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Note

Ecological Pleiotropy Suppresses the Dynamic Feedback Generated by a Rapidly Changing Trait

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abstract: Population dynamics may carry a signature of an ecology-evolution-ecology feedback, known as eco-evolutionary dynamics, when functionally important traits change. Given current theory, the absence of a feedback from a trait with strong links to species interactions should not occur. In a previous study with the *Didinium-Paramecium* predator-prey system, however, rapid and large-magnitude changes in predator cell volume occurred without any noticeable effect on the population dynamics. Here I resolve this theory-data conflict by showing that ecological pleiotropy—when a trait has more than one functional effect on an ecological process—suppresses shifts in dynamics that would arise, given the links between cell volume and the species interaction. Whether eco-evolutionary dynamics arise, therefore, depends not just on the ecology-evolution feedback but on the net effect that a trait has on different parts of the underlying interaction.

Keywords: eco-evolutionary dynamics, ecological pleiotropy, body size, predator-prey interactions.

Introduction

Population dynamics generally depend on species interactions, and a variety of cycles and other dynamical patterns can arise deterministically out of simple models of interacting species. Rapid evolution of traits known to have functional consequences for species interactions, however, can change model parameters as the dynamics unfold. As a result, rapid evolution of functional traits will generate feedbacks that alter patterns of population dynamics relative to the no-evolution state; this is known as eco-evolutionary dynamics (Thompson 1998; Palkovacs and Hendry 2010; Schoener 2011; Reznick 2013). Such feedbacks should arise regardless of whether trait change occurs through evolu-

tion or phenotypic plasticity, even though changes in dynamics mediated through plastic traits are not generally considered a form of eco-evolutionary dynamics (DeLong et al. 2014*a*; Fischer et al. 2014; Hendry 2015).

Many traits may change rapidly, but evidence for the full feedback between dynamics and trait change is somewhat limited. Several case studies clearly show eco-evolutionary dynamics arising from the rapid evolution of functionally important traits (Fussmann et al. 2003; Yoshida et al. 2003; Post and Palkovacs 2009; Carlson et al. 2011; Ellner et al. 2011; Turcotte et al. 2011; Walsh et al. 2012), but these are somewhat limited in comparison with the breadth of studies documenting rapid trait evolution (Hendry and Kinnison 1999). This dearth of evidence is at least partly due to the difficulty of documenting all of the required components of eco-evolutionary dynamics, including trait evolution (if that is the mechanism of trait change), the functional consequences, and the change in dynamics between an evolutionary and a no-evolution state (Fussmann et al. 2007). Nonetheless, changes in functionally important traits are theoretically expected to have noticeable effects on population dynamics through a link between traits and the parameters that characterize species interactions (Ellner and Becks 2011; Schielke et al. 2011; Vasseur et al. 2011; Cortez and Weitz 2014).

In contrast to these theoretical expectations, a recent study showing rapid change in a functional trait (10-fold change in body size in 6–7 generations) revealed no feedback from the trait change to the ecological dynamics (DeLong et al. 2014*a*). In this study, populations of the ciliate predator *Didinium nasutum* were grown with *Paramecium aurelia* as prey in laboratory microcosms. *Didinium* is a pursuit predator that specializes on various *Paramecium* species and can forage and grow rapidly when prey are plentiful (Hewett 1980). The abundances of both predator and prey and the cell volume of *Didinium* in the microcosms were tracked through time and fitted to a series of coupled ordinary differential equations (eqq. [1]), showing that the dynamics could be described without incorporating feedback from the changes in predator cell volume. *Didinium* cell vol-

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ume shows considerable phenotypic plasticity, and given that there was limited genetic variation in the populations, much of the 10-fold change in cell volume was due to phenotypic plasticity. Thus, two possible explanations for the absence of a feedback from cell volume changes to dynamics in this study are that (1) body size does not have functionally important consequences for this interaction and (2) traits that change through phenotypic plasticity do not cause the same feedbacks as traits that change through evolution. I argue that both of these are highly unlikely, because body size is strongly linked to functional aspects of species interactions across most taxa and because it is the phenotype, not the genotype, that determines an organism's functional interactions with other organisms (Hendry 2015).

