

Individual Variation Decreases Interference Competition but Increases Species Persistence

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Abstract

Interference competition is thought to stabilize consumer–resource systems. The magnitude of interference is linked to that of attack efficiency: when both levels are intermediate, populations are maximally stable and have high competitive ability. Individual variation can affect ecological dynamics through its effect on attack efficiency and handling time. Because interference has a non-linear effect on consumer foraging rates, individual variation in mutual interference can strongly affect ecological dynamics. Here, we explicitly incorporate individual variation in attack efficiency, handling time and interference into a dynamic consumer–resource model and show that variation increases species coexistence by depressing attack efficiency to a greater extent than predator interference. We argue that this differential effect of variation affects the

equilibrium densities of consumers and their prey, thus altering their competitive ability. Intermediate levels of variation can maximize both consumer persistence and competitive ability. Our results show the importance of quantifying individual variation in natural populations for understanding the persistence and stability of species within communities.



1. INTRODUCTION

A major goal of ecology is to understand the factors underpinning species coexistence and stability in complex ecosystems (Allesina and Tang, 2012; May, 1972, 1973; McCann et al., 1998). Seminal work by Tilman showed that when two competing species share a common resource, the one that can reduce resource density the most will outcompete the other (Tilman, 1982, 1986). However, the ability to reduce resource density and persist may depend upon the factors controlling interaction strengths and consumer–resource interactions. A number of these factors have received a lot of attention, including foraging behaviour (Abrams and Matsuda, 2004; Schmitz et al., 1997), consumer and resource body sizes (Vucic-Pestic et al., 2010) and relative velocities (DeLong, 2014; Pawar et al., 2012), prey defence mechanisms (Hammill et al., 2010; Yoshida et al., 2004), and environmental temperature (Dell et al., 2014; Gibert and DeLong, 2014; O’Connor, 2009). And while all these factors are important, the underlying assumption in ecology has historically been that populations are homogeneous collections of individuals and that mean trait values are sufficient for understanding ecological processes (Lomnicki, 1988). Unfortunately, whenever non-linear relationships between underlying traits and ecological processes of interest occur, using mean trait values can be misleading (Bolnick et al., 2011; Inouye, 2005). Because non-linearities are common in consumer–resource interactions, overlooking individual phenotypic variation may impair our capacity to fully understand species persistence and competitive ability in natural communities.

Populations often show individual-level phenotypic variation in anti-predator defences (Duffy, 2010), competitive ability (Lankau and Strauss, 2007), or resource utilization (e.g. Bolnick et al., 2003; Estes et al., 2003). Because interspecific interactions ultimately occur between individuals, individual phenotypic variation can affect interspecific interactions in multiple ways (Pettorelli et al., 2011). For instance, individual-level dietary specialization among southern sea otters (*Enhydra lutris nereis*) induces changes in the

structure of the population-level resource utilization network, which in turn can alter the structure and dynamics of the food webs in which these organisms are embedded (Tinker et al., 2012). Individual variation also can affect the strength of consumer–resource interactions by changing the parameters of the functional response connecting species pairs (Bolnick et al., 2011; Gibert and Brassil, 2014; Schreiber et al., 2011; also see Doebeli, 1996 in an evolutionary context). In particular, increasing individual variation in attack efficiency (or attack rate) and handling time decreases interaction strengths, which in turn increases species persistence and stability (Gibert and Brassil, 2014). Together, these results underscore the need to understand how individual-level phenotypic variation affects ecological processes and, through that, the structure and dynamics of entire communities.

Interaction strengths can be influenced by ‘mutual’ interference competition among predators by dampening resource uptake at higher consumer densities (Arditi et al., 2004). Therefore, mutual interference is thought to stabilize the dynamics of consumer–resource interactions (Arditi et al., 2004; DeLong and Vasseur, 2011, 2013; Forrester et al., 2006). Interference is often thought to occur through behavioural mechanisms associated with territoriality and aggressiveness (Connell, 1961; Forrester et al., 2006; Kennedy and White, 1996), but more generally, interference competition is any form of interaction among consumers that inhibits foraging. Because interference is widespread among many different taxa, it may play an important role in stabilizing natural communities (DeLong and Vasseur, 2011, 2013; Skalski and Gilliam, 2001).

The parameters of the functional response, including mutual interference, are driven by organism traits, and these traits may influence more than one parameter at a time. For example, body size influences both attack efficiency and handling time in several taxa (DeLong and Vasseur, 2012a). Also, variation in different parameters can have opposite effects on foraging rates (Bolnick et al., 2011), so it may be important to link variation in underlying controlling traits to multiple parameters simultaneously (Gibert and Brassil, 2014; Pettorelli et al., 2011). Recently, a positive trait-based link between attack efficiency and mutual interference was discovered for predatory protists, where predator velocity was thought to increase the magnitude of attack efficiency and interference competition simultaneously (DeLong and Vasseur, 2013). Thus, while increasing individual variation can increase stability by lowering interaction strengths through attack efficiency, individual variation might also lower interference competition, potentially undermining the overall stabilizing effect. Because of this, the challenge

now is to understand how individual variation in both mutual interference and attack efficiency influences the fate of interacting populations among natural communities.

Our goal is to extend recent work about how individual variation alters consumer–resource dynamics by studying its impact upon linked ecological attributes such as attack efficiency, handling time and interference competition. [Schreiber et al. \(2011\)](#) explored the effect of individual-level heritable variation in attack efficiencies in eco-evolutionary dynamics, while [Gibert and Brassil \(2014\)](#) explored the simultaneous effect of non-heritable variation in the attack efficiency and the handling time of a consumer–resource system. Here, we incorporate non-heritable individual variation in mutual interference by taking into account its functional relationship with attack efficiency ([DeLong and Vasseur, 2013](#)) and then we assess its effect upon the persistence and competitive ability of consumer–resource systems.



