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RESEARCH ARTICLE

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Linking intraspecific trait variation to community abundance dynamics improves ecological predictability by revealing a growth–defence trade-off

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Abstract

1. Intraspecific trait change, including altered behaviour or morphology, can drive temporal variation in interspecific interactions and population dynamics. In turn, variation in species' interactions and densities can alter the strength and direction of trait change. The resulting feedback between species' traits and abundance permits a wide range of community dynamics that would not be expected from ecological theories purely based on species abundances. Despite the theoretical importance of these interrelated processes, unambiguous experimental evidence of how intraspecific trait variation modifies species interactions and population dynamics and how this feeds back to influence trait variation is currently required.
2. We investigate the role of trait-mediated demography in determining community dynamics and examine how ecological interactions influence trait change. We concurrently monitored the dynamics of community abundances and individual traits in an experimental microbial predator–prey–resource system. Using this data, we parameterised a trait-dependent community model to identify key ecologically relevant traits and to link trait dynamics with those of species abundances.
3. Our results provide clear evidence of a feedback between trait change, demographic rates and species dynamics. The inclusion of trait–abundance feedbacks into our population model improved the predictability of ecological dynamics from r^2 of 34% to 57% and confirmed theoretical expectations of density-dependent population growth and species interactions in the system.
4. Additionally, our model revealed that the feedbacks were underpinned by a trade-off between population growth and anti-predatory defence. High predator abundance was linked to a reduction in prey body size. This prey size decrease was associated with a reduction in its rate of consumption by predators and a decrease in its resource consumption.
5. Modelling trait–abundance feedbacks allowed us to pinpoint the underlying life history trade-off which links trait and abundance dynamics. These results show that accounting for trait–abundance feedbacks has the potential to improve understanding and predictability of ecological dynamics.

KEYWORDS
community dynamics, density-dependent trait change, generalised additive models, growth–defence trade-offs, predator–prey experiment, trait-dependent interaction, trait–abundance feedbacks

1 | INTRODUCTION

Trait variation within species is increasingly recognised as having important impacts on the population dynamics of natural communities (Berg & Ellers, 2010; Schoener, 2011). Such variation can be driven by evolutionary selection pressures favouring certain heritable traits (Kasada, Yamamichi, & Yoshida, 2014; Thompson, 1998; Yoshida, Hairston, & Ellner, 2004). Alternatively, trait variation can be caused by phenotypic plasticity, when a single genotype produces different phenotypes under differing environments (Agrawal, 2001; Cortez, 2011; Fordyce, 2006; Tollrian & Harvell, 1999). For example, the timing of life history events or the allocation of resources to growth and defence may depend on the density of predators and resources and on environmental conditions (Finlay, 1977; Lampert, 1994; Riessen, 2015; Travis et al., 2014). Trait change can mediate significant temporal variation in ecological processes such as resource consumption, growth, birth and death (Bassar et al., 2010; Bolker, Holyoak, Křivan, Rowe, & Schmitz, 2003; Pelletier, Clutton-Brock, Pemberton, Tuljapurkar, & Coulson, 2007; Preisser, Bolnick, & Bernard, 2005; terHorst, Miller, & Levitan, 2010; Turcotte, Reznick, & Hare, 2011). When the modification of ecological interactions alters the strength or direction of trait change, a feedback loop is produced between abundance (ecologically driven) and trait dynamics (evolutionary/plasticity-driven) (Agrawal, Johnson, Hastings, & Maron, 2013; Becks, Ellner, Jones, & Hairston, 2012; Pelletier et al., 2007; Schoener, 2011; Yoshida, Jones, & Ellner, 2003; Yoshida et al., 2007).

Trait-dependent vital rates permit a broad array of community dynamics that are not expected from classical ecological theories based only on species abundances (Abrams & Matsuda, 1997; Berg & Ellers, 2010; Cortez & Weitz, 2014; Ellner & Becks, 2011; Hiltunen, Ellner, Hooker, Jones, & Hairston, 2014; Jones et al., 2009; Kishida, Trussell, Mougi, & Nishimura, 2010; Mougi, 2012; Pelletier, Garant, & Hendry, 2009). For example, in intraguild predation systems, where a predator consumes a prey and simultaneously competes for the resource of the prey, purely ecological theory predicts that peaks of resource abundance should be followed by a peak in the prey and then in the predator ("turn-taking") (Hipfner, Jones, Ellner, & Hairston, 2013; Holt & Polis, 1997). The inclusion of trait-mediated variation of interaction strengths makes possible a variety of novel dynamical behaviours, by allowing the community to have differing trajectories, at different times, despite having equal states of abundance (Ellner & Becks, 2011; Hiltunen et al., 2014). Such crossing of trajectories is not possible in ecological models lacking age, stage or trait structure. The dynamics can become increasingly complex as the number of species, interactions and trait dependencies increases (Ellner & Becks, 2011; Hiltunen et al., 2014; Jones et al., 2009; Strauss, 2014).

For trait change to substantially influence community dynamics, it must be sufficiently rapid to influence demographic processes on an ecological timescale (Berg & Ellers, 2010; Ellner, Geber, & Hairston, 2011; Hairston, Ellner, Geber, Yoshida, & Fox, 2005; Thompson, 1998). Observations of rapid trait change, in response to density-induced phenotypic plasticity or evolutionary selection processes, are increasingly being reported (Becks, Ellner, Jones, & Hairston, 2010; Bolnick et al., 2011; Boulanger, Cattet, Nielsen, Stenhouse, & Cranston, 2013; Kusch, 1993; Losos, Schoener, & Spiller, 2004; Pettorelli, Hilborn, Duncan, & Durant, 2015; Relyea & Auld, 2004; Travis et al., 2014). When rapid trait change substantially impacts ecological rates, abundance-only based ecological theories will poorly explain community dynamics and may give unreliable predictions of future abundances (Ellner & Becks, 2011; Schreiber, Bürger, & Bolnick, 2011; Shertzer, Ellner, Fussmann, & Hairston, 2002; Strauss, 2014). Therefore, we need to improve our process-based understanding of how density-dependent trait change feeds back with intraspecific trait variation to influence species interactions and population dynamics (Gibert, Dell, DeLong, & Pawar, 2015).

