

LETTER

The ecological consequences of environmentally induced phenotypic changes

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Abstract

Population dynamics and species persistence are often mediated by species traits. Yet many important traits, like body size, can be set by resource availability and predation risk. Environmentally induced changes in resource levels or predation risk may thus have downstream ecological consequences. Here, we assess whether quantity and type of resources affect the phenotype, the population dynamics, and the susceptibility to predation of a mixotrophic protist through experiments and a model. We show that cell shape, but not size, changes with resource levels and type, and is linked to carrying capacity, thus affecting population dynamics. Also, these changes lead to differential susceptibility to predation, with direct consequences for predator-prey dynamics. We describe important links between environmental changes, traits, population dynamics and ecological interactions, that underscore the need to further understand how trait-mediated interactions may respond to environmental shifts in an increasingly changing world.

Keywords

Body size, environmental change, phenotypes, predation risk, predator-prey interactions, resources.

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INTRODUCTION

Resource availability and predation risk, play major roles in determining ecological dynamics (Rosenzweig & MacArthur 1963; Abrams 1991; Houston *et al.* 1993; Kopp & Gabriel 2006; Walsh & Reznick 2009; Siebenkäs *et al.* 2016) through their direct effect on reproduction and survival (Anholt & Werner 1998; Walsh & Reznick 2009; Lucena *et al.* 2015). Ecological interactions and dynamics are also mediated by traits with functional ecological effects, such as, body size (Abrams 2001; Werner & Peacor 2003; Miner *et al.* 2005; Giometto *et al.* 2013; Gibert & Brassil 2014; Gibert & DeLong 2015; Dehling *et al.* 2016). Traits like body size can be determined in turn by resource availability and predation risk: abundant resources often allow organisms to grow large (Anholt & Werner 1998), while predation risk can lead to smaller individuals (Peckarsky *et al.* 2001; Walsh & Reznick 2009), larger individuals (Abrams & Rowe 1996; Werner & Peacor 2003; DeLong & Walsh 2015), or to dynamic changes in body size as predator-prey dynamics unfold (DeLong *et al.* 2014). Both resource availability and predation risk are known to be set by environmental conditions (Durant *et al.* 2007; Miller *et al.* 2014; Janssens *et al.* 2015), and traits can respond to environmental changes either plastically (DeLong 2012) or evolutionarily (Grant & Grant 2002). Together these results suggest that environmentally induced changes in resource availability and predation risk could lead to changes in phenotypes that may have important yet poorly understood consequences for population dynamics and predator-prey interactions.

Most organisms utilise multiple resource types, and different traits may therefore play different roles in acquiring or utilising those resources. Sometimes, a single trait can have multiple functional consequences. Body size, for example, often

sets metabolic rates (Brown *et al.* 2004), influences reproduction (Shine 1988; Arendt 2011), and determines diet breadth (Beckerman *et al.* 2006; Petchey *et al.* 2008), trophic level (Riede *et al.* 2011), food web structure (Gibert & DeLong 2014), susceptibility to predation (MacLeod *et al.* 2006; Pettorelli *et al.* 2011), and predator-prey dynamics (Yodzis & Innes 1992). This type of ecological pleiotropy [i.e. when a single trait jointly affects multiple ecological processes; (Strauss & Irwin 2004; DeLong & Gibert 2016)] could have unexpected ecological consequences whenever traits change. Quantifying the effect that environmentally induced changes in ecologically important traits like body size can have on population dynamics is thus central to our understanding of how environmental change may impact species persistence.

Here, we aim to fill this gap by addressing how resource availability and environmental conditions alter the phenotype (i.e., body size and shape), population growth, and susceptibility to predation of a mixotrophic protist by integrating microcosm experiments and a mathematical model. Mixotrophic protists are mutualists that may acquire resources heterotrophically, through the consumption of bacteria or other protists, or autotrophically, through a symbiotic relationship with zoochlorellae algae. The mixotrophic protist *Paramecium bursaria*, for example, adjusts the abundance of zoochlorellae within their cells in response to light levels (Dolan 1992), such that key traits associated with resource acquisition (i.e. the number of endosymbionts) respond to environmental signals. They are also capable of changing their body size and shape plastically, influencing their swimming speeds and thus potentially affecting encounter rates with resources and predators alike (Berger 1980).

