

Life history traits and functional processes generate multiple pathways to ecological stability

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Abstract. Stability contributes to the persistence of ecological communities, yet the interactions among different stabilizing forces are poorly understood. We assembled mesocosms with an algal resource and one to eight different clones of the consumer *Daphnia ambigua* and tracked algal and *Daphnia* abundances through time. We then fitted coupled ordinary differential equations (ODEs) to the consumer–resource time series. We show that variation in different components of stability (local stability and the magnitude of population fluctuations) across mesocosms arises through variation in life history traits and the functional processes represented by ODE model parameters. Local stability was enhanced by increased algal growth rate and *Daphnia* mortality and foraging rate. Population fluctuations were dampened by high *Daphnia* conversion efficiency and lower interaction strengths, low algal growth rate, high *Daphnia* death rate, and low *Daphnia* foraging. These results indicate that (1) stability in consumer–resource systems may arise through the net effect of multiple related stabilizing pathways and (2) different aspects of stability can vary independently and may respond in opposite directions to the same forces.

Key words: consumer–resource dynamics; *Daphnia*; differential equation fitting; diversity; functional traits; life history; paradox of enrichment; phenotypic dissimilarity; stability.

INTRODUCTION

Understanding the mechanisms underpinning stability in natural communities is essential for predicting how complex ecological communities persist (MacArthur 1955, May 1972, Tilman and Downing 1994, McGrady-Steed et al. 1997). Species richness, network structure, interaction strength, and primary productivity all influence community stability (MacArthur 1955, Rosenzweig 1971, May 1972, Tilman and Downing 1994, McGrady-Steed et al. 1997, Allesina and Pascual 2007). In addition, intraspecific variability, both genetic (Jones et al. 2004, Hughes et al. 2008, Agashe 2009, Steiner and Masse 2013) and phenotypic (Gibert and Brassil 2014, Gibert and DeLong 2015), can stabilize biological communities. This is because individuals from the same population with different phenotypes can interact with other individuals in a community in different ways, potentially

altering network structure and interaction strengths (Gamfeldt and Källström 2007, Hughes et al. 2008, Bolnick et al. 2011, Violle et al. 2012). How these stabilizing mechanisms interact and whether they simultaneously influence stability within any given community is, however, unknown.

Two distinct aspects of community stability are fluctuations, or how widely population abundance ranges through time, and local stability, or whether a population returns to an equilibrium state after a small perturbation. Although they are fundamentally related, different mechanisms may influence each aspect of stability in unique ways (McCann 2011, Donohue et al. 2013). Local stability is often closely tied to the strength of interactions among interacting populations; for example, strong interactions may lead to overexploitation of resources and prevent recovery from low population size (Yodzis 1981, McCann et al. 1998, May 2001, Gilbert et al. 2014). In contrast, fluctuations may be linked to system productivity if it influences the location of zero-growth isoclines (Rosenzweig 1971, McCauley et al. 1999). Yet whether these two aspects of stability are influenced by the same mechanisms, and how traits and system properties actually alter stability via the

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mechanisms generating the community dynamics, is poorly understood.

The stability properties of an ecological community are linked to the birth and death rates of the community's constituent species, as differences between birth and death rates drive the direction and magnitude of changes in abundance through time. Birth and death rates, in turn, are linked to the life history traits that describe how individuals allocate resources to competing fitness ends. Thus, variation in life history traits within a population could lead to variation in birth and death rates, generating variation in dynamics and stability associated with the traits (Yoshida et al. 2003). In this study, we assembled mesocosms with *Daphnia ambigua* (hereafter just *Daphnia*) consuming the alga *Scenedesmus obliquus*, which represents a simple yet critical component of most lake food webs. The *Daphnia* populations varied in genotypic composition, having been initiated with different combinations of genotypes with known variation in life history traits (DeLong and Hanley 2013). We sought to determine whether variation in *Daphnia* life history traits and genotypic composition could influence the stability properties of this consumer–resource system.