Here I propose another possibility: there is no detectable ecological feedback because the functional consequences of trait change cancel out. This kind of ecological pleiotropy (Strauss and Irwin 2004; DeLong and Gibert 2016) seems particularly plausible with a trait, such as body size, that is known to be linked to many aspects of consumer-resource interactions (Rall et al. 2012; Hudson and Reuman 2013; DeLong et al. 2015). I address this possibility by using empirically determined relationships between cell volume and consumer-resource model parameters for protists to visualize the expected dynamics that would arise from the observed cell volume changes and the functional consequences of those changes. I then do this for the complete set of known body-size-dependent parameters. These simulations show that, individually, functional links between cell volume and model parameters should alter the dynamics but that their effects cancel out when combined, indicating that ecological pleiotropy suppresses the feedback that would have resulted from changes in cell volume.

Methods

The following consumer-resource model provides a good description of the simultaneous temporal dynamics of predator abundance (C), prey abundance (R), and predator cell volume (M) for the *Didinium-Paramecium* system (see table 1 for parameter descriptions; DeLong et al. 2014*a*):

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{aRC^{m+1}}{1 + ahRC}, \tag{1A}$$

$$\frac{dC}{dt} = \frac{eaRC^{m+1}}{1 + ahRC} - \left(d_{\max} - \frac{d_{\max}R}{R + k_d}\right)C, \tag{1B}$$

$$\frac{dM}{dt} = gM(S - D). \tag{1C}$$

Equations (1A) and (1B) are a modification of the classic MacArthur-Rosenzweig predator-prey model (Rosenzweig and MacArthur 1963), where mutual interference among predators is added to the functional response (as is necessary for *Didinium*; see Salt 1974; Jost and Ellner 2000; DeLong and Vasseur 2013) and the mortality rate is dependent on prey levels (Minter et al. 2011). Equation (1C) is the dynamic version of the supply-demand model (DeLong 2012), where the supply available to the predators is some portion of the per capita amount of prey, $S = sR/C$, and the demand for resources is the maximum ingestion rate, $D = 1/h$. In this model, body size (cell volume in this case) increases whenever resource supply exceeds the demand and declines when the reverse is true. Together, equations (1) describe predator-prey interactions that drive variation in predator body size (fig. 1*A*–1*C*; data available from DeLong et al. 2014*b*).

Table 1: Parameters in equations (1), parameter descriptions, the original mean parameter estimates (DeLong et al. 2014*a*), parameter units, and allometric scaling relations for the parameters