To link trait-dependent community dynamics and density-dependent trait change, the dynamics of behavioural and morphological traits must be studied simultaneously with the dynamics of species abundances (Hiltunen, Hairston, Hooker, Jones, & Ellner, 2014). Then, the most ecologically important traits need to be identified and the trait and abundance dynamics need to be linked. However, despite the body of theoretical work suggesting the importance and interrelatedness of these processes (Abrams & Matsuda, 1997; Cortez & Weitz, 2014; Ellner & Becks, 2011), these two dynamic components remain largely empirically disconnected (Kishida et al., 2010; but see Becks et al., 2012).

Here, we present a novel framework to link a community's trait and abundance dynamics. This framework allows investigation of the role of trait variation in mediating species' interactions and the resulting community dynamics. It also allows us to examine how variation in species′ abundance and the strength of ecological interactions in turn influences trait change. The framework was applied to an experimental microbial predator–prey system, where we concurrently monitored the dynamics of community abundances and a range of relevant morphological and behavioural traits. These traits included measures of body size, swimming speed and movement characteristics.

We predict that increased predation should drive selection for prey trait change and that trait alteration should weaken the impacts of predation on prey, generating trait-mediated species dynamics. This could be achieved if trait change either (1) confers defence against predation (Tollrian & Harvell, 1999) or (2) accelerates the prey's life history to allow earlier reproduction and reduce the cost of predation

(Cole, 1954; Law, 1979). We parameterised an empirically derived trait-dependent community model, using the observed time series of both species traits and abundances. Key traits influencing species interactions were identified, and their dynamics were linked with those of species abundances. We were also able to examine how changes in species abundances caused intraspecific trait change. By evaluating the trait dependence of species interactions and the ecological dependence of trait change, we were able to investigate the feedbacks between trait and abundance dynamics.

2 | MATERIALS AND METHODS

2.1 | Empirical microcosm system

2.1.1 | Study species, community interactions and ecologically important traits

We studied the community dynamics of a tri-trophic predator–prey–resource system, consisting of a bacteria resource, *Serratia marcescens*, an intermediate bactiverous ciliate *Colpidium striatum* (Stokes 1886; referred to as the prey), and a top predator, *Stentor coeruleus* (Ehrenburg 1830). These species coexist at temperatures between 15 and 25 °C and have short generation times: *c.* 2–6 hr for bacteria, 12–24 hr for *Colpidium* and 30–42 hr for *Stentor* (Beveridge, Petchey, & Humphries, 2010; Fenchel, 1987; Griffiths, Warren, & Childs, 2015; Laybourn, 1976). *Stentor* populations consume bacteria during filter feeding, but do not persist on a purely bacterial diet, generating weak intraguild predation (Slabodnick & Marshall, 2014).

The prey species (*Colpidium*) is a selective bactiverous grazer (Thurman, Parry, Hill, & Laybourn-Parry, 2010) and exhibits morphological and behavioural responses to environmental variation. Body size is known to be reduced under highly competitive conditions or at high temperatures (Balciunas & Lawler, 1995; Jiang & Morin, 2005). Exposure to predation has also been observed to drive changes in *Colpidium* body size (Fyda, Warren, & Wolińska, 2005). The speed and tortuosity of *Colpidium* movement have also been found to depend on the composition of its community (Fronhofer, Klecka, Melián, & Altermatt, 2015). Changes in such movement behaviours influence the contact rates of individuals, and this has been found to influence predatory interactions between similar ciliate species (Beveridge et al., 2010; Luckinbill, 1973).

2.1.2 | Culturing and establishing the predator–prey system

The microcosm experiments consisted of Petri dishes containing 50 ml Chalkley's solution (Thompson, Rhodes, & Pettman, 1988), 0.7 g/L of crushed protozoan pellets (Carolina Biological Supply, USA) and three wheat seeds (Altermatt et al., 2015). All microcosms and media were autoclaved before use. Two days prior to the initiation of the experiments, the medium was inoculated with bacteria and kept at 37°C, allowing the establishment of a resource base. Protist microcosms were subsequently maintained at 20°C with a 16:8 light–dark photoperiod. The positions of microcosms within controlled temperature environments were randomised and frequently permuted. Cultures were replenished three times a week by renewing 1 ml of medium and replacing any evaporative loss with distilled water.

2.1.3 | Treatments

Microcosms were either assigned to a predator–prey–resource treatment (exposed to predation: replication = 6) or a prey–resource treatment (not exposed to predation: replication = 4). Higher replication was used to infer vital rates in the more complex and often variable predation treatment. On day zero, replicate microcosms were initiated with 100 *Colpidium*. During the first 12 days, all treatments contained just the prey and resource and were treated identically. On day 12, the microcosms exposed to predation were each invaded with 25 individuals of *Stentor*. They also received a second equal invasion 2 days later, reducing the impacts of demographic stochasticity on the initial population trajectories and preventing chance predator extinctions. The replicates in which prey was not exposed to predation received additions of equivalent volumes of *Stentor* culture medium, but sieved to remove predators. All populations persisted for the 82-day duration of the study.

2.1.4 | Sampling

Microcosms were sampled three times a week for the duration of the experiment. To count the predator's density, microcosms were agitated, then 5 ml of medium was temporarily transferred to a sterile Petri dish. This was scanned under a stereomicroscope, and the medium returned into the microcosm (Leica M205 C: surveyed at 7.8× magnification). Prey density was measured by transferring 1 ml of medium into a Sedgewick Rafter cell (S52; SPI supplies, Westchester, PA), and taking a 5 s video of a 0.044 ml sample (25 frames per second) using the stereomicroscope with a 25× magnification mounted digital CMOS camera (Hamamatsu Orca C11440; Hamamatsu Photonics, Japan). The automated digital video processing R package, BEMOVI (Pennekamp, Schtickzelle, & Petchey, 2015) was used to remove static background debris, locate and measure individual prey and reconstruct their trajectories. This allowed measurement of a range of individual-level behavioural and morphological traits including the following: body size and shape, movement speed, net displacement rate, step lengths per video frame and turning angles. These traits were examined as they are likely to influence the strength of species interactions, by modifying the rate of predation or energetic content and handling time of prey. The automated video-based counting and measurement pipeline have been carefully tested and shown to give unbiased estimates of *Colpidium* abundance and morphology (Pennekamp et al., 2015, 2017).