Here, we manipulate light and bacteria levels to test the hypotheses that (1) *Paramecium* body size (measured as cell volume) will increase with resource availability (DeLong 2012;

DeLong & Walsh 2015), (2) larger body size will decrease maximum per capita growth rate (Blueweiss *et al.* 1978; Savage *et al.* 2004), and (3) larger body size will lead to a smaller carrying capacity (Damuth 1981). We also tested (4) if cell shape, which may be responding to the same environmental cues as body size, changes with resource availability, and (5) if changes in cell shape affect population dynamics, given that shape is related to swimming speeds (Batchelor 1999), which can in turn affect intraspecific interactions. Last, because shape may affect swimming speeds, and swimming speeds typically affect predator-prey interactions (Aljetlawi 2004; Pawar *et al.* 2012), we tested (6) if changes in cell shape influence *Paramecium* susceptibility to predation by a predatory copepod (*Eucyclops gracilis*). Our results reveal complex responses of body size (measured as cell volume) and shape (length and width) to differing environmental scenarios and resource availability that impact population dynamics and interspecific interactions.

MATERIALS AND METHODS

Experimental set-up

We used *Paramecium bursaria* originally collected from a pond at the Spring Creek Prairie Audubon Center near Denton, Nebraska (Novich *et al.* 2014). We started 24 independent *Paramecium* populations by transferring six individuals from laboratory stock cultures into 24 2.5 cm diameter Petri dishes with 2 mL growth medium (protozoan medium, Carolina Biological Station, Burlington, NC, USA). Populations were grown at 24°C and 75% humidity levels in a 16–8 day/night cycle in Percival (Fontana, WI, USA) growing chambers.

The 24 replicates were separated into four groups of six populations that we then randomly assigned to different treatments. We manipulated light levels and nutrient concentration (which influences bacteria density, hence, resource availability) in a factorial design. Each treatment had two levels, low and high. Light was manipulated by changing the number of light banks kept on in the growing chambers during the light cycle. The 'low light' level corresponded to 12 000 lux, while the 'high light' level was 27 000 lux. Bacteria levels were manipulated by modifying the resources available to them, generating low and high levels of bacteria (low bacteria: 1:9 protozoan medium:spring water and high bacteria: 2:8, corresponding to twice the amount of nutrients). We thus had four different experimental conditions: high light, high bacteria (HLHB); high light, low bacteria (HLLB); low light, high bacteria (LLHB) and low light, low bacteria (LLLB).

We estimated *Paramecium* densities 3 days per week (Monday, Wednesday, and Friday) using a scaled sampling regime (DeLong & Vasseur 2012). That is, on each sampling day, we sampled 0.1 mL of the culture. When *Paramecia* were present, we estimated population density by counting individuals in the 0.1 mL sample using a stereoscopic microscope (Leica, M165), then multiplying that count by 20 to get an estimate of the total population density in each microcosm. When no *Paramecia* were present in the 0.1 mL sample, we counted the entire *Paramecium* population for the whole microcosm. After

each sample, 0.1 mL of fresh medium was added to all microcosms, and once in every week, we added 0.2 mL of new medium to control for evaporative loss of liquid and bacterial depletion.

After all populations reached carrying capacity (~24 days), we estimated susceptibility to predation by allowing the freshwater copepod *Eucyclops gracilis* to forage on *Paramecia* taken from each treatment. For that, we placed one *E. gracilis* that had been kept without food for 1 day in a 2.5 mm Petri dish with 2 mL of 1 : 9 protozoan:spring water medium and allowed it to acclimate for 5 min. This environment closely resembles the medium in which *Paramecium* grew and matches the medium in which copepods were maintained. This has the dual benefit of avoiding osmotic stress for *Paramecium* and stress in copepods, while putting *Paramecium* from both low and high bacteria treatments in similar conditions. Any resulting differences in foraging levels is thus presumably due to differences in the prey themselves or in their behaviour. Twenty individual *Paramecia* were then placed in the experimental dish. After 15 min of foraging, the remaining *Paramecia* were counted. This was done at least once for each replicate microcosm within each treatment ($n = 27$). Foraging experiments occurred in controlled laboratory light conditions (ambient lighting), and were thus at comparable, albeit lower, than both experimental conditions. Prey were only exposed to these light conditions for exactly 15 min, i.e. for the duration of the foraging trials and thus did not have enough time to adjust to their new environment. Finally, we processed *Paramecium* populations from all replicates using a FlowCAM to quantify cell volume, cell length, and cell width; all measured at the individual level (total sample = 2174 individuals).

