

IDEA AND
PERSPECTIVEIntegrating physiological, ecological and
evolutionary change: a Price equation approach

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Abstract

We use a general quantitative framework – the Price equation – to partition phenotypic responses to environmental change into separate physiological, evolutionary and ecological components. We demonstrate how these responses, which potentially occur over different timescales and are usually studied in isolation, can be combined in an additive way; and we discuss the main advantages of doing this. We illustrate our approach using two worked examples, concerning the emergence of toxin resistance within microbial communities, and the estimation of carbon uptake by marine phytoplankton in high-CO₂ environments. We find that this approach allows us to exclude particular mechanistic hypotheses with regard to community-level transformations, and to identify specific instances where appropriate data are lacking. Thus Price's equation provides not only a powerful conceptual aid, but also a means for testing hypotheses and for directing empirical research programmes.

Keywords

Carbon dioxide, community composition, community function, diuron, eco-evolutionary change, global change, levels of selection, microbial community ecology, toxin resistance.

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INTRODUCTION

Over arbitrary scales of time and space, the properties of natural communities may change owing to changes in the physiology of individual organisms, changes in the genetic composition of species and changes in species composition of communities. These causes of change have traditionally been considered in isolation by physiologists, evolutionary biologists and ecologists, respectively, with surprisingly little overlap between disciplines. This separatist approach has yielded insight into the mechanisms particular to each level. Examples include: how light levels mediate the expression of genes involved in photosynthesis (physiology); the effect of interactions such as cross-feeding or predation between species on community diversity (ecology); and describing the genetic changes that correlate with of the emergence of toxin resistance (evolution).

However, it is well known that ecological processes can influence evolutionary change, and *vice versa*, such that it becomes difficult or impossible to explain the properties of a population without taking both processes into account. All communities undergo both ecological and evolutionary change. On human timescales, one obvious example where

ecological and evolutionary processes are likely to co-occur is in microbial communities. For example, the presence of predators may mediate the degree of evolutionary diversification in bacterial communities (Hall *et al.* 2008). Similarly, rapid evolution of resistance to viruses can attenuate the impact of viral infection upon nutrient cycling (Lennon & Martiny 2008). Hence, a reasonably complete explanation for community-level change requires that researchers integrate ecological changes (shifts in community composition in terms of species or functional groups) and evolutionary changes (genetic change within species). Such studies primarily focus upon mechanistic models that show how incorporating ecology (e.g. interactions between trophic levels) affects how evolutionary processes (e.g. diversification) occur. However, they neither provide a general framework for partitioning the contributions of ecological and evolutionary change to transformations of the community as a whole, nor do they explicitly account for relatively rapid changes, such as physiological acclimation.

In this study, we show that Price's (1972) equation can be used to describe the separate effects of physiological, evolutionary and ecological change in an exact and completely general way. This approach allows the total

change at the community level to be expressed as a simple sum of these three effects. The approach is exact, and completely general, because it does not rest upon particular mechanistic assumptions. For this reason, it does not deliver the usual concrete results expected of mathematical modelling approaches. To illustrate the usefulness of a Price equation approach, we provide two worked examples. First, we apply the partition to changes in a microbial community's tolerance to a toxin (diuron), and we explicitly test the hypothesis that increases in community tolerance are primarily attributable to the elimination of sensitive species rather than to physiological change, or the evolution of resistance in sensitive species (McClellan *et al.* 2008). Second, we use the Price equation to systematically take stock of our ability to predict changes in carbon uptake (CU) by marine phytoplankton as a long-term response to elevated atmospheric CO₂ levels associated with climate change, highlighting a poverty of data that is easily remedied by more focused, theory-driven empiricism. Thus, we show that the Price equation provides a conceptual aid, facilitates testing of competing hypotheses, and suggests avenues for more fruitful empirical research.