Bacteria density was estimated using flow cytometry, based on a 20 µl sample of medium and stained with the SYBR Green I nucleic acid binding dye (Data S1). Analysis of the flow cytometry measurements of scatter and fluorescence absorbance, associated with each observation, allows the groups with similar qualities to be distinguished. It

also provides information about the biological differences between the groups, with respect to size, shape and DNA content (Data S1A). As a characteristic background noise pattern was identified across samples, a Gaussian mixture model (GMM) was constructed to filter noise observations from the bacterial signal (Fraley & Raftery, 2002; Data S1A). To identify different components in the bacterial resource, the signal observations were grouped into clusters of observations with differing characteristics. Model-based clustering was undertaken to achieve this and to determine the number of bacterial classes in the data (Data S1B). During this process, a set of GMM's was fitted, each hypothesising a different number of clusters in the data. Model comparison was then applied, based on Bayesian information criterion scores, to identify the most parsimonious model.

Observations were then classified into bacterial categories. Two main distinct bacterial classes were identified, and the proportion in each class calculated for every sample. Based on analysis of the flow cytometry data, the bacteria in the main resource class (most numerous overall) were likely smaller (less forward scatter), had a smoother or more spherical shape (lower sideways scatter) and contained less red pigmentation (lower intensity of red wavelength fluorescence) compared to the secondary resource. These characteristics suggest that the secondary resource class may represent bacterial clumps or a modified strain of *S. marcescens* (Data S1C). Clumping is known to confer defence against protist predation, but comes with the cost of producing secondary metabolites (Friman, Diggle, & Buckling, 2013; Queck, Weitere, Moreno, Rice, & Kjelleberg, 2006).

2.2 | Model inference

2.2.1 | Empirically derived trait-dependent community model

Deriving a community model of traits and abundance

To describe the linked dynamics of species traits and abundances, we formulated a community model accounting for trait-dependent species interactions (Holt & Polis, 1997) and fitness-dependent trait selection (Abrams, Matsuda, & Harada, 1993). We then derived nonparametric regression model structures from this theoretical model (Data S2). These empirical models describe changes in community abundances and trait values between observations as smooth functions of species densities and mean trait values. This allowed trait-dependent community interactions and ecological impacts on trait dynamics to be described flexibly, without strong constraints on the functional forms of the model equations (Wood, 2006). The trait dependence model could be generalised to incorporate discontinuous changes in the strength of interactions at a specific species density (e.g. if prey exhibit density-dependent behavioural switching).

The community dynamics were discretised into the following system of difference equations:

$$E\left(\log\left(\frac{R^{t+1}}{R^t}\right)\right) = g_{RR}(R, Y_R) - f_{RN}(R, Z_i, Y_R)\frac{N}{R} - f_{RP}(R, P)\frac{P}{R} \quad (1a)$$

$$E\left(\log\left(\frac{N^{t+1}}{N^t}\right)\right) = \alpha_{RN} f_{RN}(R, Z_i, Y_R) - f_{NP}(N, Z_i)\frac{P}{N} - d_N \quad (1b)$$

$$E\left(\log\left(\frac{P^{t+1}}{P^t}\right)\right) = \alpha_{NP} f_{NP}(N, Z_i) + \alpha_{RP} f_{RP}(R, P) - d_p \quad (1c)$$

$$E\left(\log\left(\frac{Z^{t+1}}{Z^t}\right)\right) = s_z(R, N, P, Z_i) \quad (1d)$$

These equations describe the expected (E) log change in species abundances and trait values between sampling occasions. The densities of the resource, prey and predator are, respectively, R, N and P. Ecologically relevant prey traits influencing dynamics are denoted by Z_i (the subscript i indicates a specific behavioural or morphological trait). The proportion of the resource composed of the rare bacterial class is denoted Y_R. The quantities f_{ab} are smooth functional response terms describing the dependence of the consumption rate, of species a by species b. The arguments of these functions are the species abundances, prey trait values (in prey containing terms) and the resource composition (in resource containing terms). For example, $f_{NP}(N, Z_i)$ describes the density- and trait-dependent predation of prey by the predator. Similarly, the term $g_{RR}(R, Y_R)$ is a smooth function describing the intraspecific density dependence of growth in the resource and its dependence on the resource composition. The per capita mortality term of species a (d_a) and the conversion efficiency between species i and j (α_{ij}) are constants to be estimated. Finally, $s_Z(R, N, P, Z_i)$ is the density-dependent rate of trait change and is proportional to the ecological selection pressure acting on the trait.

Model parameterisation

Prior to model fitting, individual trait measurements were square root transformed to reduce skew in the data. Mean trait measurements were then calculated for each replicate at each sample point. Population abundance and trait dynamics were interpolated, using cubic hermite splines, to obtain data with equidistant time intervals and then standardised to have a standard deviation of one. The finite rate of change of each species population abundance (X_s) was calculated, based on nonstandardised measurements and log-transformed to provide a measure of the observed linearised per capita rate of population growth: $\log\left(\frac{X_s(t+1)}{X_s(t)}\right)$. Similarly, the first log difference of dynamics of each trait (Z_i) was also calculated: $\log\left(\frac{Z_i(t+1)}{Z_i(t)}\right)$.

We used the "MGCV" package in R to fit generalised additive models describing the linked community dynamics (Equations 1; Wood, 2006). To account for heavy-tailed response variables, we used a scaled t-distribution model. To avoid overfitting, the model degrees of freedom in the generalised cross-validation score was inflated by a factor of 1.2, following recommendations of Gu (2013) and Hiltunen et al. (2014). Numerical optimisation, using a box-constrained variable metric algorithm (Limited-memory Broyden–Fletcher–Goldfarb–Shanno quasi-Newton method), was applied to identify the remaining constants (d_a and α_{ij}).

Formulation and comparison of candidate hypotheses

Competing hypotheses about the trait dependence of species interactions and community dynamics were formalised as a set of candidate regression models. These candidate models differ in how

population growth and consumption rates depended upon different behavioural and morphological traits as well as species abundances. The impact of trait change on species interactions was allowed to vary with species abundances, by describing trait-dependent interactions in Equation 1a–c (e.g. $f_{NP}(N, Z_i)$) using multivariate tensor product smooths (Wood, 2006). Similarly, a set of hypotheses about the impacts of species abundances on trait dynamics was also formalised (Equation 1d). Here, candidate regression models were constructed in which the rate of trait change depended upon the abundance of different species, again using a multivariate tensor product smooth.