2. METHODS

2.1 The general model

To include mutual interference among consumers, we used a Rosenzweig–MacArthur consumer–resource model with a Hassell–Varley functional response ([Hassell and Varley, 1969](#); [Rosenzweig and MacArthur, 1963](#)). The Hassell–Varley functional response introduces interference competition as a negative exponent, m , on the consumer density in both the numerator and denominator of the functional response (e.g. [Arditi and Akçakaya, 1990](#); [DeLong and Vasseur, 2011](#); [Hassell and Varley, 1969](#)). The dynamic model is thus:

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - C \frac{\alpha RC^m}{1 + \alpha \eta RC^m}, \\ \frac{dC}{dt} &= \varepsilon C \frac{\alpha RC^m}{1 + \alpha \eta RC^m} - \beta C\end{aligned}\tag{1}$$

where r is the maximal growth rate of the prey, K its carrying capacity, ε is the conversion efficiency, β is the mortality rate of the consumer, α its attack efficiency, η its handling time and m is the parameter that represents interference competition.

If $m = 0$, the model reduces to the classic Rosenzweig–MacArthur formulation, and if $m = -1$, it reduces to the ratio-dependent formulation (e.g. [Arditi and Ginzburg, 1989](#)). The level of interference, m , varies

continuously in nature from 0 to -2.5 , although it frequently takes intermediate values (Abrams and Ginzburg, 2000; DeLong and Vasseur, 2011, 2013). In the case of the predatory protist *Didinium nasutum* preying upon *Paramecium aurelia*, the magnitude of m is linked to that of attack efficiency (α) by:

$$m = -0.26 \ln(\alpha) - 0.67, \quad (2)$$

which was determined by estimating the functional response of the consumer across replicate populations (DeLong and Vasseur, 2013) (Fig. 1A). This relationship will later be used to introduce individual variation in interference.

2.2 Individual variation

Following previous theoretical studies we incorporated individual variation by assuming that both attack efficiency and handling time depend on the value of a normally distributed trait (Gibert and Brassil, 2014; Rall et al., 2012; Schreiber et al., 2011), x , with mean \bar{x} , variance σ^2 and probability density:

$$p(x, \bar{x}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(x - \bar{x})^2}{2\sigma^2}\right]. \quad (3)$$

We assumed that the consumer's attack efficiency $\alpha(x)$ is maximal at a given optimal trait value $x = \theta_\alpha$ and decreases away from that maximum as:

$$\alpha(x) = \alpha_{\max} \exp\left[-\frac{(x - \theta_\alpha)^2}{2\tau^2}\right], \quad (4)$$

where α_{\max} is the maximal attack efficiency and τ^2 determines how steeply the attack efficiency declines away from θ_α (Fig. 1B). The handling time, $\eta(x)$, was assumed to be minimal at a given optimal value $x = \theta_\eta$ and to increase away from that minimum as:

$$\eta(x) = \eta_{\max} - (\eta_{\max} - \eta_{\min}) \exp\left[-\frac{(x - \theta_\eta)^2}{2\nu^2}\right], \quad (5)$$

where η_{\max} and η_{\min} are the maximal and minimal handling time, respectively, and ν^2 determines how steeply the handling time increases away from θ_η (Fig. 1C).

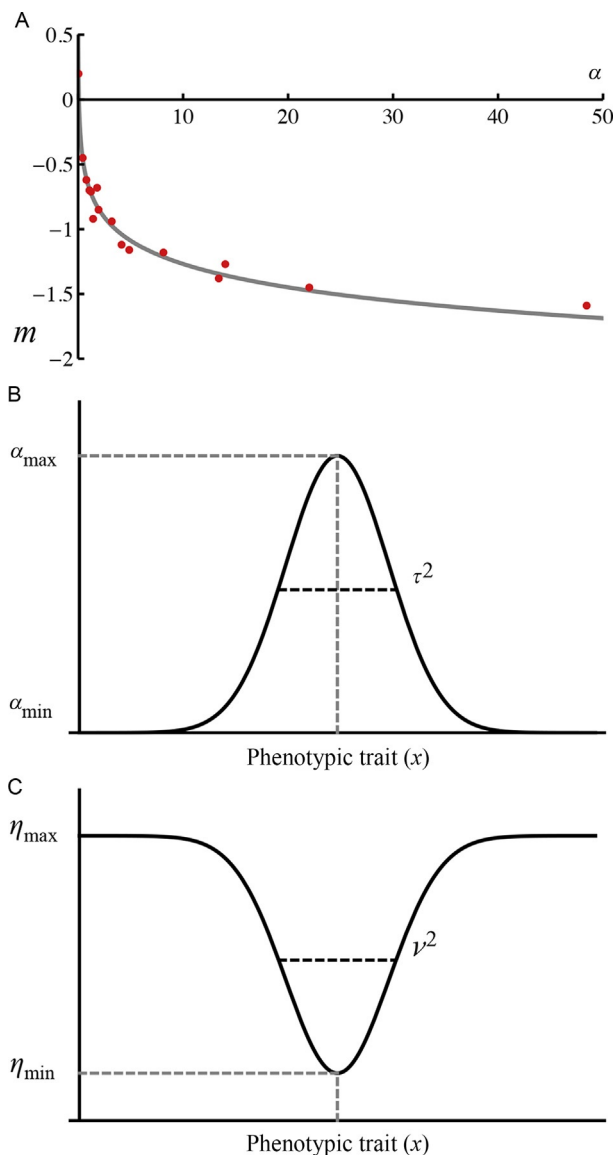


Figure 1 (A) Plot of the empirically observed relation between the coefficient of mutual interference (m) and the attack efficiency (α) in replicate populations of *Didinium nasutum* preying upon *Paramecium aurelia*. As attack efficiency increases, mutual interference becomes stronger. (B) Plot of the assumed relation between the attack efficiency (α) and the underlying phenotypic trait (x). (C) Plot of the assumed relation between the handling time (η) and the underlying phenotypic trait. *Panel (A): modified from DeLong and Vasseur (2013); Panels (B) and (C): modified from Gibert and Brassil (2014).*