PRICES EQUATION: COMBINING PHYSIOLOGICAL, EVOLUTIONARY AND ECOLOGICAL CHANGE

The Price equation is a mathematical theorem that can be applied to any system that undergoes a transformation (Price 1972; Frank 1995; Gardner 2008). It was originally developed to model evolutionary changes of biological populations (Price 1970), and now provides the formal basis for the theory of social evolution (Hamilton 1970, 1975; Price 1972; Frank 1998; Okasha 2006), although in recent years it has been applied to problems in a range of other disciplines including epidemiology (Day & Gandon 2005, 2007), community ecology (Loreau & Hector 2001; Fox 2005, 2006; Fox & Harpole 2008), economics (Andersen 2004) and linguistics (Jäger 2008). Its usefulness lies in its ability to describe the transformation of any character in an exact and completely general way, and to partition this total change into separate and meaningful components.

The Price equation is both exact and completely general, owing to the way that it emerges from notational definitions instead of specific mechanistic assumptions. Rather than modelling mechanistic processes directly, and using these to predict how a system will move from its present to future state, the Price equation takes both present and future states as given, and applies a partition that illuminates the change that has occurred (see worked example in the 'Emergence of community tolerance to toxins'). This does not mean that the Price equation cannot be used for predictive purposes. As a conceptual aid and organizational tool it can be used to point out productive paths of inquiry leading to scientific

progress on topics of real-world interest (see worked example in the 'Predicting carbon uptake by marine phytoplankton in a high CO₂ world').

Here, we are interested in describing dynamical transformations that occur within a multispecies community. We provide a hierarchical description of the community, assigning every species a unique index i and, within each species, assigning every lineage a unique index j (I is the set of species indices, and J_i is the set of lineage indices in species i). We census the community at times t_1 and t_2 , and we employ the Price equation to describe the change in community-average value for a character of interest ($\Delta\bar{x}$) over the intervening time period as:

$$\Delta\bar{x} = E_I(E_{J_i}(\Delta x_{ij})) + E_I(\text{cov}_{J_i}(w_{ij}, x'_{ij})) + \text{cov}_I(w_i, x'_i), \quad (1)$$

where: E and cov denote the statistical expectation (arithmetic average) and covariance, respectively, taken over the sets indicated by subscripts; x_{ij} and $x'_{ij} = x_{ij} + \Delta x_{ij}$ denote the value of the character of interest exhibited by lineage j in species i at times t_1 and t_2 , respectively; \bar{x}_i denotes the average value, over all lineages in species i at time t_1 , of the character at time t_2 ; and w_{ij} and w_i denote the relative growth factor of lineage ij and species i , respectively, within the community (mathematical details given in Appendix 1).

Equation (1) states that the change in the average value of the character across the whole community during this time interval is given by the sum of three terms. The first term, which corresponds to the change in the value of the character exhibited by a lineage (Δx_{ij}), averaged over all lineages in the community, defines the *physiological* change. This captures any overall tendency for lineages to change their character value in a particular direction. The second term, which is given by the covariance between a lineage's new character value (x'_{ij}) and its relative growth factor (w_{ij}), averaged over all species in the community, defines the *evolutionary* change. This is non-zero, if there is a tendency for lineages with higher or lower character values to increase in relative abundance within their species. Finally, the third term, the covariance between a species' new character value (\bar{x}'_i) and its relative growth factor (w_i), defines the *ecological* change. This captures any tendency for species with higher or lower character values to increase in relative abundance within the community. These three effects are illustrated in Fig. 1.

As shown in the Appendix 1, eqn (1) follows directly from notational definitions and hence is exact and completely general so long as the notation holds. However, for concreteness and to aid meaningful interpretation, a number of simplifying assumptions might be made. While we have conceptualized the average change within lineages as a