There was a high degree of collinearity between the measurements of several traits. Those showing strong correlation, such as body length and width, were reduced to a single variable. The resulting candidate predictor variables describing prey traits were as follows: body size (Z_{size}; area μm^2), swimming speed (Z_{speed}; μm/s), displacement rate (Z_{disp} describing the linear distance of habitat explored; μm/s) and turning angle variability (Z_{turn}; describing the variability of movement direction; radians turned per second). Finally, the composition of the resource population was also used as a putative predictor of changes in species abundances (Y_R), using the proportion of the total resource that was categorised into the secondary rarer bacterial class as an additional candidate model covariate. We constructed the models described in Equation 1, including (or excluding) each prey trait individually, and including (or excluding) the resource composition information.

Model comparison

To test whether the inclusion of trait information improved our ability to explain and predict community dynamics, the trait-dependent community models were compared with the null model based on abundance only. Models that are trained and cross-validated out of sample are expected to predict observed dynamics very poorly if they are overfitted and do not describe biological processes that produce signal in the data. Leave-one-replicate-out cross-validation was used to compare the predictive ability of each candidate model. To achieve this, all but one replicate was used to parameterise a candidate model and the remaining replicate was used to quantify the model's predictive performance. Predicted population changes between each observation were compared against the observed data and the root-mean-square error (RMSE) was calculated to quantify model prediction error. For each model, this process was repeated, sequentially leaving out each replicate and measuring RMSE.

3 | RESULTS

All populations persisted for the duration of the experiment and the observed dynamics were consistent between replicates. We observed substantial variation in the species abundances, traits and the resource composition over time (Figure 1). Resource density showed a declining trend, but spikes of increased abundance were consistently found (Figure 1a). Prey density initially increased rapidly with an estimated growth rate of 1.01 cell divisions per day (±0.11), prior to the invasion of predators. This is highly consistent with previous estimates under similar experimental conditions (Beveridge et al., 2010; Laybourn, 1976). Prey abundance plateaued and subsequently declined after 40–50 days (Figure 1b). Predator density increased after its invasion at an initial growth rate of 0.46 cell divisions per day (±0.10). Predator density fluctuated and declined around the same time as the prey (Figure 1c).

Prey body size decreased substantially over the course of the experiment (66% reduction), with synchronous fluctuations identifiable across replicates (Figure 1d). The highly significant body size reduction was found when comparing prey from populations that were exposed to predation over the course of the experiment with populations that were not exposed to predation but were kept in otherwise identical environmental conditions (n = 535, df = 6, χ^2 = 387.08, p < .001; Data S3). Finally, the resource composition also showed marked variation in the relative frequency of different bacterial types over the duration of the experiment. The rarer resource class fluctuated in relative abundance, accounting for between 20% and 40% of the total population (Figure 1e).

3.1 | Predicting community trait–abundance dynamics

The dynamics of all species densities and the body size of the prey were accurately captured by the best-performing trait-dependent community model (Figure 1; model prediction lines vs. coloured data points). We compared the predictive ability of community models that included different information about prey traits and the resource composition (Figure 2). Including prey body size and resource composition information produced the largest reduction in the community models prediction error. The greatest explanatory power was obtained by both (1) allowing prey body size to influence predators–prey (f_{NP}) and prey–resources (f_{RN}) interactions and (2) letting the resource composition influence its growth rate (g_{RR}) and its consumption by prey (f_{RN}; Table 1). The inclusion of these factors individually was not sufficient to greatly reduce prediction error, but together they gave a 16.3% reduction in out of sample cross-validation prediction error and improved the models predictive ability, increasing the average r^2 from 34% to 57% (Table 2).

The inclusion of behavioural prey traits in combination with the resource composition information provided smaller improvements in the models predictive performance (Figure 2). Contributions of these behavioural and morphological traits may further influence species interactions. If enough dynamic variability is observed in abundance time series, the combined impacts of multiple prey traits could be tested. However, such models would require many more parameters and risk over fitting to the current dataset.

3.2 | Projecting community dynamics with/without feedbacks

Without the inclusion of the trait–abundance feedback, the growth rate of the prey cannot be reconciled with the subsequent dynamics of other species (Figure 3, second row) and the dynamics of prey