We defined the quantities $d_\alpha^2 = (\bar{x} - \theta_\alpha)^2$ and $d_\eta^2 = (\bar{x} - \theta_\eta)^2$ as the distance between the mean trait in the population and the optimal value at which attack efficiency is maximal and handling time is minimal (referred to as phenotypic mismatch; see [Raimundo et al., 2014](#); [Schreiber et al., 2011](#) for similar definitions). Because the optimal value is set by past and existing selective pressures ([Anderson et al., 2010](#)), the phenotypic mismatch can be seen as a measure of how well adapted the consumer species is at attacking and handling a particular resource ([Gibert and Brassil, 2014](#)). The larger the mismatch is, the smaller the attack rate and the larger the handling time.

We explored three scenarios. We first recapitulated some of the results of [Gibert and Brassil \(2014\)](#) as a baseline for comparison, by including variation in attack efficiency and handling time only. Second, we included only variation in mutual interference, and, third, we included individual variation in all three parameters simultaneously. For the first scenario (variation in attack efficiency and handling time), the consumer–resource model is:

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{K} \right) - C \int_{-\infty}^{+\infty} \frac{\alpha(x) RC^m}{1 + \alpha(x)\eta(x)RC^m} p(x, \bar{x}) dx, \\ \frac{dC}{dt} &= \varepsilon C \int_{-\infty}^{+\infty} \frac{\alpha(x) RC^m}{1 + \alpha(x)\eta(x)RC^m} p(x, \bar{x}) dx - \beta C \end{aligned} \quad (6)$$

where m is constant. For the second scenario (variation in interference only), the model is:

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{K} \right) - C \int_{-\infty}^{+\infty} \frac{\alpha RC^{m(\alpha(x))}}{1 + \alpha\eta RC^{m(\alpha(x))}} p(x, \bar{x}) dx, \\ \frac{dC}{dt} &= \varepsilon C \int_{-\infty}^{+\infty} \frac{\alpha RC^{m(\alpha(x))}}{1 + \alpha\eta RC^{m(\alpha(x))}} p(x, \bar{x}) dx - \beta C \end{aligned} \quad (7)$$

where $m(\alpha(x)) = -0.26 \ln(\alpha(x)) - 0.67$ and all other parameters are as in Eq. (1). Notice that in this model, α is only allowed to change with variation in the underlying trait x inside function $m(\alpha(x))$, but not outside it. Because this is not realistic, we only do it as a way of understanding variation in mutual interference alone while acknowledging that variation ought to be considered in multiple parameters at the same time. This leads to the third scenario, where variation is now being considered in all three parameters simultaneously (variation in attack efficiency, handling time and interference):

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K} \right) - C \int_{-\infty}^{+\infty} \frac{\alpha(x) RC^{m(\alpha(x))}}{1 + \alpha(x)\eta(x)RC^{m(\alpha(x))}} p(x, \bar{x}) dx \\ \frac{dC}{dt} &= \varepsilon C \int_{-\infty}^{+\infty} \frac{\alpha(x) RC^{m(\alpha(x))}}{1 + \alpha(x)\eta(x)RC^{m(\alpha(x))}} p(x, \bar{x}) dx - \beta C.\end{aligned}\tag{8}$$

We analysed these three scenarios for varying levels of phenotypic mismatch using intermediate values for the maximal attack efficiency and mutual interference, as this combination of parameters is thought to be the most likely in nature (DeLong and Vasseur, 2013). Considering different combination of parameters does not qualitatively affect our results.

The objective of our simulations was to assess the effect of individual variation on the equilibrium of the system (i.e. the intersection of the consumer and resource isoclines). Because of the way we incorporated individual variation in Eqs. (6)–(8), solving for these isoclines (the conditions at which $dR/dt=0$ for the prey isocline and the conditions at which $dC/dt=0$ for the predator isocline) and their intersection is now impossible analytically, so it was done numerically. The farther away this equilibrium is from the axes, the less likely consumers and resources are to go extinct due to random fluctuations. Finally, to assess the effect of variation upon community structure, we investigated its effect upon the persistence of consumers through their equilibrium density, C^* , as well as their competitive ability, through the equilibrium density of the resource, R^* . Low equilibrium resource densities (R^*) are associated with strong competitive ability of the consumers (Tilman, 1982, 1986). We therefore define the quantity $1/R^*$ as a measure of competitive ability: the larger the quantity, the larger the competitive ability of the consumer and vice versa.



3. RESULTS

Overall, individual variation can have a strong effect on equilibrium densities and species persistence when interference competition is considered. The effect of individual variation on interference competition depends on the levels of phenotypic mismatch in the trait that controls the consumer–resource interaction (Fig. 2). This effect seems to be mediated mainly by the interplay between attack efficiency and interference competition and ultimately affects the equilibrium densities of the interacting pair, resulting in differential persistence and competitive ability for the consumer at different levels of individual variation (Fig. 3).