Analyses

To quantify whether *Paramecium* underwent any phenotypic changes across treatments, we used Linear Mixed Models (LMMs) with the trait of interest as the response variable (cell volume as a measure of body size, as well as length, width, and the length:width ratio, as measures of shape), light and nutrient treatments as the explanatory variables, and replicate as a random intercept, to control for the hierarchical structure in our data (individuals within replicate populations within treatments). To assess how different treatments affected *Paramecium* population dynamics, we fitted the solution to the logistic growth differential equation (i.e. $N(t) = KN_0/[N_0 + (K - N_0)e^{-rt}]$) to the density time series from each treatment and for all replicates using the `nls` function in R 2.14 (R Core Team 2013), where K is the carrying capacity, N_0 is the initial population size (with $N_0 = 6$), and r is the per-capita growth rate. To test our hypothesis that larger cell size would lead to smaller carrying capacity (K) and maximum per capita growth rate (r), we estimated both quantities within each replicate microcosm and treatment and regressed them against mean body size for each replicate and for all treatments. We replicated this analysis with cell shape (length:width ratio) as an explanatory variable to test the hypothesis that cell shape affects population dynamics. To assess whether susceptibility to predation was affected by

phenotypic changes resulting from our treatments, we ran a linear model with observed *Eucyclops* foraging rates as the response variable and treatment as the explanatory variable (the foraging rates were treated as a continuous variable, and the data was not overdispersed).

RESULTS

The different combinations of bacteria and light treatments had significant effects on *Paramecium* shape (Fig. 1a and b) but not cell volume (see Table I in Appendix S1 of the Supporting Information). Individuals from the high bacteria treatments became longer and thinner than individuals from all other treatments regardless of light levels (Fig. 1, Tables II and III in Appendix S1), while individuals from low bacteria treatments became generally shorter and thicker (Fig. 1, Tables II and III in Appendix S1). Light levels seemed to have only marginal effects, if any, on phenotypes (Tables II and III in Appendix S1), and changes in cell shape occurred along a trade-off line between cell length and width (Fig. 1a), with cells becoming more fusiform at higher bacteria levels (Fig. 1b, Table IV in Appendix S1).

The different treatments also resulted in qualitatively different population growth trajectories (Fig. 2, see Appendix S2 for residual plots). High bacteria *Paramecium* populations had the highest carrying capacities ($K_{\text{HLLHB}} = 1312 \pm 86$ (SE) cells mL^{-1} , $K_{\text{LLHB}} = 1059 \pm 55$, $P < 0.05$ for both) compared to low bacteria treatments ($K_{\text{HLLB}} = 763 \pm 56$ (SE) cells mL^{-1} , $K_{\text{LLLHB}} = 621 \pm 40$, $P < 0.05$ for both), with light treatments having an additive effect (Fig. 2). Maximum per capita growth rates were on average larger for high bacteria populations ($r_{\text{HLLHB}} = 0.47 \pm 0.02$ (SE) day^{-1} , $r_{\text{LLHB}} = 0.44 \pm 0.02$,

$P < 0.05$ for both), comparably large for low bacteria/low light populations ($r_{\text{LLLHB}} = 0.44 \pm 0.02$ (SE) day^{-1} ; $P < 0.05$) and lowest for low bacteria/high light treatments ($r_{\text{HLLB}} = 0.36 \pm 0.02$; $P < 0.05$), implying an interactive effect between light and bacteria levels (although notice that HLLB maximum per capita growth rates may have been underestimated by our model).

We observed no relationship between cell volume and population growth parameters ($P = 0.56$ for K and $P = 0.19$ for r , Fig. 3a and b) or between cell shape (as length:width ratio) and the maximum per capita growth rate ($P = 0.59$ for length and $P = 0.09$ for width, Fig. 3d). However, the carrying capacity was positively linked to *Paramecium*, carrying capacity increasing by 516.3 ± 189.9 (SE) individuals with a unit increase in length: width ratio ($P = 0.016$, Fig. 3c). Last, the *Paramecium* from low light treatments were more susceptible to predation by *Eucyclops* than those from high light treatments, with no effect of bacteria levels (estimate = 2.2 ± 1.1 SE, $P = 0.045$, Fig. 4).