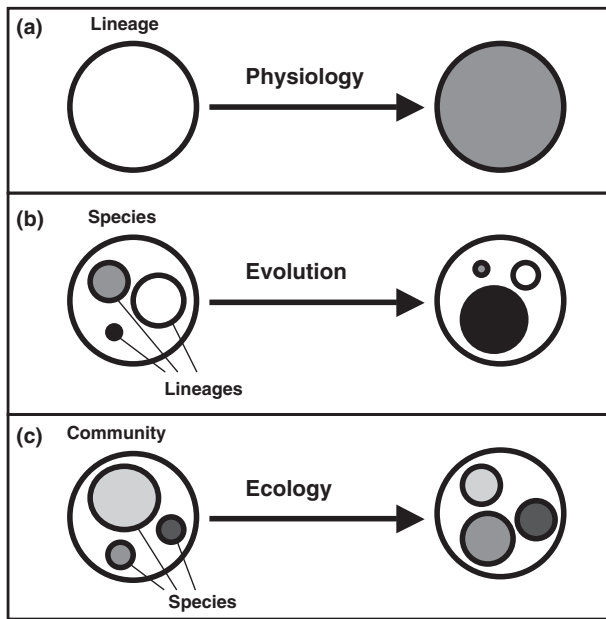


Figure 1 Physiological, evolutionary and ecological change in a trait of interest. (a) Physiological change in a focal lineage. The total physiological change at the community level is the average physiological change of all constituent lineages, weighted by their initial abundances. (b) Evolutionary change in the focal species, owing to changes in relative abundance of constituent lineages differing in their initial trait values. Note that this does not include the effect of physiological changes within lineages. The total evolutionary change at the community level is the average evolutionary change of all constituent species, weighted by their initial abundances. (c) Ecological change in the community, owing to changes in relative abundance of species differing in their initial trait values. Note that this does not include the effects of physiological change within lineages, nor of evolutionary change within species.

‘physiological’ effect, processes such as mutation (which are not usually considered physiological) are likely to contribute to this term. Hence, by using this terminology we essentially make the simplifying assumption that standing genetic variation, rather than novel mutational input, accounts for most of the response to selection during the time interval of interest. This may be a reasonable approximation for large microbial populations in which every genetic variant can be considered present (at perhaps vanishingly low initial frequency) from the start. More generally, the components of change (and their additivity) do not necessarily reflect the underlying mechanistic processes (and the ways in which these potentially interact). For example, a lineage’s physiology might be mediated by the species composition of its community, and hence changes in the latter might induce changes in the former; this would be classified as ecological change (i.e. owing to changes in species composition), rather

than physiological change or an ecology–physiology interaction.

This Price equation provides a useful means of understanding scenarios where physiological, ecological and evolutionary processes are likely to occur over the timescale of interest. First, being a statistical tautology, it is completely general and exact, and so we can be sure that eqn (1) has not neglected any key effects. All possible biological, chemical and physical processes are accounted for, albeit in an implicit way. Second, because no particular mechanistic assumptions are made, eqn (1) holds for any particular mechanistic model that has been or could be devised. Hence, our notational model provides a ‘meta-model’ that allows researchers to translate between, and to generalize from, particular mechanistic models. Third, it provides a proof of concept, namely that physiological, evolutionary and ecological effects are distinct, that they add up to give the total phenotypic change, and that there is no *a priori* reason to assume that any of these effects are unimportant.

EMERGENCE OF COMMUNITY TOLERANCE TO TOXINS

The use of antimicrobial agents is ubiquitous in our lives, from antimicrobial soaps and household cleaners, to prescription antibiotics to commercial antifouling agents. Exposure to high levels of toxin is a classic example of strong selection that has been used in experimental evolution studies to select specifically for evolved lineages that are resistant to toxins (Reboud *et al.* 2007), so it is not surprising that microbial lineages that survive the initial exposure to the toxin may undergo rapid microevolution. Additionally, the presence and abundances of different species in microbial communities may change in response to toxin exposure, further affecting the community-level tolerance to a toxin. We often have a vested interest in understanding the basis of the emergence of toxin tolerance in microbial communities for health, economic or ecological reasons, yet it is often unclear how community tolerance to toxins emerges in cases where both evolutionary and ecological responses to the toxin occur. For example, we may wish to assess the toxicity of antifouling agents released into the environment on microbial communities that are responsible for primary production in aquatic ecosystems. Here, environmental risk assessments are often carried out using either acute or chronic exposure of single-species populations of microbes (Lin *et al.* 2005). Alternatively, species sensitivity distributions – which estimate the concentration of toxin at which 95% of the species would be unaffected – may be used (Roelofs *et al.* 2003). However, recent work where microbial assemblages were exposed to varying levels of toxin for 3 months found that the community-level effects, which included increased tolerance

to the toxin, were not predictable from single-species tests (McClellan *et al.* 2008). Here, we use the Price equation to evaluate the specific explanation that poison-induced community tolerance (PICT) is the result of more tolerant species replacing less tolerant species (McClellan *et al.* 2008). This demonstrates how explicitly separating and accounting for physiological, ecological and evolutionary responses to an environmental change can aid in interpreting results from particular studies.