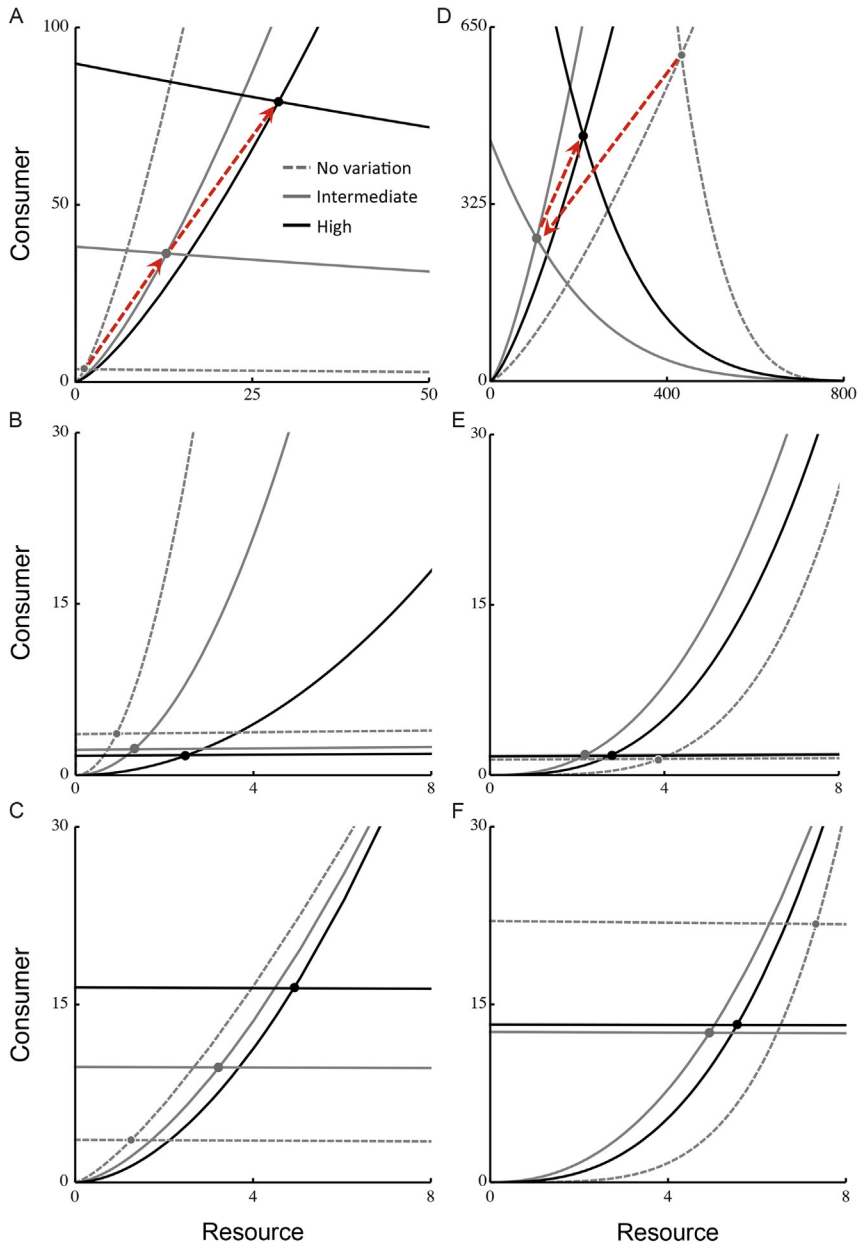


Figure 2 Phase-plane plots of consumer and resource isoclines for different levels of individual variation where the isoclines (values at which a species does not grow or decline) for consumers and resources are represented for different levels of individual variation. The intersection of the isoclines marks the equilibrium densities. Panels in the
(Continued)

3.1 Low phenotypic mismatch

When phenotypic mismatch is low ($d_\alpha \sim 0$ and $d_\eta \sim 0$), individual variation in attack efficiency and handling time increases equilibrium densities of both the consumer and the resource, moving them away from extinction thresholds (Fig. 2A). By doing so, individual variation potentially increases species persistence, as extinction due to demographic stochasticity is less likely to occur.

When it occurs only in interference, individual variation reduces the equilibrium density of the consumer but increases that of the resource (Fig. 2B). This makes consumers simultaneously less competitive due to a high R^* and more prone to extinction due to a low C^* . The change in equilibrium abundance for a given change in individual variation, however, is less pronounced than that observed when variation in both attack efficiency and handling time is considered (Fig. 2A and B).

The net effect of individual variation in interference competition, attack efficiency and handling time combined is intermediate to the effect produced when individual variation is included only in interference competition or in both the attack efficiency and the handling time. This is because the effects are opposite of each other. Individual variation increases the equilibrium density of consumers and resources, moving them away from the extinction threshold (Fig. 2C), which is qualitatively different from what happened when variation only in interference was included (Fig. 2B). However, this effect is also less pronounced than in a scenario with variation only in attack efficiency and handling time (notice the magnitude of the change in

Figure 2—Cont'd left column refer to cases with low phenotypic mismatch, and panels in the right column to cases with large phenotypic mismatch. For the panels in the top row, individual variation was only considered in attack efficiency and handling time. In the second row, individual variation in interference competition only was considered. In the third row, individual variation in attack efficiency, handling time and interference is included. Variation in attack efficiency and handling time increases equilibrium densities (intersection moves away from axes) whenever mismatch is small, and decreases then increases densities whenever mismatch is large. Variation in mutual interference results in a small effect. The latter explains why variation in attack efficiency, handling time and interference results in a tempered version of the first case. Parameter values kept constant across all plots: $\alpha_{\max} = 1.38$, $\eta_{\max} = 0.08$, $\eta_{\min} = 0$, $e = 0.15$, $r = 1.9$, $K = 841$, $\beta = 0.1$, $\tau = 1$, $\nu = 1$, $d_\eta^2 = 0$. Parameters that changed: (A) $d_\alpha^2 = 0$, $\sigma^2 = 0$ (grey, dashed), $\sigma^2 = 2.26$ (grey), $\sigma^2 = 14.19$ (black); (D) $d_\alpha^2 = 2$, $\sigma^2 = 0$ (grey, dashed), $\sigma^2 = 1.31509$ (grey), $\sigma^2 = 16.7242$ (black); (B), (C), (E), and (F) as in (A) but for $d_\alpha^2 = 0$ for (B) and (C) and $d_\alpha^2 = 2$ for (E) and (F).