To uncover the mechanisms linking life history traits to stability properties, we employ a comparative ordinary differential equation (ODE) fitting approach (Ellner et al. 2002, Raue et al. 2009, DeLong et al. 2014). By fitting a consumer–resource ODE to the abundance time series for each mesocosm, we identified model parameters and estimated local stability for each mesocosm. The model parameters themselves are not life history traits, as they are composite parameters that aggregate multiple underlying processes. We thus refer to model parameters (such as parameters of the functional response) as functional processes, which we can then use to identify mechanistic links between life history traits and stability. In this way, we combine theoretical and empirical approaches to generate new insights about how traits influence ecological stability. Our results indicate that stability is multifaceted, even in a relatively simple consumer–resource system. Different aspects of stability are simultaneously influenced by different mechanisms involving the joint effect of life history traits, species interactions, and the processes of finding, capturing, and digesting prey.

MATERIALS AND METHODS

We constructed 28 replicate 20-L mesocosm communities with *Daphnia ambigua* (*C*) consuming the alga *Scenedesmus obliquus* (*R*). These organisms represent key components of naturally occurring freshwater food webs, and because both can reproduce clonally, they are particularly well suited as a model system to address our questions. We used COMBO medium (Kilham et al. 1998) and included one, two, four, or eight *Daphnia* genotypes that were randomly selected from a pool of 12 genotypes hatched from sexually produced ephippia collected from Bride Lake (East Lyme, Connecticut, USA). Algae were

added first at a concentration of 1 mg C/L, and then 40 adult *Daphnia* of approximately the same size and age (16 of which were carrying eggs) were added to each mesocosm five days later. Equal proportions of each genotype and equal numbers of *Daphnia* with and without eggs for each genotype were added to each polyculture (two, four, and eight genotypes), minimizing differences in the initial size, age, and egg number of *Daphnia*. We included in our analysis only the time from *Daphnia* additions onward. Algal population densities at the beginning of the experiment were 43,000–128,000 cells/mL. The experiment was conducted indoors at room temperature (~22°C) with a light:dark cycle of 18 h:6 h; temperature and light intensity were monitored regularly and each mesocosm was stirred daily.

We monitored population densities of both species two or three times per week for ~60 d. For algal density, each mesocosm was stirred prior to sampling, 3–5 mL were collected from the center of the mesocosm using a pipette, and cell density was quantified (based on four replicate counts) using a laser particle counter (Spectrex PC-2200, Redwood City, California, USA). For *Daphnia* density, each mesocosm was stirred prior to sampling, and 1 L was collected using a pipette, ensuring relatively equal representation of different depths and locations. Each sample was filtered using 80- μ m mesh, preserved in 70% ethanol, and subsequently counted to determine *Daphnia* density. After each *Daphnia* sampling, we added 1 L COMBO medium to each mesocosm to maintain consistent volume during the experiment. Both *Daphnia* and the algae persisted in all mesocosms for the whole time frame.

In a previous study (DeLong and Hanley 2013), we measured juvenile growth rate, asymptotic size, and fecundity for 10–14 individuals (third or fourth clutch neonates) of each clone included in the current experiment. We used a fit of the von Bertalanffy growth equation to time series of body size to estimate asymptotic size, daily changes in juvenile size to estimate juvenile growth rate, and counts of clutch sizes to determine fecundity. We calculated population-level mean traits from the identities of constituent genotypes, and Euclidean distances between life history traits provided a measure of phenotypic dissimilarity (a proxy for phenotypic variability) in multi-clone mesocosms.

We fit ordinary differential equations (ODEs) to each mesocosm time series using the Potterswheel toolkit in Matlab (Maiwald and Timmer 2008) to identify the parameters that drive variation in the dynamic properties of each community. We used a Lotka–Volterra type consumer–resource model with logistic growth for the algae:

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - aRc \quad (1)$$

$$\frac{dc}{dt} = eaRc - dC. \quad (2)$$

In this model, r is the intrinsic rate of growth of *Scenedesmus*, K is its carrying capacity, a is the space clearance

rate of the consumer *Daphnia* (i.e., the volume of habitat cleared of prey per predator per time), e is the efficiency of converting algae into new *Daphnia* (i.e., the number of *Daphnia* produced per alga consumed), and d is *Daphnia*'s background death rate. These model parameters represent important functional aspects of the consumer–resource interaction, such as finding prey (a) and transforming prey energy into new consumers (e), and vital rates such as per capita growth (r) and death rate (d). We thus refer to model parameters as *functional processes* that reflect the underlying functional allocation of energy to growth, reproduction, and maintenance. More complex models that included a type II functional response and interference competition (DeLong et al. 2014) produced marginally better fits (i.e., lower χ^2 values), but Akaike information criterion corrected for sample size (AIC_c) values indicated that the model with fewer parameters (Eqs. 1, 2) avoided overfitting and was better supported for nearly all communities given the data (Appendix S1: Table S1). All of the model parameters in Eqs. 1, 2 were identifiable with profile likelihood-estimated 95% confidence intervals (Appendix S1: Table S2; Raue et al. 2009). In contrast, confidence intervals for several parameters were not identifiable when fitting the more complex models, and thus our data indicate that these parameters are functionally zero in this context. The tested models were nested, with the first adding handling time and the second adding interference to Eqs. 1,2. Therefore, parameters that are identified as zero reduce the model to the next simpler version. We emphasize that our inability to detect handling time and interference competition in this analysis may reflect the particular state space the systems traversed rather than the absence of those processes for *Daphnia* consuming algae generally (Hansen et al. 1997). Thus, our use of the simpler model for analysis represents a conservative approach that focuses on the processes actually identifiable in our data.

For six of the 28 replicates, the fitting procedure was unable to find parameter sets that described the data well (Appendix S1: Fig. S4), regardless of model, so 22 replicates were used in this study (10 mesocosms with one, six with two, three with four, and three with eight genotypes). Excluding the six poor-fitting replicates greatly reduced uncertainty in our correlation analysis. In addition, the six omitted time series replicates reduced our sample size by about the same amount (17–25%) within each genotype richness treatment, minimizing the chance of potential bias caused by excluding some richness treatment replicates at a higher rate than others.

We estimated local stability for each mesocosm using the real part of the dominant eigenvalue from the Jacobian matrix for Eqs. 1 and 2 evaluated at equilibrium, parameterized with the mesocosm-specific parameters obtained from model fits. We used the coefficient of variation (CV) of algal population density as a measure of the magnitude of fluctuations; since all mesocosms were initiated with the same densities, the CV provides a

measure of how widely populations swing during the initial cycle. We calculated interaction strength (IS) as the ratio of algal carrying capacity to the equilibrium abundance of algae in the presence of the consumer (Gilbert et al. 2014), using the same parameters as represented in Eqs. 1 and 2: $IS = Keald$. Many other interaction strength metrics are available, but this metric integrates several aspects of the consumer–resource interaction and characterizes the strength of the flux of energy from resource to consumer, making it an informative metric (Novak and Wootton 2010, Gilbert et al. 2014). Although links between model parameters and IS are expected given the way we calculated IS, limited variation in parameters across mesocosms and/or correlations among parameters might alter the net effect of life history traits and functional processes on stability. We used correlation analysis to assess relationships among life history traits, functional processes, and stability metrics, and we also tested whether any of these correlations were nonlinear using a quadratic term in a regression model. We then used these correlations to suggest possible pathways of stabilization in this system.

RESULTS

For the 22 mesocosms used in this study, the time series were well described by Eqs. 1 and 2, even with considerable variation in the dynamics of the communities across mesocosms (Fig. 1). All fitted models had negative dominant eigenvalues, indicating that all mesocosm communities were locally stable (Appendix S1: Fig. S1). The two aspects of stability, level of fluctuations and local stability, were influenced by different aspects of the system. A correlation analysis suggests three distinct possible pathways for stabilization in this consumer–resource system: a life history-fluctuations pathway, a functional processes-fluctuations pathway, and a functional processes-return time pathway (Fig. 2). Within-species variability in the form of genotypic richness and phenotypic dissimilarity had no effect on any model parameter or stability metric (Appendix S1: Fig. S2). Similarly, algal carrying capacity K , which could indicate variation in mesocosm productivity, had no effect on other model parameters or stability metrics (Appendix S1: Fig. S2). Below we highlight the significant correlations among life history traits, functional processes (model parameters), and stability metrics, and all correlations are shown in Appendix S1: Fig. S2.