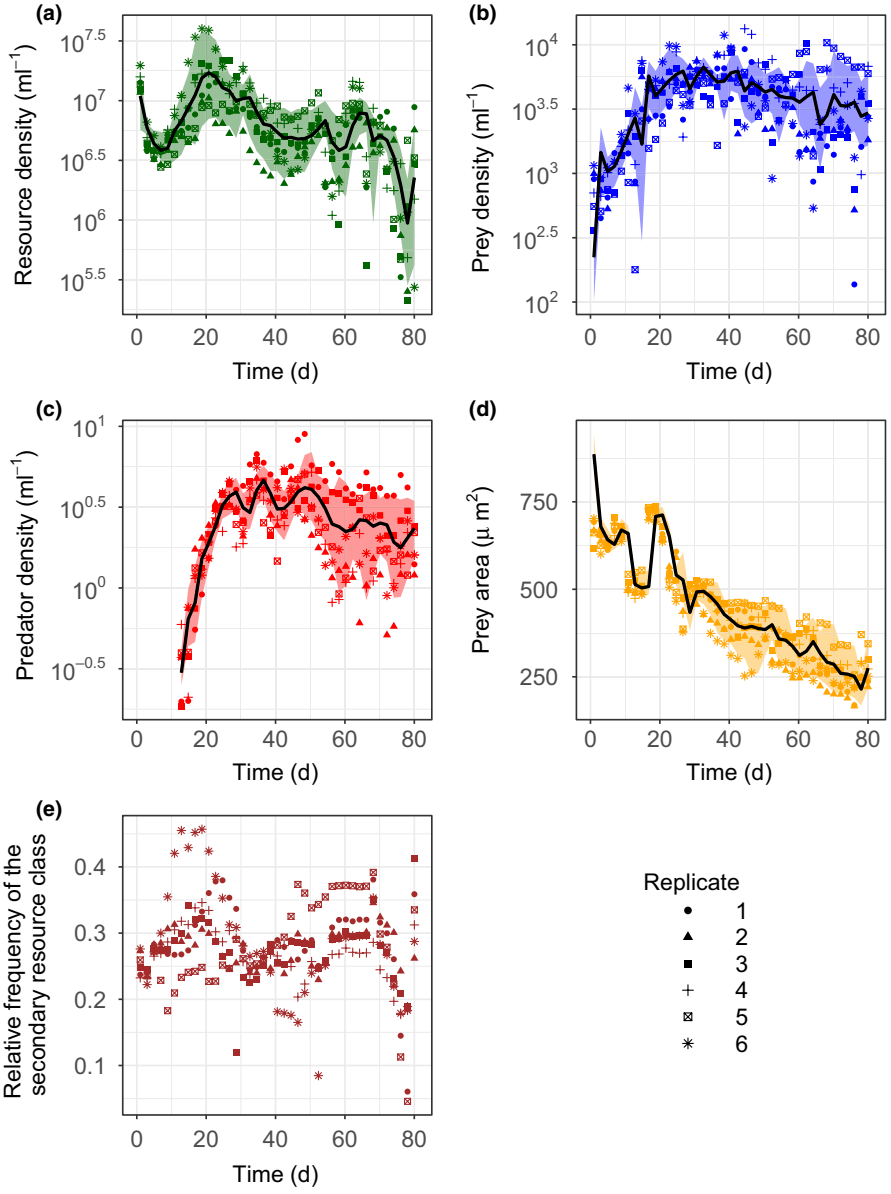

FIGURE 1 The observed and predicted dynamics of (a) resources, (b) prey, (c) predators, (d) prey body size and (e) the resource composition over the experiment. Predator additions were first made on day 12. Observations are shown by points which vary in shape according to the replicate. The mean one-step-ahead predictions of the best-performing trait-dependent community model are indicated by the black lines. The coloured shaded regions indicate the range of the states predicted across all replicates at a given time. The trait-dependent community model did not provide predictions of the resource composition dynamics and so only data points are presented

body size were not explained (Figure 3, bottom row). Linking species abundance dynamics with the prey body size dynamics improved the accuracy of the community models in describing the observed prey and resource time series and provided smaller improvements in the projection of predator abundances (Figure 3, third row; Table 2). Incorporation of predator traits would likely allow further improvement in the projection of this species' dynamics. By linking species abundances with trait dynamics, the dynamics of prey body size could also be explained (Figure 3, bottom row).

3.3 | Rate–trait relationships

The trait-dependent community models allowed a detailed understanding of the relationships between species' abundance and trait dynamics. The parameterised model revealed density-dependent processes and species interactions that were consistent with theoretical expectations (Figure 4). The resource growth rate showed negative density dependence, as expected when a finite nutrient supply limits population growth (Figure 4a). Consumption rates of both the predator and the prey increased with the density of their respective prey. The consumer interactions between the prey and the resource (Figure 4b) exhibited a functional form similar to a type I functional response when prey individuals were large and similar to a type II functional response when prey individuals were small (Holling, 1965). A similar pattern of trait-dependent consumption of prey by the predator was also found (Figure 4c).

Inclusion of resource composition information into the community model revealed that the resource growth rate depended upon its composition. Resource growth decreased as the population became increasingly comprised of the secondary resource class (Figure 4a; line transparency). The consumption rate of resources by the prey was also influenced by the resource composition, but the effect was overwhelmed by the effect of the prey's size. Initially, when prey was

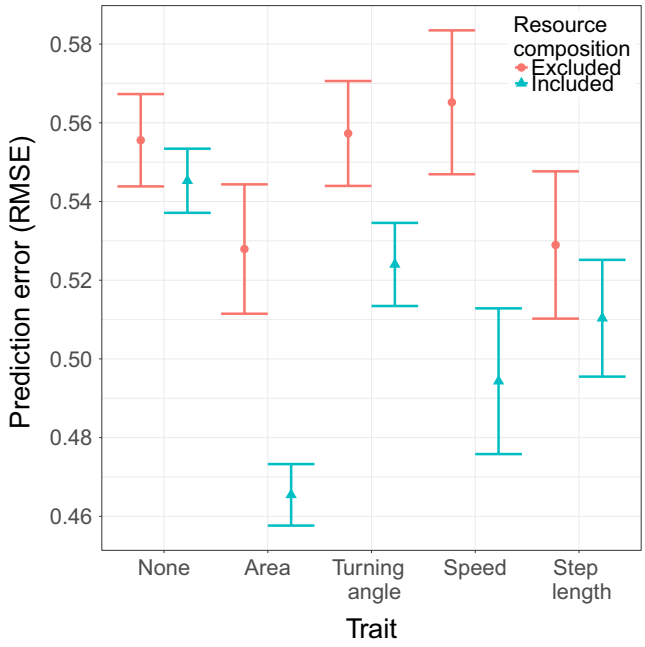

FIGURE 2 Predictability of changes in species abundances in population models containing different combinations of information about prey traits (*x*-axis) and the resource composition (bar colour). The predictability is quantified by measuring the prediction error between the observed rates of change of species abundances and model predictions, based on the root-mean-square error (RMSE) of predictions during cross-validation (lower RMSE is better; *y*-axis truncated). Error bars show the confidence interval of the prediction error observed between rounds of the cross-validation, the midpoint being the mean prediction error

added to the bacterial resource, they were relatively large and consumed resources at a fast rate. The prey gradually became smaller and consumed resources more slowly (Figure 4b; line colour). The initially high per capita consumption rate of the prey, along with minimal prey search durations and lower resource defence, produced the rapid initial declines in resource density. The consumption rate of prey by the predator was also dependent on the size of prey, with larger prey being more rapidly consumed (Figure 4c; line colour). As prey individuals gradually became smaller, they were consumed less by predators and ingested resources at a lower rate.

The considerable decline in prey size (Figure 1d, Data S4) was related to higher densities of predators (Figure 4d; line colour) and prey (Figure 4d; *x*-axis). The latter effect of prey abundance may reflect a delayed feedback from resource availability, as current resource abundance did not help explain body size change. The negative effect of increased predator abundance on body size indicates that predation pressure is either directly selecting for smaller individuals or indirectly causing altered resource allocation to growth.