We partition the response of a simple phytoplankton community to chronic, environmentally relevant levels of diuron exposure. Diuron is a well-studied photosystem-2 inhibitor and commonly used antifouling agent (Sabater *et al.* 2007). In most published studies and measures of toxicity the phenotype of interest (\bar{z}) is the photosynthesis rate per unit chlorophyll. Here, we take advantage of a study by McClellan *et al.* (2008) where phytoplankton communities were exposed to sublethal levels of diuron for 3 months,

and where the total change in community phenotype was reported, as well as changes in community composition. The resolution of community composition is not at the level of individual species, but rather at the level of functional groups (diatoms vs. cyanobacteria). Hence, whilst we may define a quasi-ecological effect in terms of the change in photosynthetic rate that can be ascribed to changes in the relative abundances of functional groups, and a quasi-evolutionary effect in terms of the change that can be ascribed to changes in the relative abundances of lineages within functional groups, some true ecological change (owing to changes in the relative abundance of species within functional groups) is necessarily left out of the former effect and incorrectly attributed to the latter effect. However, the aim here is to provide a proof of principle, and to illustrate how the Price equation partition could be applied to more detailed data. Hence, we proceed by treating the functional groups in the McClellan *et al.* (2008) dataset

Table 1 Breakdown of terms used in partitioning the emergence of community tolerance to diuron

	Relative photosynthesis rate	Inhibition of photosynthesis(%)	Absolute photosynthesis rate \bar{z}			
Total difference in community phenotype						
\bar{z} Community	100	0	2.65			
\bar{z}' Community	85	14.28571429	2.2525			
Change in phenotype	-0.3975					
	Initial frequency a_i	Initial photosynthesis rate \bar{z}_i	Inhibition of photosynthesis (%)	Final photosynthesis rate \bar{z}_i'	Total photosynthesis rate for group	
Physiological change						
Diatoms	0.9	2.5	85	2.125	1.9125	
Cyanobacteria	0.1	4	90	3.6	0.36	
Change in phenotype					-0.3775	
	Initial frequency a_i	Final frequency a_i'	Final photosynthesis rate \bar{z}_i'	Photosynthesis weighted by frequency $(a_i' - a_i)\bar{z}_i'$	Lineage growth factor w_i	Average fitness (all groups)
Ecological change						
Diatoms	0.9	0.5	2.125	-0.85	0.55	1.0
Cyanobacteria	0.1	0.5	3.6	1.44	5	
Change in phenotype						0.59
	Total change in phenotype	Physiological contribution	Ecological contribution			
Evolutionary change						
Community	-0.3975	-0.3775	0.59			
Change in phenotype	-0.61					

All absolute photosynthesis rates are in $\mu\text{g C}\cdot\mu\text{g Chl}\cdot\text{h}^{-1}$. All data are for subacute diuron exposure ($0.4\text{--}0.8\mu\text{g L}^{-1}$ of diuron) (Source: Avramescu *et al.* 1999; Soukupová *et al.* 1999; Coles & Jones 2000; McClellan *et al.* 2008).

as species in the framework of eqn (1). Note that the choice of levels does not affect the mathematical validity of eqn (1), but it does affect our interpretation of each of the three components of change. Throughout the calculations, we use data for phytoplankton exposed to 0.4–0.8 $\mu\text{g L}^{-1}$ of diuron, which falls within the range of concentrations measured in chronically exposed areas and is well below concentrations needed to provoke an acute response (4–9 $\mu\text{g L}^{-1}$) (Sabater *et al.* 2007). All calculations are summarized in Table 1. The sources for each value and particular calculations for this example can be found in the supplementary version of Table 1 (Table S1).

Total difference in community phenotype

The total difference in community phenotype is simply the decrease in the photosynthesis rate per unit chlorophyll of the community after long-term exposure to diuron, and can be taken directly from published data. This is reported as the percent inhibition of photosynthesis in most studies, but can easily be transformed into absolute rates. Here, the total difference in community phenotype is -0.40 , or a 40% reduction in photosynthesis per unit chlorophyll.