In the life history-fluctuations pathway, three inter-correlated life history traits, asymptotic size, juvenile growth rate, and fecundity, influenced stability through a chain of effects (Fig. 2). Although asymptotic size and fecundity were correlated with juvenile growth rate, only juvenile growth rate was related to stability. Juvenile growth rate was negatively correlated with conversion efficiency e , which positively influenced interaction strength and thus the magnitude of fluctuations. These

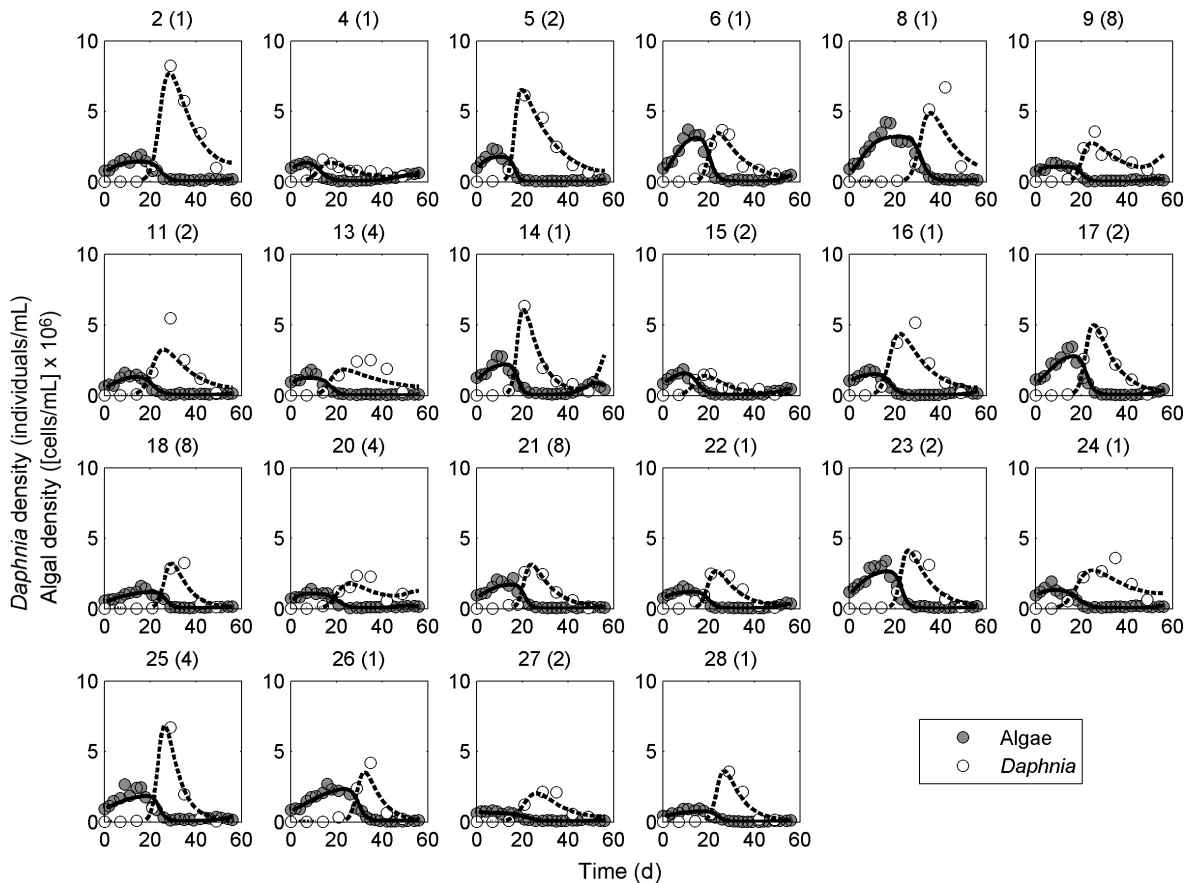


FIG. 1. Time series for 22 mesocosms of *Daphnia* and *Scenedesmus* communities with fitted model trajectories for each. The number in the title indicates mesocosm number and number of *Daphnia* genotypes in parentheses. Dashed line is *Daphnia* model prediction and solid line is algal model prediction.

three life history traits were not directly connected to any of the other model parameters.