4 | DISCUSSION

In this study, we identified traits that were modified by the ecological conditions and simultaneously influenced demographic rates and community dynamics. This allowed us to quantify the trait dependence of species' growth and consumption rates. It also allowed us to understand how changes in species' densities feedback to drive trait change. Our results revealed a rich network of relationships among traits and resource, prey and predator abundances and demonstrated how inclusion of trait–abundance feedbacks increase the ability to predict ecological dynamics (Figure 5). We found that the temporal changes in species' trait-dependent interactions were consistent with the development of costly defences against predation. The findings indicate that changes in prey size can be understood through a consideration of growth–defence trade-offs in resource allocation.

4.1 | Body size-dependent prey interactions

Body size mediates the strength of predator–prey interactions in many ecological systems (Brooks & Dodson, 1965; Tucker, Hipfner, & Trudel, 2015; Yoshida et al., 2004; Zaret & Kerfoot, 1975). The substantial two-third reduction in prey body size observed over the course of our experiment was found to be coupled with two important community processes: the top-down effect of predation and the bottom-up effect of resource availability and consumption. We identified that temporal changes in *Colpidium* body size modified its vulnerability to predation by *Stentor* and its per capita resource consumption rate. As body size declined, partially driven by reduced resource availability, the vulnerability of prey (*Colpidium*) to predation decreased, but they also consumed resources at a lower rate. These ecological impacts may result from changes in either the life history or resource allocation of the prey.

The reduced vulnerability to predation at small sizes could have been attained through some combination of: (1) reduced frequency of predator encounter, (2) investment in physical defence, (3) improved escape/avoidance behaviour when encountering predators or (4) predator saturation through increased consumption time, for example if smaller individuals invest in the production of tissues that are difficult to digest. If high predator density caused prey to reduce their movement and foraging in order to reduce predator contacts, we would have expected the inclusion of movement rate information into our community model to have improved our ability to explain changes in species abundances. We found that including movement rate information (along with resource information) provided some improvement in model prediction. However, the role of changes in movement characteristics appears much smaller than the impacts of body size. It is plausible that behavioural modifications occurred very rapidly, making the effects difficult to detect. For example, an improved ability to escape following predator encounters may have occurred rapidly if *Colpidium* utilise chemical cues or developed an aversion to the vortex of *Stentor's* filtering. Such mechanisms have been proposed to be common in ciliates (Kusch, 1993; Roberts, Legrand, Steinke, & Wootton, 2011). However, we have no direct measurements of such kairomones or rapidly induced aversion behaviours in *Colpidium*. There was also no obvious evidence of physical defence in *Colpidium*. Chemical defences are

TABLE 1 Comparisons between the performance of alternate community models. Models differ in whether they include (+) or exclude (−) impacts of prey size (Z_{Area}) and the resource composition (Y_R) on resource growth rate (g_{RR}), the prey–resource interaction (f_{RN}) and the predator–prey interaction (f_{NP})

f_{RN} (Z_{Area}, …)	f_{NP} (Z_{Area}, …)	g_{RR} (Y_R, …)	f_{RN} (Y_R, …)	log Likelihood	*df*	AIC	ΔAIC	Rank
+	+	+	+	−252.8	38.8	699.6	0.0	1
+	+	+	−	−320.4	35.3	711.5	11.9	4
+	+	−	+	−322.6	36.7	718.6	19.0	5
+	−	+	+	−338.0	32.5	741.1	41.5	7
−	+	+	+	−322.1	32.9	709.9	10.4	2
+	+	−	−	−371.9	32.1	808.0	108.4	14
+	−	+	−	−345.5	28.5	747.9	48.3	11
+	−	−	+	−341.9	30.4	744.6	45.0	10
−	+	+	−	−325.6	29.9	711.1	11.6	3
−	+	−	+	−335.0	29.1	728.3	28.7	6
−	−	+	+	−344.4	26.8	742.3	42.7	8
+	−	−	−	−396.7	24.1	841.5	141.9	16
−	+	−	−	−376.6	26.5	806.1	106.5	13
−	−	+	−	−348.1	23.7	743.5	43.9	9
−	−	−	+	−353.9	23.0	753.9	54.3	12
−	−	−	−	−398.4	19.8	836.5	137.0	15

The community model with the highest degree of support is coloured grey.

TABLE 2 Comparison of the proportion of variance (R^2) in species population densities explained by models including or excluding a feedback between species abundances and the dynamics of the ecologically important trait of body size

	Coefficient of determination (R^2)	
Predicted state variable	Trait–abundance feedback model	Trait-independent model
Resource density	0.4	0.1
Prey density	0.6	0.4
Predator density	0.7	0.5
Prey body size	0.7	—

usually associated with protist species that have pigmented granules (Miyake, Harumoto, & Iio, 2001). Finally, the handling time of captured prey may have increased if predators required longer to capture, subdue and digest prey. Such changes have previously been reported in similar protist systems and may be related to an altered cellular composition (Hammill, Petchey, & Anholt, 2010). The lower resource consumption in smaller prey is likely an acclimatory response to low energy inflow by switching to a life history strategy that uses minimal resources. Several previous studies provide evidence that *C. striatum* responds to decreased productivity or lower effective prey availability by decreasing cell size (Balciunas & Lawler, 1995; Jiang & Morin, 2005). Predator-induced changes in growth rates and defence have also been observed (Fyda et al., 2005; ter-Horst et al., 2010); however, the links between individual traits, demographic rates and community dynamics have not previously been made (Kishida et al., 2010).

4.2 | Prey trait change: feedback with species densities underpinned by a growth–defence trade-off

Changes in the abundance of predators, competitors and resources drive trait change in many ecological systems (Brooks & Dodson, 1965; Pelletier et al., 2009; Travis et al., 2014). Such trait changes can influence ecological and evolutionary dynamics in wild populations (Pelletier et al., 2007; Pettorelli et al., 2015; Travis et al., 2014). We linked the observed body size reduction in prey during the experiment with increases in the abundance of both predators and conspecific competitors. As body size was also found to influence the abundance of these species, by influencing trait-mediated interactions; a feedback loop was identified between the ecological impacts of the trait change and the future selection pressure on the body size trait in the prey.