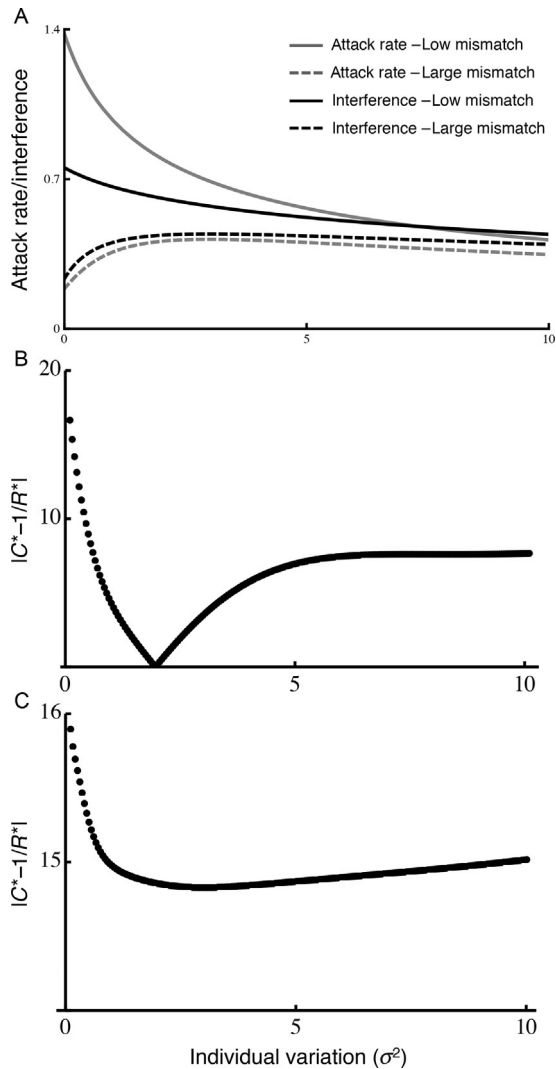


Figure 3 (A) Plot of the attack efficiency (grey) and interference competition (black) against individual variation under low phenotypic mismatch (solid) and large phenotypic mismatch (dashed). Variation decreases attack rates to a larger extent than interference competition when mismatch is small, and the effect on both parameters is comparable when mismatch is large. Parameter values as in Fig. 2. (B) Plot of the absolute value of the difference between consumer equilibrium density, C^* , and consumer competitive ability $1/R^*$, as a function of individual variation under low phenotypic mismatch. Variation maximizes both simultaneously whenever the curve is at its lowest point. (C) Same as in (B) but for large phenotypic mismatch. Parameter values as in Fig. 2.

Fig. 2A) and more similar in magnitude to a scenario with variation only in interference (notice the magnitude of the change in Fig. 2B).

3.2 Large phenotypic mismatch

When phenotypic mismatch is large ($|d_\alpha| \gg 0$) in a scenario with variation in both attack efficiency and handling time, low levels of individual variation decrease equilibrium densities, but high levels of variation increase equilibrium densities for both consumers and prey (Fig. 2D). These changes in equilibrium densities occur much farther away from extinction thresholds than in a scenario with small phenotypic mismatch (Fig. 1A), but are of larger magnitude.

Individual variation in interference decreases the equilibrium density of the resource at first, but it then increases as variation gets larger (Fig. 2E). This practically has no effect on consumer equilibrium densities and the overall effect of variation is comparatively small in magnitude.

The net effect of individual variation in interference competition, attack efficiency and handling time is, again, intermediate to the effect produced in the previous scenarios. Indeed, the densities for both resource and consumers behave as if only variation in attack efficiency and handling time was considered (Fig. 2F and D), but these fluctuations are of a much smaller magnitude, as in a scenario with only variation in interference (Fig. 2F and B).

3.3 Interference, attack efficiency consumer persistence and competitive ability

Individual variation has the same overall effect on interference competition as it has on attack efficiency (Fig. 3). If phenotypic mismatch is low, both attack efficiency and interference competition decrease with individual variation, but the effect seems to be more pronounced on attack efficiency than on interference (Fig. 3A). When phenotypic mismatch is large, however, both attack efficiency and interference increase with variation at first, and then decrease (Fig. 3A). The magnitude of this effect is comparable for both parameters.

Because variation on attack efficiency and interference alters the equilibrium densities of both consumers and resources (Fig. 2), it will ultimately affect consumer persistence as well as its overall competitive ability. For the full model (Eq. 8), when phenotypic mismatch is low, the consumer equilibrium density, C^* , increases with variation but its competitive ability,

measured as $1/R^*$, decreases. Because variation maximizes C^* and $1/R^*$ simultaneously whenever the absolute value of that difference is small, our results suggest that intermediate levels of variation maximize the consumer's ability to persist (C^*) and to compete ($1/R^*$) (Fig. 3B). When phenotypic mismatch is large, the consumer equilibrium density decreases with individual variation at first and then increases slowly. Consumer competitive ability, however, increases with variation and then decreases. Interestingly, intermediate levels of variation maximize the consumer's ability to persist and to compete (Fig. 3C), despite the larger phenotypic mismatch.