In the functional processes-fluctuations pathway, three correlated model parameters, *Daphnia* death rate d , *Daphnia* space clearance rate a , and algal growth rate r , were linked to the temporal fluctuations through conversion efficiency e and the subsequent effect on interaction strength (Fig. 2). Increasing space clearance rate and algal growth rate were linked to greater interaction strength and thus the magnitude of fluctuations, while increasing death rate decreased interaction strength and fluctuations.

In the functional processes-return time pathway, these same three parameters, *Daphnia* death rate, *Daphnia* space clearance rate, and algal growth rate, were connected to stability through the dominant eigenvalues (Fig. 2). In this pathway, space clearance rate and algal growth rate were negatively correlated with eigenvalues (increased stability), and death rate was positively correlated with eigenvalues (decreased stability). All of these patterns were the same when fitting our data with a model that included handling time in a type II functional response rather than a type I (Appendix S1: Table S3).

Several fitted model parameters were correlated across the mesocosms (Fig. 3). It is possible that some of these correlations are structural (i.e., built into the model) or an artifact of the fitting procedure. For example, the product of conversion efficiency (e) and space clearance rate (a) is important to consumer growth, so different combinations of inversely correlated e and a may give similar rates of growth. We therefore tested our fitting procedure by generating simulated time series from Eqs. 1 and 2 with independently drawn random parameters for each correlated pair of parameters and using mean values from our empirical fitting for the other parameters. We then fitted the model to the simulated time series. If the correlation was generated as a statistical artifact or a structural correlation, we would expect to see a spurious correlation arise between the parameters estimated by our fitting procedure, even though the input parameters were independent. We conducted 100 simulations and fittings for each correlated parameter pair, and in all cases, the fitting procedure recovered the parameters and did not generate spurious correlations (Appendix S1: Fig. S3). Thus, the correlations between parameters reflect real

