faster-growing ciliates they were often more frequent (especially during the exponential growth phase towards the start of the time series). Furthermore, the strain studied have substantial diversity in life history, physiology and growth rate. It is therefore possible that important dynamics took place between sampling events which were not captured in the model and, furthermore, that these

missed dynamics may be strain-specific and therefore difficult to disentangle. While this is an unavoidable limitation in studies of population dynamics, it is important to note, and faster-growing strains (e.g. *Tetrahymena*) and microcosms in environmental conditions which promote faster growth (e.g. the temperature treatment, T) are more susceptible to this kind of error. Additionally, we fit the models using only a single time-step lag, i.e. only the immediately preceding time step influences the growth rate at a given time. However, it may be that changes in densities and traits are partially driven by points further in the past (e.g. due to residual waste products that have not yet been removed or degraded).

We could not monitor the drivers of trait changes, i.e. plasticity or evolution. While plastic responses have been observed in the two systems at the time scales considered (Lovindeer et al. 2021, Gibert et al. 2022), we cannot exclude mutations in the initially clonal populations. The potential for mutations to take place during the course of the experiments may differ between the two model systems due to their different population sizes and number of generations (Barrick and Lenski 2013). Assuming approximate cell division rates of once per hour and once per day for the ciliate and cyanobacteria systems, respectively, (Binder and Chisholm 1995, DeLong and Hanson 2009) and accounting for experiment length ($\leq$ 37 days and 10 days), average population density (1.04×10^3 and 2.23×10^7 cells), and microcosm volumes (100 and 6 ml) gives the number of cell divisions as 9.20×10^7 for the ciliate system and 1.34×10^9 for the cyanobacteria system. Therefore, we expect that the cyanobacteria system possessed somewhat greater potential for evolution during the course of the experiment, as it is likely that more cell division events took place. This increased likelihood of mutation events may have resulted in more prominent trait–density coupling in the cyanobacteria system.

We did not find a large potential for feedbacks for both systems and across all environmental conditions. However, in multispecies communities, the potential for feedbacks grows considerably, as indirect interactions may manifest across multiple species' densities and traits (Zelnik et al. 2024). However, one challenge will be that the net result of such feedbacks at the level of population and trait dynamics can be hard to identify, let alone be predicted.

Finally, it is possible that these relationships between traits and population density may be nonlinear, requiring more complex fitted models (e.g. effects of body size on growth may be described by a Gaussian function, Fernández-González and Marañón 2021).

Conclusions

We found that the relationships between populations and functional traits vary with model system and environmental context. While reciprocal interactions between density and traits were apparent within the cyanobacteria system, we did not find general support for strong feedbacks between population and trait change. More work is needed to unveil the context dependence of growth–trait connections. One approach to do this is by means of a space-for-time approach, where one experimentally crosses density and trait values, and then monitors short-term growth and trait change (Wieczynski et al. 2021). While experimentally demanding, and manipulating traits is challenging, strict control over density and traits may be needed to more systematically explore density–trait interactions.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bzkh189m1 (Holmes et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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