Physiological change

The part of the community level change that can be ascribed to physiology is defined as the average (over all lineages within the community, weighted by their initial abundance) change in photosynthesis rate per unit chlorophyll. In other words, it is the part of the total change that is not due to changes in the abundance of lineages within each functional group or changes in the abundance of functional groups within the community. The available data do not discriminate individual lineages within functional groups, so it is not possible to measure this effect directly. However, upon the assumption that physiological change occurs relatively quickly and evolutionary and ecological effects occur relatively slowly, we can estimate the physiological change simply by measuring the difference in photosynthesis for each functional group after physiological acclimation to diuron exposure. Short-term diuron exposure tests are typically carried out over days in the studies used here. For this community, the physiological response is -0.38 , or a 38% reduction in photosynthesis per unit chlorophyll in the community (details in Table 1).

Ecological change

The part of the community level change that can be ascribed to ecology is equal to the covariance (over functional groups, weighting according to their initial abundance) of a functional group's (post-physiological change) photosynthe-

sis rate and its relative growth factor in the community. In other words, the ecological effect is that which is due to changes in the relative abundances of functional groups in the community. We have estimated the physiological change for each functional group above, and relative growth factor is readily calculated as the ratio of final vs. initial relative abundance, where the final abundance is measured in the chronically diuron-poisoned environment and the initial abundance is measured in the unexposed environment. This gives a change of $+0.59$, or a 59% increase in photosynthesis per unit chlorophyll in the community (Table 1).

Evolutionary change

The part of the community level change that can be ascribed to evolution is equal to the average (over functional groups) covariance within each functional group of a lineage's (post-physiological effect) photosynthesis rate per unit chlorophyll and its relative growth factor within the community. Thus, the evolutionary effect describes the part of the community-level change that is due to changes in the relative abundance of lineages within functional groups. As outlined above, the available data do not allow discrimination of individual lineages. However, the evolutionary effect is obtained by subtracting the sum of physiological and ecological effects from the total change, and hence can be estimated by difference, since the other terms in the equation are known. For this example, the evolution term is -0.61 , or a 61% decrease in photosynthesis per unit chlorophyll in the community (see Table 1). Calculating this term on its own would require information on the variation within functional groups for photosynthesis inhibition by diuron, as well as some measure of how degrees of photosynthetic inhibition covary with fitness within functional groups.

DISCUSSION

One of the striking features of PICT that is exposed by using our Price equation approach is that the ecological and evolutionary effects are both large, but in the opposite direction. In this particular case, they are of roughly equal magnitude, and nearly cancel each other out. If only the physiology term was measured, this could easily be misinterpreted to support the idea that PICT can be explained by the physiology term alone, and that long-term community tolerance can be predicted from weighted averages of single-species acclimation data. However, the changes in community composition, both in terms of functional groups present and in terms of the lineages that make up the functional groups, has changed drastically.

Even though both functional groups decrease photosynthesis rates after exposure to diuron, cyanobacteria have photosynthesis rates that are less sensitive to low

concentrations of diuron, and also increase in frequency in communities that are exposed to diuron. There is a shift from a diatom-dominated community (90% diatoms and 10% cyanobacteria) before diuron exposure to a community where cyanobacteria are 50% of the community. Since cyanobacteria have much higher absolute levels of photosynthesis/chlorophyll here, changes in community composition lead to a large increase in the community photosynthesis rate per unit chlorophyll.

The large negative evolution term indicates that within each functional group, the relative fitness of lineages that photosynthesize more slowly increases under chronic diuron exposure. There are several reasons that this might be the case. First, species or lineages with lower photosynthesis rates may be less affected by diuron, in that they may experience a lower percent inhibition of photosynthesis. This would require that there be a positive correlation between diuron sensitivity (measured as percent inhibition of photosynthesis) and uninhibited photosynthesis rates, as well as a negative correlation between photosynthesis rate and competitive fitness in the presence of low concentrations of diuron. Alternatively, lineages with lower uninhibited photosynthesis rates may be less affected by diuron poisoning because the same percent reduction in photosynthesis rate corresponds to a lower absolute loss in energy for the cells such that the fitness effect of a given amount of photosynthesis inhibition is smaller. This would not require any correlation between photosynthesis rates and percent inhibition by diuron. One would instead expect to see that the fitness cost per percent inhibition of photosynthesis is positively correlated with the absolute rate of uninhibited photosynthesis. Our framework cannot distinguish between these two possibilities. However, it does produce a set of expectations that allow a simple experiment to be carried out that would measure the covariances between photosynthesis rates, diuron sensitivity and fitness (growth rate or competitive ability).