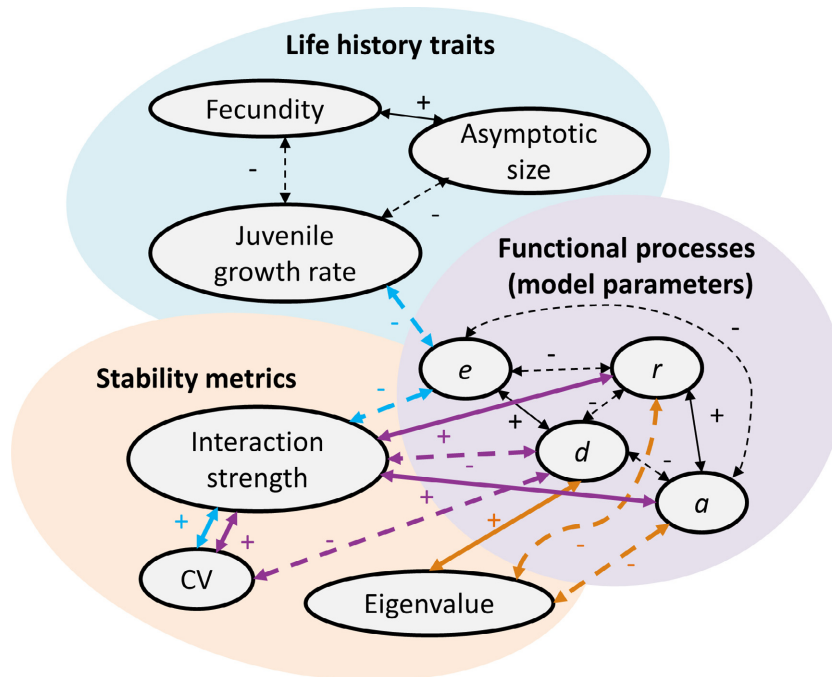


FIG. 2. Summary of significant correlations and pathways of stabilization in the *Daphnia ambigua*–*Scenedesmus obliquus* consumer–resource system. Positive correlations among variables indicated with a (+) and solid lines and negative correlations with a (–) and dashed lines. Colored arrows represent stability pathways: life history–fluctuations pathway (blue arrows), functional processes–fluctuations pathway (purple arrows), and functional processes–return time pathway (orange arrows). Eigenvalues indicate local stability and reflect the rate of return to equilibrium after a perturbation, and CV is the coefficient of variation that reflects fluctuations through time. Functional processes (model parameters) are *a* (*Daphnia* space clearance rate), *r* (algal intrinsic rate of growth), *d* (*Daphnia* death rate), and *e* (*Daphnia* conversion efficiency).

biological variation that arose across mesocosms rather than spurious, statistical artifacts. Two of these relationships were nonlinear, as indicated by a significant quadratic term in the model (Fig. 3). We nonetheless report correlation coefficients of all linear relationships for consistency in Table 1.

DISCUSSION

We detected three separate pathways through which variation in life history traits and functional processes across mesocosms were linked to stability in the *Daphnia*–*Scenedesmus* consumer–resource system (Fig. 2). The results revealed complex interactive effects of life history and functional processes that influenced the two aspects of stability (magnitude of fluctuations [CV] and return times [dominant eigenvalues]) in different, and sometimes opposite, directions. Surprisingly, none of these pathways involved the expected effects of increasing intraspecific diversity (neither genotypic nor phenotypic in this case) or productivity on stability (Rosenzweig 1971, Agashe 2009, Steiner and Masse 2013). However, there was evidence for the role of genotypic identity on stability through variation in life history traits and the functional processes represented by model parameters.

The first stabilization pathway involved links from life history traits to the coefficient of variation (Table 1, Fig. 2). Larger and more fecund *Daphnia* have young with slower juvenile growth rates, and juvenile growth rate was negatively linked to conversion efficiency. In principle, conversion efficiency is directly linked to asymptotic body size and fecundity (i.e., lifetime fecundity), as efficiency is higher when the consumers have more offspring and lower when consumers are larger (DeLong and Vasseur 2012). Nonetheless, in this experiment, conversion efficiency was correlated with juvenile growth rate and not asymptotic body mass or fecundity. This suggests that juvenile growth rate is integrating the effects of size and fecundity on conversion efficiency of *Daphnia*. Conversion efficiency was in turn negatively linked to interaction strength, which had a positive effect on the magnitude of fluctuations as expected (McCann 2011, Gilbert et al. 2014). This potential pathway represents a novel mechanistic depiction of how variation in life history traits actually leads to ecological stability.

The second pathway involved a set of inter-correlated functional processes linked to interaction strength and thus again the magnitude of fluctuations (Table 1, Fig. 2). All functional processes (model parameters) were correlated with each other across mesocosms except