Similar predator-driven changes in body size that follow the expectations of growth–defence trade-offs appear to be common in microbial and various other systems (Kishida et al., 2010; Kratina, Hammill, & Anholt, 2010; Wiackowski & Starońska, 1999). For example, Fyda et al. (2005) observed that *Colpidium* exposed to predation by *Euplotes* or *Stylonychia*, became shorter and wider. In systems where predators hunt for prey more active, such as fish–zooplankton communities (Brooks & Dodson, 1965; Travis et al., 2014), predation is often size selective. Predators may preferentially attack larger individuals to obtain greater energetic gains per attack. Although *Stentor* is known to exhibit preferential feeding on certain prey species, prey consumption is thought to be unrelated to prey size (Rapport, Berger, & Reid, 1972; Tartar, 1961). Therefore, direct size selective predation may not have been the major driver of the reduction in prey size. Instead, it may have been largely an indirect outcome of modified prey energetic

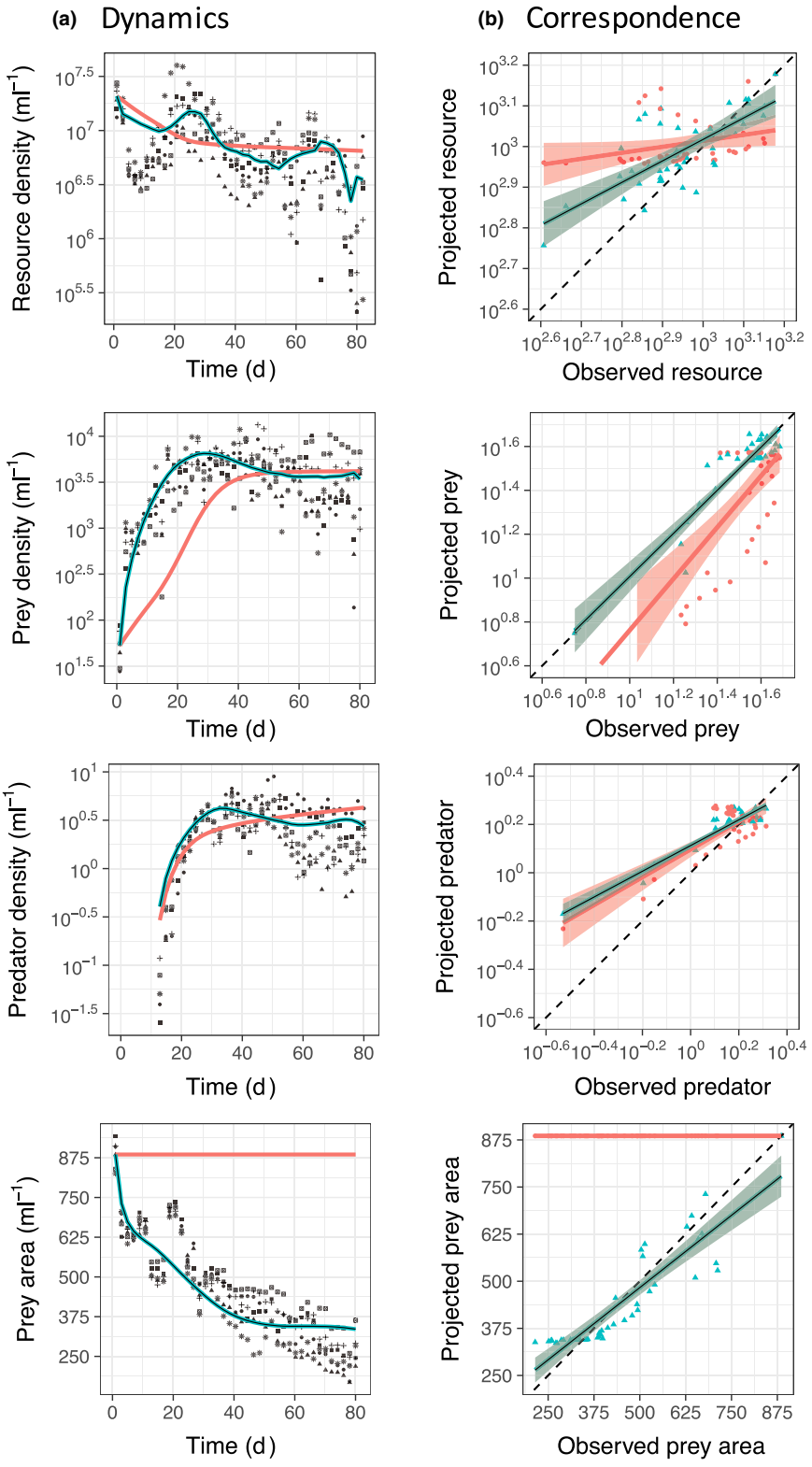

FIGURE 3 Comparison between observed abundance/trait values and the projections of models including trait–abundance feedbacks (blue) or excluding them (red). In subpanel (a), the dynamic projections of the deterministic skeleton of the trait-dependent (red) and trait-independent (blue) community models are overlaid on the observed species abundance and prey body size dynamics. Projections are made for the entire duration of the experiment using the model and only the initial conditions of the system. In subpanel (b), the correspondence between model projections and the mean empirical observations at each time point are presented. Linear regression is used to summarise the relationship, and shaded regions show the standard errors of the regression. Dashed black lines indicate the 1:1 relationship between observations and predictions

investment, driven by the trade-off between growth and defence. That is, prey may have reduced their resource investment into somatic growth due to an energetic cost of defence (Bolker et al., 2003; Riessen & Sprules, 1990; Schmitz, Beckerman, & Brien, 1997) or by modifying their life history strategy to allow earlier cell division (Finlay, 1977; Travis et al., 2014).