Parameter	Description	Original static estimates	Units	Allometric relationship with cell volume (M)
r	Prey intrinsic growth rate	.78	day^{-1}	
K	Prey carrying capacity	1,300	cells mL^{-1}	
a	Space clearance rate	9.06	mL pred^{-1} day^{-1}	$1.59 \times 10^{-5}M^1$
h	Handling time	.038	days	$49 \times M^{-.54}$
m	Mutual interference	−1.06	...	
e	Conversion efficiency	.046	...	$34.6 \times M^{-.5}$
$d_{\max}$	Maximum predator death rate	.9	day^{-1}	$42 \times M^{-.29}$
k_d	Death half-saturation constant	.0026	cells mL^{-1}	
g	Transmission efficiency	.015	...	
s	Fraction of prey available	.14	...	
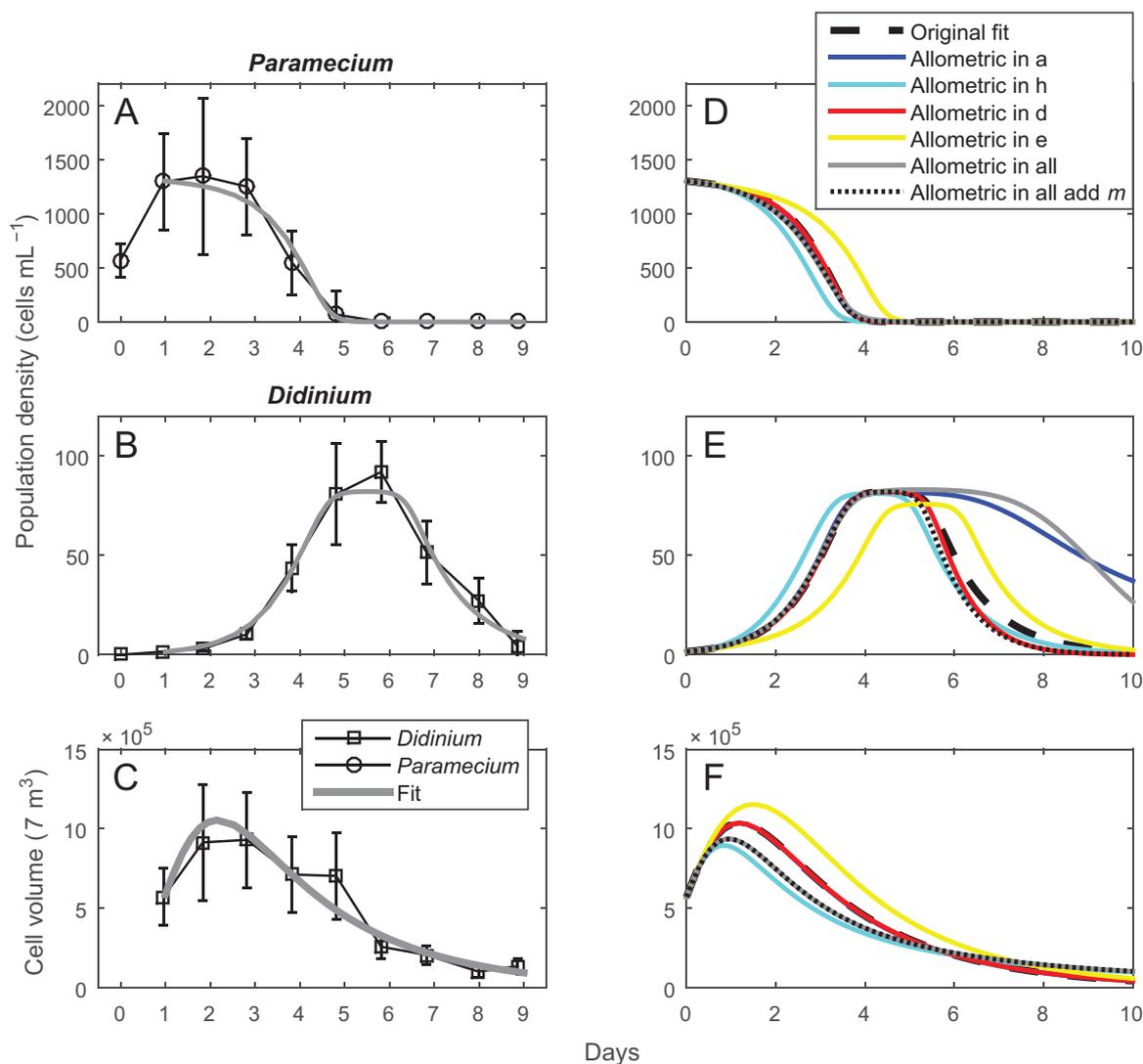
Figure 1: Population densities for *Paramecium aurelia* (*A*, *D*) and its predator *Didinium nasutum* (*B*, *E*), growing together, and *D. nasutum* cell volume (*C*, *F*). In *A*–*C*, original data ± SD, along with an overall fit of equations (1) to the data, are shown (redrawn from DeLong et al. 2014*a*). In *D*–*F*, the overall fit is shown (dashed black line), along with the expected dynamics if each of four parameters (*a*, *h*, *d*, and *e*) are allometrically linked to the predator cell volume changes seen in *C*. When the allometric relationships for all four parameters are included, a net effect arises that appears to be dominated by the effect of the *a* (space clearance rate) parameter ("Allometric in all"). When the known relationship between *a* and *m* (mutual interference) is included, the expected dynamics are nearly indistinguishable from the observed dynamics ("Allometric in all add *m*"), indicating that the pleiotropic effects of cell volume on multiple functional processes suppress the feedback from trait change to ecological dynamics.

I then used the allometric functions for each predator-linked parameter (*a*, *e*, *d*, and *h*; DeLong and Vasseur 2012; DeLong et al. 2015) to assess the expected change in dynamics that would arise, given the functional link between cell volume and the parameters. The allometric functions are of the form $y = b_0 M^b$, where y is the parameter of interest, b_0 is the value of the parameter when $M = 1$, and b is an estimated scaling exponent. Because *Didinium*'s parameters do not fall exactly on the allometric curve, the intercepts of all allometric curves were adjusted so that the

allometric equation used produces the original parameter estimate from DeLong et al. (2014*a*) at the starting body size (5.71 × 10⁵ μm³). I solved equations (1), substituting the fixed parameter with the appropriate allometric expression for each parameter in turn. To evaluate how all the effects interact together (ecological pleiotropy), I solved the model with all four allometric functions included. Finally, although there is no clear dependence of mutual interference on body size (DeLong 2014), interference is positively correlated with space clearance rate in *Didinium* (DeLong

and Vasseur 2013) by the relation $m = -0.26 \ln a - 0.49$. It is hypothesized that this relationship arises because any behavior that increases encounters with potential prey may increase encounters with competitors, causing a positive correlation between the two parameters (note that m is negative). Therefore, in addition to including the allometric effect of space clearance rate, in the fully pleiotropic model I also include interference as a function of space clearance rate.