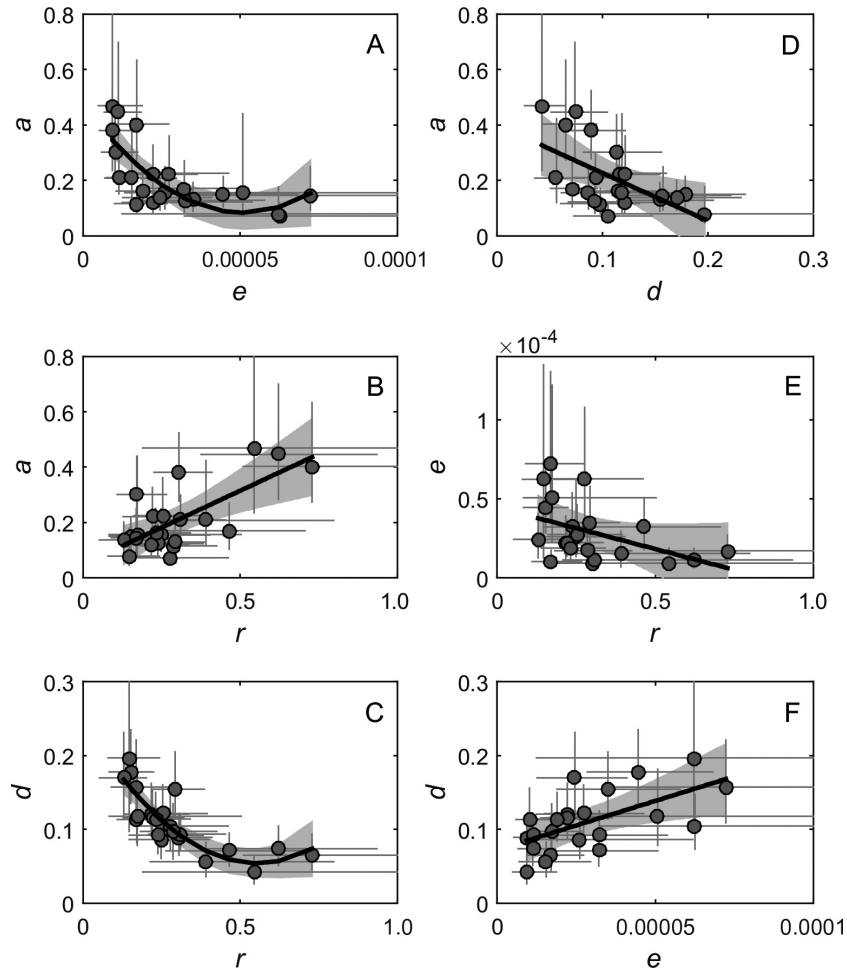


FIG. 3. Correlations among functional processes. Gray lines indicate 95% confidence intervals for each estimated parameter, black lines indicate the mean, and gray regions indicate 95% confidence band for the linear regression of each parameter on the other. Functional processes are a (*Daphnia* space clearance rate), r (algal intrinsic rate of growth), d (*Daphnia* death rate), and e (*Daphnia* conversion efficiency).

that space clearance rate (a) was not correlated with conversion efficiency (e) and algal carrying capacity (K) was not correlated with any other model parameter. These correlations have an unknown but real biological underpinning, as our simulation analysis indicates that the fitting procedure does not produce the correlations spuriously (Appendix S1: Fig. S3). The model parameters algal growth rate, space clearance rate, and *Daphnia* death rate all influenced interaction strength directly, and thus influenced the magnitude of fluctuations, but these parameters may also have had an indirect effect on interaction strength through conversion efficiency. Interestingly, some of the direct and indirect effects worked in opposite directions. For example, *Daphnia* death rate was negatively linked to interaction strength directly ($r = -0.71$), but positively linked to it via space clearance rate ($r = -0.61$), which then was positively linked to interaction strength ($r = 0.5$). In this case, the link between death rate and stability was tighter along the

direct pathway to interaction strength (higher correlation coefficients; Tables 1, 2), but a mix of different pathways indicates stabilization through linked functional processes is multifaceted.

The third pathway involved the same set of functional processes as in the second pathway, this time through their direct effect on dominant eigenvalues and thus the time it takes for the system to return to equilibrium after a perturbation (McCann 2011). Higher *Daphnia* death rates tended to make the system less stable, while higher algal growth rate and higher space clearance rate both increased system stability. These effects are somewhat surprising, as more effective consumers (with a higher space clearance rate) can rapidly exploit their resource base and generate fluctuations (Gilbert et al. 2014). Space clearance rate, however, did not vary independently of other model parameters, such that a higher space clearance rate was accompanied by a higher algal growth rate and a lower *Daphnia* death rate.

TABLE 1. Significant correlations among life history traits, model parameters, and stability metrics ($n = 22$ for all correlations).