DISCUSSION

Understanding the links between environmental factors, resource availability, susceptibility to predation, phenotypic changes, and ecological dynamics is a central and pressing challenge in ecology (Pimm 2009; Schnell *et al.* 2013; Bateman *et al.* 2015). With a simple factorial experiment, we showed that resource availability in the form of changes in bacteria density and light levels determine the shape, but not the body size (here: volume), of the mixotrophic protist *Paramecium bursaria*. We show this change in phenotype to be linked to changes in carrying capacity, and thus, population dynamics.

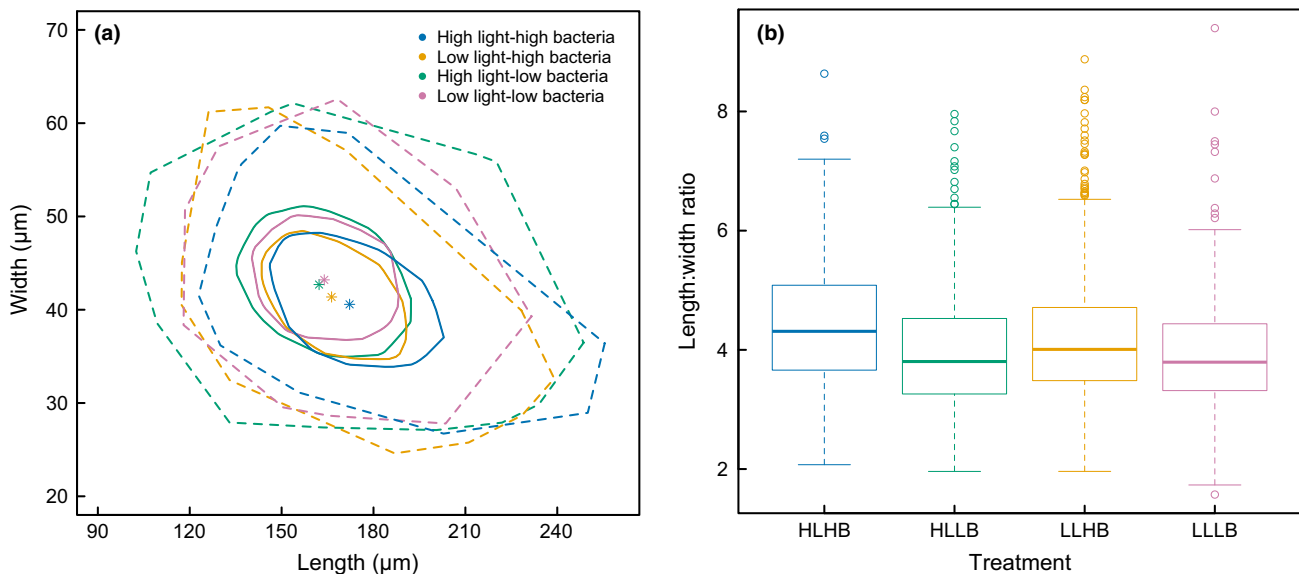


Figure 1 (a) Bagplot of the cell width and length of *Paramecium bursaria* across treatments. A bagplot consists of a center (here an asterisk) marking the median for both width and length, a bag (solid line) which contains at most 50% of the data, and a loop (dashed line), which is a convex hull of the outermost data points not considered outliers. The bagplot is a bivariate extension of the classic boxplot, and helps visualising location, spread, correlation, skewness, and tails of the data (Rousseeuw *et al.* 1999). Here, it can be seen that width and length trade-off, and how the different treatments affected the shape of *Paramecium* through changes in their cell width and length. (b) Length:width ratio across experimental treatments (colors as in (a)). It can be seen how high bacteria treatments (blue, yellow) are generally longer but thinner than low bacteria treatments (green, pink).