Results

Equations (1) with the original fitted parameters provide a good fit to the raw data for the abundances of *Didinium* and *Paramecium* and the *Didinium* cell volume (fig. 1*A*–1*C*). With each of the four parameters (a, e, d, and h) substituted in turn with their allometric functions, all but the death rate indicate that deviations from the observed dynamics should arise (fig. 1*D*–1*F*). When all four parameters are included together as allometric functions, the expected dynamics appear to be dominated by the effect of the a parameter (gray line). However, when the empirically established relationship between a and m is included, the expected dynamics converge on the observed dynamics (compare dashed and dotted black lines). Thus, when the body-size-dependent effects of five parameters are included, the expected outcome is one with no detectable feedback from trait changes to the ecological dynamics.

Discussion

My results suggest that a shift in ecological dynamics may not be detectable even when substantial changes in functionally important traits have occurred (fig. 1). That is, even when a trait is changing rapidly and is strongly tied to the functional processes that set the dynamics, the outcome may not be different from that predicted by a model with no feedback from the trait. In this case, the dominant effects appeared to be space clearance rate and interference competition that canceled out the feedback as *Didinium* grew and declined in cell volume and population size (Holdridge et al. 2016). These results suggest that whether eco-evolutionary dynamics arise may in many cases depend on ecological pleiotropy and how broadly linked a particular trait is to the dynamics. One possibility is that traits influencing one or two functional processes may be more likely to generate detectable feedbacks than traits with more effects, such as body size.

These results are unexpected from recent theory on eco-evolutionary dynamics. The field of eco-evolutionary dynamics has grown logically out of observations that the evolution of functionally important traits may occur very rapidly, approaching the timescale of ecological dynamics (Hairston et al. 2005; DeLong et al. 2016). If they occur fast enough and do indeed have functional consequences, then even relatively short-term ecological processes may not be independent of evolution and may show signatures of rapid evolution (Post and Palkovacs 2009; Schoener 2011; Walsh et al. 2012). Thus, ecological models may have to incorporate evolution or risk being unable to accurately describe or predict the dynamics of natural systems. My results suggest that this need not be the case, however, and being able to predict when ecological pleiotropy might obscure feedbacks would be helpful for knowing whether evolution need be explicitly included in ecological models.

Another way in which the action of rapid evolution can be masked by ecological dynamics is through cryptic dynamics (Yoshida et al. 2007). Cryptic dynamics occur when the frequencies of different genotypes in a population change in a counterbalancing way, leaving the overall population size relatively stable. These types of dynamics are cryptic because the fluctuations of specific genotypes may go unseen at the population level. When occurring for prey or hosts in predator-prey or host-parasite systems, cryptic dynamics also obscure the underlying species interactions. Thus, antagonistic ecological pleiotropy obscures the functional consequences of trait change, while cryptic dynamics obscure the species interaction.

In contrast to the antagonistic ecological pleiotropy suggested by my *Didinium-Paramecium* results, other forms of ecological pleiotropy may not suppress the feedback to ecological dynamics. For example, a series of studies on the dynamics of chemostat systems with rotifers consuming algae suggest fluctuating selection on algal defense traits (Fussmann et al. 2003; Yoshida et al. 2003, 2007; Becks et al. 2012). Since the algal traits that minimize consumption by the rotifers also may influence the algae's own growth rate, this is a form of ecological pleiotropy. Instead of canceling out, however, as the algae increase in defensive characteristics, decreased growth and consumption rates may work together to briefly stabilize the system until grazing risk declines and reverses the selection on defensive traits.