4. DISCUSSION

4.1 Variation and interference

Individual variation in traits controlling ecological attributes such as attack efficiency and handling time can increase species persistence in consumer–resource interactions (Bolnick et al., 2011; Gibert and Brassil, 2014). In classic consumer–resource models, an increase in the attack efficiency increases interaction strengths, resulting in a decrease of species persistence and overall stability (e.g. Rosenzweig and MacArthur, 1963). Individual variation weakens interaction strengths by decreasing attack efficiencies, which in turn increases species persistence and stability (Gibert and Brassil, 2014). Our results suggest that this effect also occurs when consumer interference is considered. Interference is generally stabilizing (Ginzburg and Jensen, 2008), so it might be expected that individual variation in interference alone could have destabilizing effects, potentially leading to species extinctions. However, it seems to either decrease consumer equilibrium densities and increase resource equilibrium densities, or have negligible effects on both. When we consider variation in attack efficiency and link that to mutual interference through their empirically determined negative relationship (Fig. 1A), the net effect of variation is to increase species persistence. This may be due to a larger effect of individual variation in attack efficiency than in interference that would overcome the negative effect of variation in interference only. These results highlight the importance of considering possible functional relationships between dynamic parameters such as attack efficiency and interference as well as the importance of considering individual variation in the traits controlling these parameters in order to fully understand population dynamics and stability (DeLong and Vasseur, 2012b, 2013; Yodzis and Innes, 1992).

4.2 Variation and competitive ability

Our results also have important consequences for understanding community assembly. If phenotypic mismatch is low, the equilibrium resource density increases with individual variation, which decreases consumer competitive ability. If phenotypic mismatch is large, some variation can reduce resource density at first, momentarily increasing competitive ability. However, large phenotypic mismatch generally decreases competitive ability regardless of variation, meaning that poorly adapted species are in general poor competitors and populations that are already well adapted to their niche become less competitive when they become more variable. In the case of the *Didinium*–*Paramecium* system, after which our model is parameterized, if interference is too large, consumer uptake is heavily impaired, resulting in deterministic extinction (DeLong and Vasseur, 2013). If interference is low, however, equilibrium densities increase up to a point where the competitive ability of the populations is reduced (DeLong and Vasseur, 2013; Tilman, 1982, 1986). A similar rule might apply to individual variation when it affects both attack efficiency and interference. If variation is too small, populations are close to their extinction threshold. If variation is too large, their equilibrium densities increase to a point where it may impair their competitive abilities, threatening their persistence in the community. Variation in interference thus seem to counter the effect of variation in attack efficiency, naturally leading to the existence of an intermediate amount of variation that both minimizes the chance of extinction and maximizes the competitive ability of populations in a community.

4.3 Eco-evolutionary feedbacks

Individual variation can be important for ecological dynamics, but it also is the raw material upon which natural selection acts (Dobzhansky, 1937). In addition, evolutionary processes have been increasingly recognized to occur at ecological timescales, altering ecological processes and dynamics as they unfold (Grant and Grant, 2002; Hairston et al., 2005; Thompson, 1998). The interplay between ecological and evolutionary processes, or eco-evolutionary feedbacks, thus needs to be considered in future work. In this sense, individual variation has been recognized to increase species coexistence in eco-evolutionary dynamics (Schreiber et al., 2011; Vasseur et al., 2011), but variation has been assumed to be constant through time. However, phenotypic variation generally scales with mean trait values, a pattern known as Taylor's power law (Taylor, 1961) and prevalent across systems

and taxa (DeLong, 2012). Thus, individual variation in a given trait will track the evolution of the mean trait value, potentially leading to changes in community structure due to alterations in competitive ability that are a consequence of changes in individual variation that track the evolution of underlying traits. This makes it paramount to also track the evolution of variation over time to understand eco-evolutionary and the stability and persistence of ecological systems in nature.

The effect of individual variation may also depend on the strength of selection acting on the traits that control the consumer–resource interaction (Gibert and Brassil, 2014; Yoshida et al., 2003). Strong stabilizing selection may reduce individual variation through time, with consequences for population stability and competitive ability. Unstable and uncompetitive populations will not fare well in communities, which implies that selection that reduces variation and increases mean fitness within populations may have negative effects for the population in a community. Populations may thus be the subject of antagonistic effects of natural selection (Raimundo et al., 2014). Together, this suggests that the interplay between ecological and evolutionary processes is central to understanding how communities are structured in nature (Bolnick et al., 2011; Fontaine et al., 2011; Guimarães et al., 2011; Thompson, 2005). Individual variation may be the key to bridging the gap between ecology and evolution.

4.4 Underlying controlling traits

Considering what traits operate as ‘controlling’ traits that influence parameters such as attack efficiency, handling time and interference is also important. For instance, the amount of variation in the controlling trait is linked to mutation rates, the amount of phenotypic plasticity and the strength of selective forces operating on the trait. Thus, by identifying probable controlling traits, we may have a deeper grasp of the processes controlling the variation ultimately affecting consumer–resource dynamics. It is possible that some traits, such as body size, might act as ecological ‘magic traits’. In an evolutionary context, magic traits are involved in both mating and ecological activities, and when they experience disruptive selection they can lead to adaptive speciation (Gavrilets, 2004; Raimundo et al., 2014). Ecological magic traits would be traits influencing many dynamic parameters at once (e.g. DeLong and Vasseur, 2012b), while other traits only influence a limited set of parameters, if any. Specific links between traits, their optima and dynamic population parameters are needed to fully understand how

individual variation influences consumer–resource dynamics. Identifying such traits and quantifying their distribution and their effect upon ecological processes of interest should be a major goal of ecology in the upcoming future (Gibert and Brassil, 2014; Pettorelli et al., 2011; Violle et al., 2012a,b).