Correlation between variables	r_p	P
r and a	0.72	<0.001
r and d	-0.74	<0.001
r and e	-0.45	0.036
a and d	-0.60	0.003
a and e	-0.63	0.002
d and e	0.61	0.002
a and eigenvalue	-0.59	0.004
r and eigenvalue	-0.79	<0.001
d and eigenvalue	0.51	0.014
r and interaction strength	0.76	<0.001
a and interaction strength	0.51	0.015
d and interaction strength	-0.71	<0.001
e and interaction strength	-0.44	0.04
d and coefficient of variation	-0.45	0.036
e and juvenile growth rate	-0.48	0.024
Interaction strength and coefficient of variation	0.78	<0.001
Asymptotic size and juvenile growth rate	-0.75	<0.001
Asymptotic size and fecundity	0.83	<0.001
Fecundity and juvenile growth rate	-0.62	0.002

Notes: Abbreviations are r (algal growth rate), a (space clearance rate), d (*Daphnia* death rate), e (conversion efficiency). Pearson's correlation coefficient (r_p) and significance level (P) are shown.

Previous experimental works have found a direct link between genetic diversity and stability (Agashe 2009, Steiner and Masse 2013). In this study, however, neither genotypic richness nor phenotypic dissimilarity was linked to stability. It is possible that an effect of phenotypic variation per se was swamped by the effects of specific genotypes, as there was clear evidence that life history traits (e.g., juvenile growth rate) that vary across genotypes played a strong role in determining interaction strength. Alternatively, individual variation in phenotypic traits can reduce interaction strength depending on the circumstances. For systems where the consumer is very well matched to its prey, more individual variation offsets the phenotype of individuals close to the optimum, lowering interaction strength. For systems where the consumer is less well matched to its prey, more individual variation can increase interaction strength for

some individuals, limiting the effect of variation on interaction strength (Gibert and Brassil 2014). Thus, we do not argue that individual variation is unimportant for stability in general, but that the effect may be more obvious for other consumer–resource pairs.

There has been a rich tradition of investigating the role of single factors in stabilizing communities (Rosenzweig 1971, May 1972, Tilman and Downing 1994, McCann et al. 1998, Arditi et al. 2004, Allesina and Pascual 2007, Agashe 2009). Our results demonstrate that stability in even simple two-species consumer–resource systems involves a complex tapestry of integrated effects. Furthermore, different components of stability were influenced by different pathways and were not correlated. Indeed, the three correlated parameters algal growth rate, *Daphnia* death rate, and space clearance rate influenced both aspects of stability but did so in opposite directions. For example, a high algal growth rate lowered eigenvalues (stabilized) and increased interaction strength (destabilized). Thus, actual stabilization in any specific natural system may arise through the net effect of multiple stabilizing pathways that may reinforce or conflict with each other (Donohue et al. 2013).

In conclusion, we leveraged the power of experimental diversity manipulations with a comparative ODE fitting approach. The results revealed multiple mechanisms of stabilization in a consumer–resource system that is critical to many lake food webs. Life history traits, interaction strengths, and multiple functional processes represented by model parameters all simultaneously altered the dynamics and stability properties of the system. Our analysis contributes important mechanistic insights into the generation of stability, which are essential to help predict the fate of ecological systems in the face of global environmental change.

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TABLE 2. Regression results for parameters on stability metrics, where slopes indicate relative magnitude of the effects.

Correlation between variables	Slope (95% CI)	P
a – eigenvalue	-0.067 (-0.11 to -0.024)	0.004
r and eigenvalue	-0.066 (-0.09 to -0.042)	<0.001
d and eigenvalue	0.17 (0.038 to 0.30)	0.014
r and interaction strength	1.18×10^6 (4.62×10^3 to 7.04×10^5)	<0.001
a and interaction strength	1.09×10^6 (2.41×10^5 to 1.95×10^6)	0.015
d and interaction strength	-4.36×10^6 (-6.40×10^6 to -2.32×10^6)	<0.001
e and interaction strength	-5.90×10^9 (-1.15×10^{10} to -2.96×10^8)	<0.001

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2070/supinfo>

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8h8q0>.