Documenting eco-evolutionary dynamics is fairly challenging, requiring at a minimum documenting changes in traits, their functional links to dynamics, and a comparison of the dynamics with those of a no-evolution state (Fussmann et al. 2007). However, my results suggest that failing to see a difference between dynamics with changing traits and those with static traits is not sufficient to demonstrate that rapid trait change is not altering the interaction. Finally, it may be worth remembering that in the simple *Didinium-Paramecium* laboratory system, the effects of trait changes on other food web components is absent, so some consequence of the change in cell volume might still be relevant to more natural communities. The downstream consequences of the changes in *Didinium* size could influence interactions with other species and selection on other traits due to those interactions (terHorst et al. 2015).

Acknowledgments

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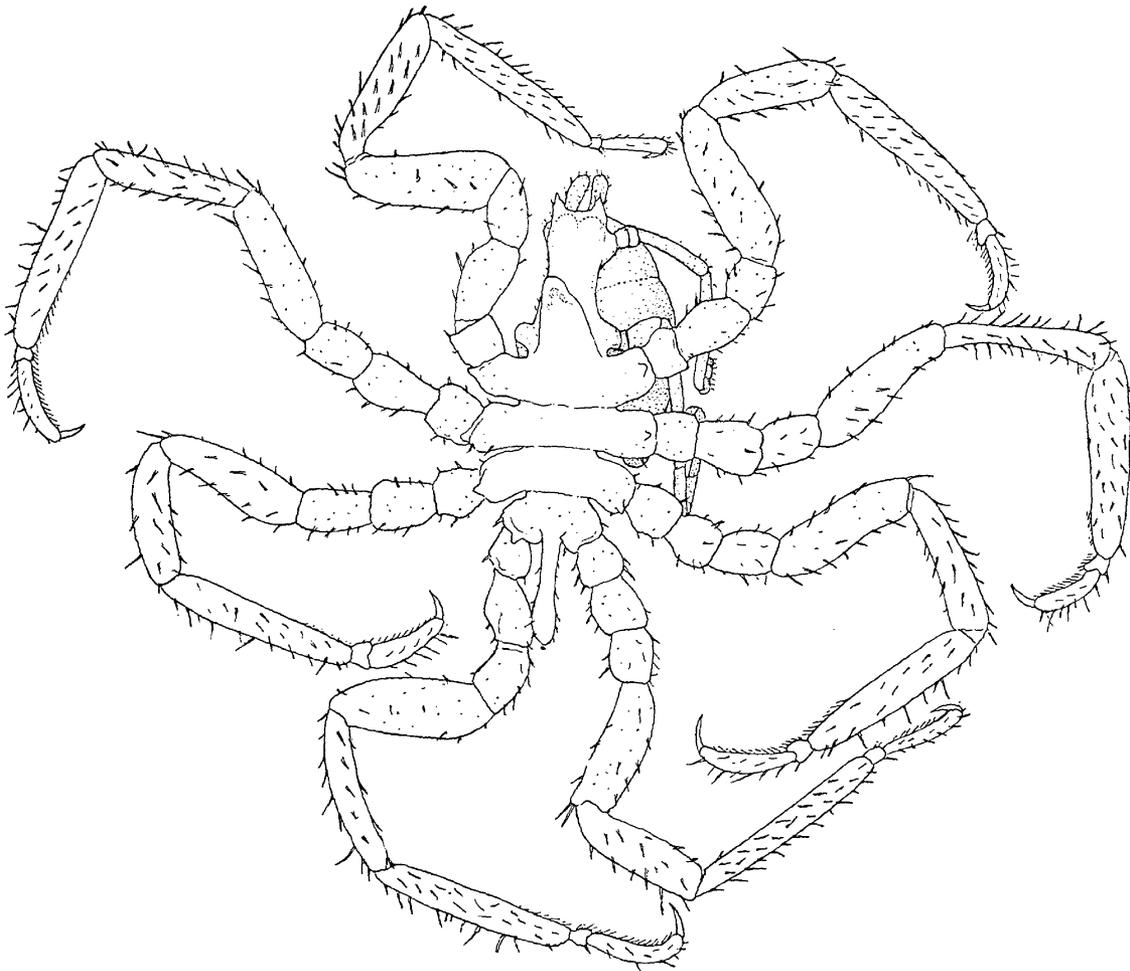
"Mr. Thomas Barbour has kindly turned over to me for examination a single pycnogonid taken upon the expedition made by himself, in company with Dr. G. M. Allen and Mr. Owen Bryant, to the Bahama Islands in the summer of 1904." Figured: dorsal view of *Barana latipes* female. From "A New Pycnogonid from the Bahamas" by Leon J. Cole (*The American Naturalist*, 1906, 40:217–227).