4.5 Testable predictions from the theory of individual variation

To help move toward that goal, we can make some simple testable predictions as to how individual variation can affect interaction strengths in a system with interference competition. If the per-capita foraging rate of a consumer preying upon a resource is:

$$f(R, C) = \frac{\alpha RC^m}{1 + \alpha \eta RC^m}, \quad (9)$$

then, we can find an expression for the average foraging rate that explicitly depends upon individual variation by integrating over the functional response and the underlying trait distribution. We thus get:

$$\overline{f(R, C)} = \int_{-\infty}^{+\infty} \frac{\alpha(x)RC^m}{1 + \alpha(x)\eta(x)RC^m} p(x, \bar{x}) dx, \quad (10)$$

where m can be a function of the attack efficiency or a constant. In this case, we can see that while under some conditions increasing individual variation reduces foraging rates and thus, interaction strengths, this effect increases with resource density (Fig. 4A) and decreases with consumer density (Fig. 4B and C). These predictions can be tested in foraging experiments where the resource and consumer densities are manipulated in the same way it would be done for quantifying the parameter of mutual interference, m (DeLong and Vasseur, 2013). A measure of individual variation across treatments and one or several traits such as body size would need to be quantified as well. The latter is particularly doable in microcosms with protists (DeLong, 2012; DeLong and Vasseur, 2013) or mesocosm experiments with metazoan grazers and algae (Fussmann et al., 2003; Yoshida et al., 2003, 2004).



5. CONCLUSION

Because of their effect on population persistence and stability, understanding the interplay between individual variation and interference competition is central in ecology. Using dynamic models that explicitly take into account individual variation, we have shown that increasing individual

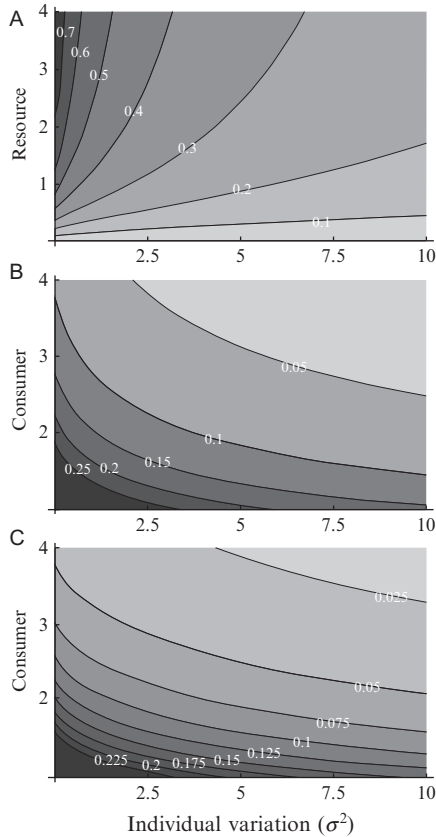


Figure 4 Plots of the effect of individual variation and either resource (A) or consumer density ((A) and (B): foraging rate as in Eq. 10, (C): foraging rate as in Eq. 8)) upon foraging rates (grey scale). Individual variation and consumer and resource densities have a joint effect upon foraging rates and should thus not be studied separately: foraging rates increase with resource density, decrease with consumer density and decrease with individual variation. Parameter values as in Fig. 2. R and C where kept constant and equal to 1 whenever the other quantity was varied.

variation simultaneously affecting attack efficiency, handling time and mutual interference can increase species persistence and stability as well as consumer competitive ability. Moreover, as variation is affected by selection, we argue that evolutionary processes may deeply affect the way communities are structured. Finally, our results underscore the need for comprehensive studies that quantify the level of individual variation in natural populations, making specific testable hypotheses as to how individual variation can interact with resource and consumer densities to alter foraging rates and through that, interaction strengths.

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REFERENCES

- Abrams, P.A., Ginzburg, L., 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* 15, 337–341.
- Abrams, P.A., Matsuda, H., 2004. Consequences of behavioral dynamics for the population dynamics of predator–prey systems with switching. *Popul. Ecol.* 46, 13–25.
- Allesina, S., Tang, S., 2012. Stability criteria for complex ecosystems. *Nature* 483, 205–208.
- Anderson, B., Terblanche, J.S., Ellis, A.G., 2010. Predictable patterns of trait mismatches between interacting plants and insects. *BMC Evol. Biol.* 10, 204.
- Arditi, R., Akçakaya, H.R., 1990. Underestimation of mutual interference of predators. *Oecologia* 83, 358–361.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326.
- Arditi, R., Callois, J.-M., Tyutyunov, Y., Jost, C., 2004. Does mutual interference always stabilize predator–prey dynamics? A comparison of models. *C.R. Biol.* 327, 1037–1057.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulseley, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161, 1–28.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42, 710–723.
- Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J. Anim. Ecol.* 83, 70–84.
- DeLong, J.P., 2012. Experimental demonstration of a “rate–size” trade-off governing body size optimization. *Evol. Ecol. Res.* 14, 343–352.
- DeLong, J.P., 2014. The body-size dependence of mutual interference. *Biol. Lett.* 10, 20140261.
- DeLong, J.P., Vasseur, D.A., 2011. Mutual interference is common and mostly intermediate in magnitude. *BMC Ecol.* 11 (1), 8.
- DeLong, J.P., Vasseur, D.A., 2012a. A dynamic explanation of size–density scaling in carnivores. *Ecology* 93, 470–476.
- DeLong, J.P., Vasseur, D.A., 2012b. Size–density scaling in protists and the links between consumer–resource interaction parameters. *J. Anim. Ecol.* 81, 1193–1201.
- DeLong, J.P., Vasseur, D.A., 2013. Linked exploitation and interference competition drives the variable behavior of a classic predator–prey system. *Oikos* 122, 1393–1400.
- Dobzhansky, T., 1937. *Genetics and the Origin of Species*. Columbia University Press, New York, p. 364.
- Doebeli, M., 1996. An explicit genetic model for ecological character displacement. *Ecology* 77, 510–520.
- Duffy, M.A., 2010. Ecological consequences of intraspecific variation in lake *Daphnia*. *Freshw. Biol.* 55, 995–1004.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., Lyon, B.E., 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *J. Anim. Ecol.* 72, 144–155.