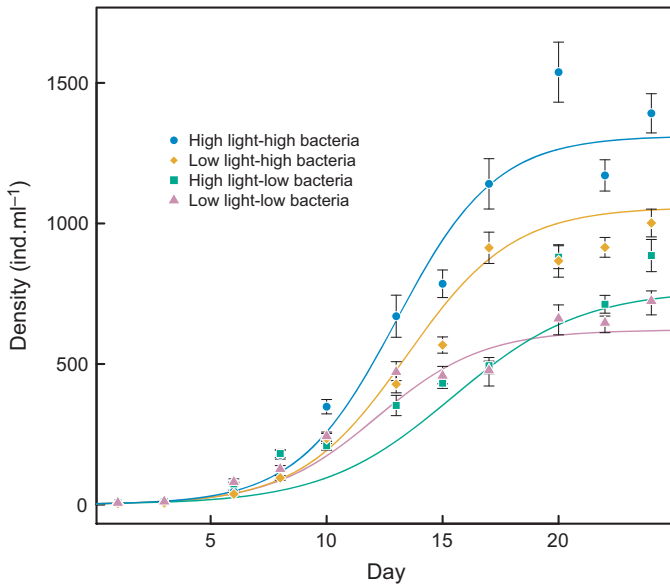


Figure 2 Time series of the density of *Paramecium* across treatments. Dots represent mean densities across replicate populations ($n = 6$ in all cases) and bars represent standard errors. Solid lines represent the fits of the logistic growth equation for each treatment separately.

Interestingly, it is the cell length to width ratio –a measure of how fusiform cells are–, but not their body size, that seems to be linked to the parameters controlling ecological dynamics. These phenotypic changes may be determined by the biomechanical constraints of organisms moving in liquids, as the drag force, which controls how energetically expensive swimming is, ultimately depends on the shape, but not the size, of the organism. Last, we showed how resource and light treatments also affected susceptibility to predation by the copepod *E. gracilis*, further suggesting an important connection between resources, phenotypes and multi-species interactions.

Previous studies have shown that phenotypes can often respond to changes in environmental conditions and resource levels in specific ways (Anholt & Werner 1998; Peckarsky et al. 2001; Walsh & Reznick 2009; DeLong 2012). For example, organisms may become smaller when resources are less abundant due to increased competition among individuals or can grow larger for the opposite reasons (Walsh & Reznick 2009). How phenotypes respond to simultaneous changes in different, complementary resources, is more difficult to foresee. *Paramecium bursaria* face a unique challenge, as acquiring resources through bacterivory implies allocating intracellular space to the vacuoles where digestion takes place after bacteria are ingested (Dolan 1992). Acquiring resources through