4.3 | Resource growth–defence trade-off

The rapid emergence of defence appears to be common in the basal trophic levels of experimental aquatic food chains (Lampert, 1994; Yoshida et al., 2003, 2004). Protist grazing on a bacterial resource can lead to rapid changes in bacterial morphology, providing defence

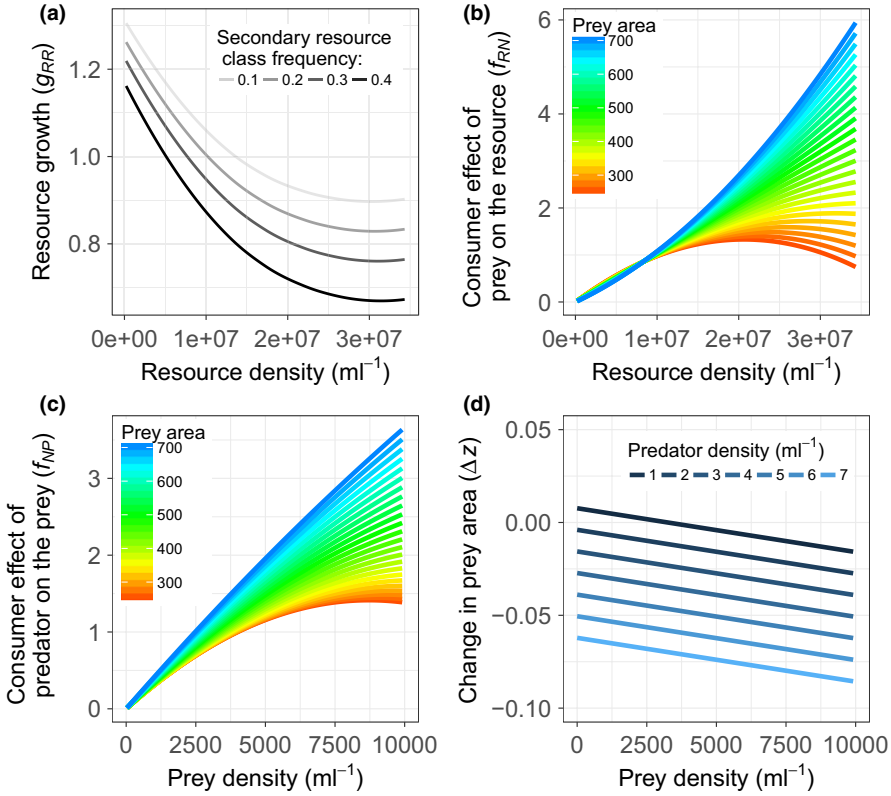

FIGURE 4 The trait and density dependence of community processes and the density dependence of trait change, identified in the empirically derived community model. The model revealed the following: (a) the impact of the resource composition on its density-dependent population growth (line transparency), (b) the impact of prey body size (colour) on the preys' rate of resource consumption, (c) the impact of prey body size on the predators' rate of prey consumption and (d) the impact of predator and prey density (brightness of blue) on prey body size. Subpanels show slices through the continuous functions describing (a) resource composition-dependent resource growth (b/c) trait-dependent consumer–resource interaction surfaces

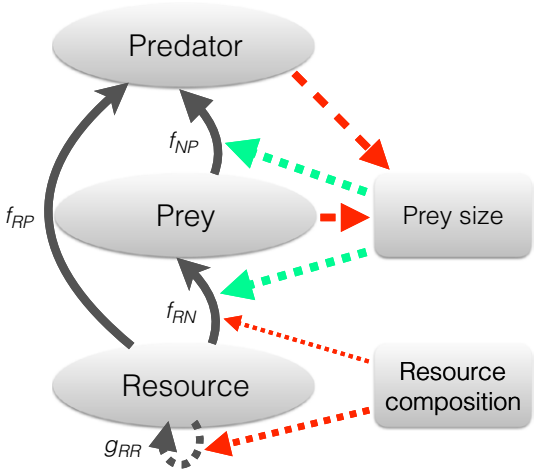

FIGURE 5 The key relationships identified in the predator–prey–resource microbial system. Ecological interactions between species are depicted by curved solid arrows and labelled with the model function describing each process. The dashed circular line signifies resource density-dependent growth rather than an interspecific interaction. Prey body size and resource composition influenced species consumptive interactions and density-dependent population growth (coloured dashed lines). Positive relationships between consumption rates and the preys body size are signified by green arrows. Negative relationships between resource growth/prey consumption rates and the proportion of the resource composed of the secondary resource type are signified by red arrows. Predator and prey density negatively influenced prey body size (red dashed lines), creating feedbacks between the dynamics of species traits and population abundance

against predation and incurring an energetic cost to the bacteria (Corno & Jürgens, 2006; Hahn & Höfle, 1999; Pernthaler, Posch, & Simek, 1997). The reduction in prey consumption rate and population growth was linked to an increase in the rarer secondary resource class. As the *Colpidium* prey is known to show selective feeding behaviour (Thurman et al., 2010), it is likely that this shift in resource composition was driven by the strong consumptive selection pressure, representing a transition towards a population dominated by better defended and slow-growing bacteria. The developmental of traits promoting microcolonies have been shown to confer resistance to protist predation in *S. marcescens*, and the characteristics of the secondary resource class match these expectations (Friman et al., 2013; Queck et al., 2006). Direct observations of the bacterial population would help to determine whether the mechanism driving the increased defence of the bacterial resource results from intra- or interspecific changes.

Overall, our results provide evidence of a feedback between trait change and species dynamics. The feedback appears to be underpinned by a growth–defence trade-off in resource allocation, mediated by changes in the defence or life history of the species being consumed. Our findings indicate that theoretical frameworks for understanding trait or community dynamics will perform poorly in isolation. Theories of trait-dependent ecological interactions and ecological dependent trait change are now well developed; however, there is a clear empirical gap. A more mechanistic understanding of the nature of defence is required across ecological systems as well as a quantification of fitness costs and benefits. This will allow an improved understanding of the process driving the trait dependence of ecological

rates and the rates of trait change. Empirically derived models are needed to link these empirical insights with theoretical frameworks to understand the feedbacks between trait and abundance dynamics. This study shows the value of including trait information for improving predictive power and pinpointing underlying mechanisms driving community abundance and trait dynamics. It also shows the relative ease with which the approach could be implemented in a reasonably complex community. It therefore makes a convincing case for wider adoption of the framework for linking community trait and abundance dynamics.

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AUTHORS' CONTRIBUTIONS

J.I.G., D.Z.C. and O.L.P. conceived the ideas and designed methodology; J.I.G. and F.P. developed empirical methodologies and collected the data; J.I.G. and D.Z.C. analysed the data; J.I.G. and D.Z.C. led the writing of the manuscript. All authors contributed critically to multiple drafts and gave final approval for publication.

DATA ACCESSIBILITY

The experimental dataset generated and analysed in this study is available from the Dryad Digital Repository https://doi.org/10.5061/dryad.675mr (Griffiths, Petchey, Pennekamp, & Childs, 2017).

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