- Fontaine, C., Guimarães Jr., P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., van Veen, F.J.F., Thébault, E., 2011. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181.
- Forrester, G.E., Evans, B., Steele, M.A., Vance, R.R., 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia* 148, 632–640.
- Fussmann, G.F., Ellner, S.P., Hairston Jr., N.G., 2003. Evolution as a critical component of plankton dynamics. *Proc. Biol. Sci.* 270, 1015–1022.
- Gavrilets, S., 2004. *Fitness Landscapes and the Origin of Species*. Princeton University Press, Princeton.
- Gibert, J.P., Brassil, C.E., 2014. Individual phenotypic variation reduces interaction strengths in a consumer-resource system. *Ecol. Evol.* 4, 3703–3713.
- Gibert, J.P., DeLong, J.P., 2014. Temperature alters food web body-size structure. *Biol. Lett.* 10, 20140573.
- Ginzburg, L.R., Jensen, C.X.J., 2008. From controversy to consensus: the indirect interference functional response. *Verh. Int. Ver. Limnol.* 30, 297–301.
- Grant, P.R., Grant, B.R., 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707–711.
- Guimarães Jr., P.R., Jordano, P., Thompson, J.N., 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14, 877–885.
- Hairston Jr., N.G., Ellner, S.P., Geber, M.A., Yoshida, T., Fox, J.A., 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8, 1114–1127.
- Hammill, E., Petchey, O.L., Anholt, B.R., 2010. Predator functional response changed by induced defenses in prey. *Am. Nat.* 176, 723–731.
- Hassell, M.P., Varley, G.C., 1969. New inductive population model for parasites and its bearing on biological control. *Nature* 223, 1133–1137.
- Inouye, B.D., 2005. The importance of the variance around the mean effect size of ecological processes: comment. *Ecology* 86, 262–265.
- Kennedy, E.D., White, D.W., 1996. Interference competition from house wrens as a factor in the decline of bewick's wrens. *Conserv. Biol.* 10, 281–284.
- Lankau, R.A., Strauss, S.Y., 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* 317, 1561–1563.
- Lomnicki, A., 1988. *Population Ecology of Individuals*. Princeton University Press, Princeton.
- May, R.M., 1972. Will a large complex system be stable? *Nature* 238, 413–414.
- May, R.M., 1973. Qualitative stability in model ecosystems. *Ecology* 54, 638–641.
- McCann, K.S., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798.
- O'Connor, M.L., 2009. Warming strengthens an herbivore-plant interaction. *Ecology* 90, 388–398.
- Pawar, S., Dell, A.I., Savage, V.M., 2012. Dimensionality of consumer search space drives trophic interaction strengths. *Nature* 486, 485–489.
- Pettorelli, N., Coulson, T., Durant, S.M., Gaillard, J.-M., 2011. Predation, individual variability and vertebrate population dynamics. *Oecologia* 167, 305–314.
- Raimundo, R.L.G., Gibert, J.P., Hembry, D.H., Guimarães, P.R., 2014. Conflicting selection in the course of adaptive diversification: the interplay between mutualism and intraspecific competition. *Am. Nat.* 183, 363–375.
- Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., Petchey, O.L., 2012. Universal temperature and body-mass scaling of feeding rates. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367, 2923–2934.
- Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator-prey interactions. *Am. Nat.* 97, 209–223.

- Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399.
- Schreiber, S.J., Bürger, R., Bolnick, D.I., 2011. The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92, 1582–1593.
- Skalski, G.T., Gilliam, J.F., 2001. Functional responses with predator interference: viable alternatives to the holling type II model. *Ecology* 82, 3083–3092.
- Taylor, L.R., 1961. Aggregation, variance and the mean. *Nature* 189, 732–735.
- Thompson, J.N., 1998. Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329–332.
- Thompson, J.N., 2005. *The Geographic Mosaic Theory of Coevolution*. The University of Chicago Press, Chicago, p. 443.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, New Haven, p. 296.
- Tilman, D., 1986. Resources, competition and the dynamics of plant communities. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell scientific publications, Oxford, pp. 51–75.
- Tinker, M.T., Guimarães Jr., P.R., Novak, M., Marquitti, F.M.D., Bodkin, J.L., Staedler, M., Bentall, G., Estes, J.A., 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecol. Lett.* 15, 475–483.
- Vasseur, D.A., Amarasekare, P., Rudolf, V.H.W., Levine, J.M., 2011. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am. Nat.* 178, E96–E109.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012a. The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012b. Viva la variance! a reply to Nakagawa & Schielzeth. *Trends Ecol. Evol.* 27, 475–476.
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G., Brose, U., 2010. Allometric functional response model: body masses constrain interaction strengths. *J. Anim. Ecol.* 79, 249–256.
- Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. *Am. Nat.* 139, 1151–1175.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F., Hairston Jr., N.G., 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424, 303–306.
- Yoshida, T., Hairston Jr., N.G., Ellner, S.P., 2004. Evolutionary trade-off between defence against grazing and competitive ability in a simple unicellular alga, *Chlorella vulgaris*. *Proc. Biol. Sci.* 271, 1947–1953.