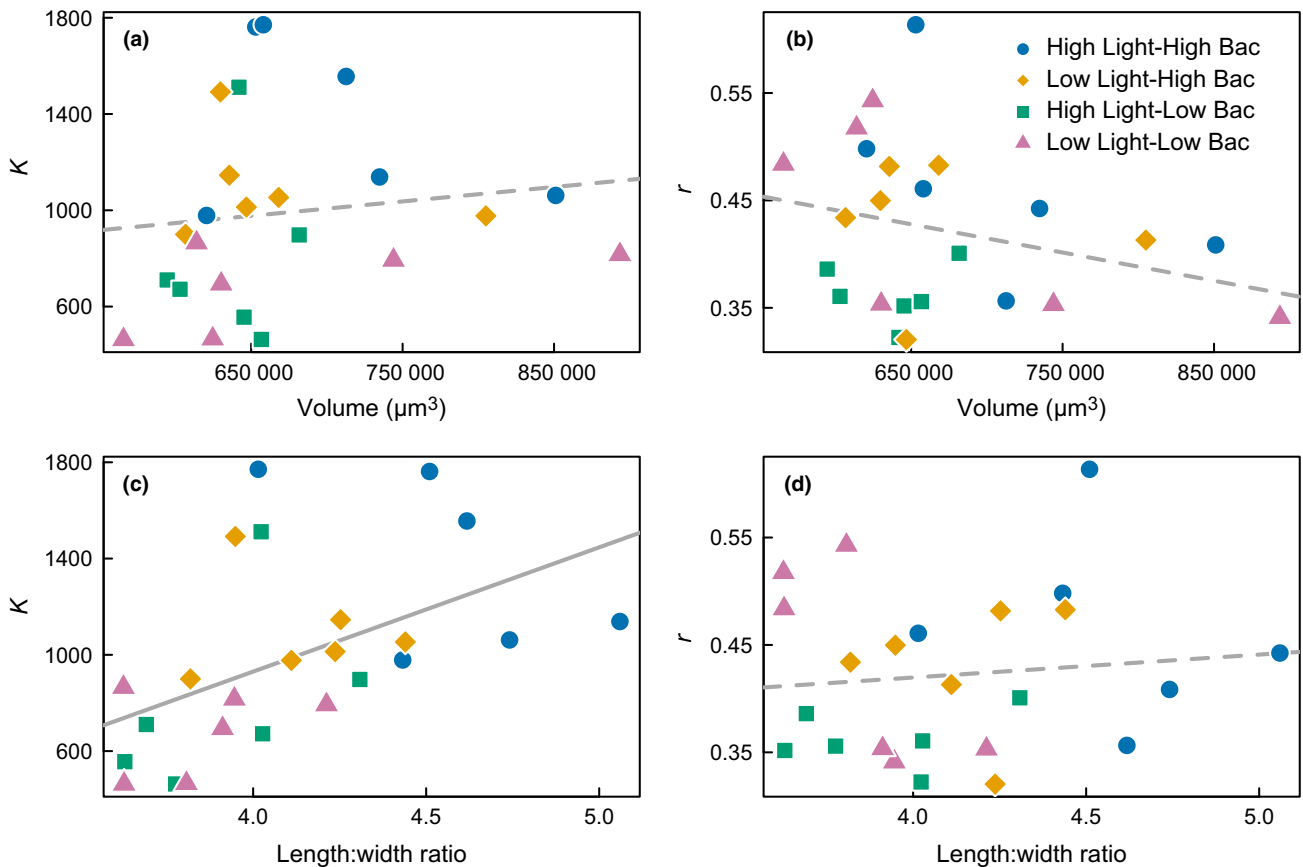


Figure 3 Plots of carrying capacity (K) and maximum per capita growth rate (r) against volume (a and b respectively) and K and r against the length:width ratio (c and d respectively). The dots represent the estimated r or K for a given replicate population within a given treatment against a mean variable of interest within that replicate (Length:width ratio or volume). Grey lines represent significant (solid) or non-significant (dashed) regressions.

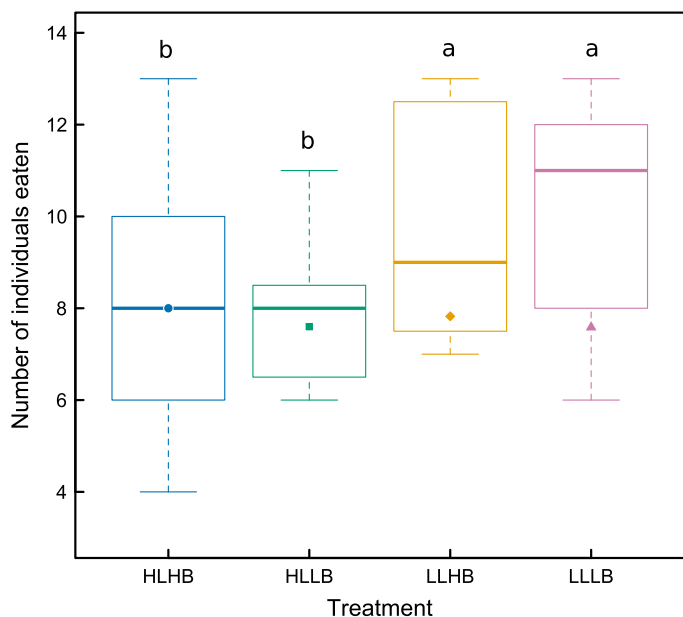


Figure 4 Box plot of the foraging rates for the predatory copepod *Eucyclops gracilis* across treatments (namely; high light/high bac = HLHB, high light/low bac = HLLB, low light/high bac = LLHB and low light/low bac = LLLB). *Paramecia* from low light level treatments (a) get eaten significantly more than high light treatments (b) ($P = 0.045$). Dots represent foraging rate predictions using the model presented in the discussion and the supporting information, parameterised with respect to HLHB. Only taking shape and size into account does not correctly predict predation risk.

photosynthesis, on the other hand, involves allocating intracellular space to symbiotic zoochlorellae algae (Dolan 1992), thus creating a space trade-off between the two resource acquisition modes. A priori, the trade-off would not exist if *Paramecium* could grow ever larger in response to different resource levels. However, and contrary to what we hypothesised, this is not what we observed. Rather, while some marginal changes in total volume might have occurred, the most important effects involved changes in the cell length:width ratio, implying that *Paramecium* may be able to grow in length or width, but not both, in response to changes in resource levels, at least for the levels of resource we provided. Our results thus show that phenotypic responses can be complex, especially whenever trade-offs between alternative resource acquisition modes are in existence.

Although body size often plays a major role in determining the way in which many ecological processes occur (Yodzis & Innes 1992; Brose *et al.* 2005; DeLong *et al.* 2015), how important the role body size plays relative to that of other traits is unknown and difficult to assess. Here, we show that it is a change in the cell shape, but not body size (cell size), that is linked to how *Paramecium* populations grow in response to resource levels. Our results thus go against our hypothesised – and often observed elsewhere – relationship between body size and population dynamics, but support our hypotheses that cell shape affects population dynamics. Indeed, the cell length:width ratio determines *Paramecium* carrying capacity, although no effect was observed on maximum per capita growth rates

(Fig. 3). *Paramecia* from the high bacteria treatments have generally larger carrying capacities, and are also longer but thinner. Long but thin body shapes help reducing drag (Batchelor 1999), and thus lead to faster swimming velocities. Larger velocities in turn allow these individuals to capture more bacteria by increasing the encounter rate (Aljetlawi 2004; Pawar *et al.* 2012). The more bacteria they capture, the more energy there is available to grow and reproduce, potentially providing a mechanism through which more fusiform cell shapes may lead to larger carrying capacities, as observed in this study.

Our predation experiments suggest that adjustments to light, but not bacteria levels, influence predation risk. To interpret these results, we used a model that merges how predator attack rates depend on predator and prey velocities, and how *Paramecium* swimming velocities in turn depend on their shape (Appendix S2). Parameterising this model with the results of the high light/high bacteria treatment, we predicted the expected change in foraging rates given the observed changes in cell shape, which tended to be lower than observed in the low light treatments (Fig. 4, markers within box plots). Based on this, it was possible to assess what changes in the parameters of the model could lead to foraging rates like those observed in our experiment (Appendix S2). We conclude that the observed predation risk may be due to changes in some of the parameters controlling the interaction, other than shape, such as *Paramecium* detectability across treatments (being 1.15 times higher for low light/high bacteria and 1.45 times higher for low light/low bacteria compared to high light/high bacteria, see Appendix S2), or a change in cilia density (being 1.32 times higher in low light/high bacteria or 2.12 times higher in low light/low bacteria compared to high light/high bacteria, see Appendix S2), contrary to what we hypothesised. Together, our foraging experiment and modelling results thus suggest a possible behavioural adjustment in swimming speeds, as already observed in other *Paramecium* species (Hammill *et al.* 2010), or, alternatively, changes in cilia density, in response to exposure to different environmental conditions with consequences for predator-prey interactions. *Paramecium bursaria* has been shown to have higher predation risk when apochlorotic (i.e. without zoochlorellae), than in normal conditions (i.e. with zoochlorellae), perhaps because of secondary metabolites produced by the symbionts that discourage predators (Berger 1980). These results may provide an alternative explanation as to why light levels, but not bacteria, are the primary determinants of predation risk in our study and further underscore the need to look beyond body size to further understand the processes controlling ecological dynamics and interactions, as a recent study also suggested (Kalinowski & DeLong 2016).

We would like to point out, however, that the population dynamics for the high light, low bacteria treatment (green, Fig. 2), may be underestimated by the logistic model. This may result in smaller estimates of the maximum per capita growth rates (r) for these microcosms than they might really be, and thus, such estimates need to be interpreted with caution. In fact, larger per capita growth rates for *Paramecium* in the high light/low bacteria treatment could potentially result in a significant relationship between body size and r . So, although our results conclusively show that cell shape, but not body size, is linked to carrying capacity, they may not

conclusively show that body size is not related to maximum per capita growth rates.

Overall, we show that changes in phenotype, induced by changes in resource acquisition modes in response to resource availability and environmental conditions, are linked to changes in population growth. These changes in phenotype lead to changes in susceptibility to predation that cannot be solely explained by purely morphological changes such as body size or cell shape, implying broad simultaneous shifts in sets of traits, from morphology to behaviour. Our results show how the environment sets resource levels, and through that, organismal traits, which has consequences for ecological interactions and dynamics.

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AUTHORSHIP

JPG and JPD designed the study; JPG, RA and RH performed the experiments, JPG analysed the data, did the mathematical modelling and wrote the first draft; all authors contributed to subsequent versions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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