Our partition of the Price equation lends very limited support to the hypothesis that PICT is attributable to the elimination of sensitive species. While the change in functional group frequencies is consistent with community tolerance increasing when a more sensitive group (diatoms) declines in frequency, changes within functional groups appear to be related to differences in photosynthesis rates. The sign difference between the ecology and evolution terms highlights that eqn (1) can also be used to force the clarification of a hypothesis and expose implied assumptions. Here, we see that the hypothesis that more sensitive groups are eliminated assumes that diuron sensitivity has a strong negative correlation with competitive fitness regardless of the level of biological organization upon which selection is acting. Furthermore, since a single explanation for PICT is proposed for the entire community, it is also

assumed that selection acts in much the same way on competition between functional groups as it does on competition between species or lineages within functional groups. From eqn (1) we observe that this is not the case, and that it is likely that selection acts differently between functional groups and between lineages.

Another key consideration is that traits other than photosynthesis levels may be interesting or important. Our partition shows that there is scope for selection in this system. For covariances between traits to be non-zero, variances in traits must be larger than zero. We have shown that covariances in this system are non-zero, which demonstrates that traits other than photosynthesis also have the potential to evolve in response to chronic exposure to low levels of diuron. This could warrant concern in some cases. For example, some cyanobacteria produce toxins, and here we have a shift towards communities with a higher proportion of cyanobacteria, along with probable changes in the species of cyanobacteria present.

PREDICTING CARBON UPTAKE BY MARINE PHYTOPLANKTON IN A HIGH CO₂ WORLD

Currently, there is much interest in predicting the biological consequences of climate change. One major point of interest is in evaluating the responses of oceans to global change, where an important goal is to better understand how future populations of phytoplankton may differ from contemporary ones (Falkowski *et al.* 2000). This is not surprising, since phytoplankton CU and fixation comprises *c.* 40% of global photosynthesis, and makes up the biological carbon sink in the ocean (Falkowski 1994). Because phytoplankton have large population sizes and relatively fast generation times, it is possible that changes in physiology, species succession (ecological change) and genetic change within species (evolutionary change) occur on human time scales, and there is limited experimental evidence that evolutionary change in CU (Collins & Bell 2004; Collins *et al.* 2006) is likely to occur in response to elevated CO₂. Recent work has called for an integration of physiological, ecological and evolutionary responses of phytoplankton to elevated CO₂ (Bell & Collins 2008; Rost *et al.* 2008). However, there has been confusion as to whether these three aspects of change are actually distinct (for recent examples illustrating this see Riebesell *et al.* 2007; Iglesias-Rodriguez *et al.* 2008; Wohlers *et al.* 2008). Additionally, no attempt has yet been made to quantitatively combine existing empirical data on physiological, ecological and evolutionary effects. Instead, experimental studies on responses of marine phytoplankton to elevated CO₂ rely on qualitative descriptions of how these different levels may interact (e.g. see Riebesell *et al.* 2008, Piontek *et al.* 2009). The contribution of applying the Price equation here is to

show – in all possible models, rather than in one toy model – that the three components of change are indeed distinct and that none of them can be dismissed *a priori*. Our goal in this worked example is not to produce a numerical prediction, but to illustrate how published data may be used (and what data are needed) to obtain a meaningful numerical calculation over these levels of biological organization. In other words, our partition of the Price equation can be used to make a specific and practical ‘to do’ list that may be useful in organizing interdisciplinary efforts, and indicating which items have been ‘checked off’ and which remain to be performed. Such a list could be compiled without any overarching quantitative framework, but using the Price equation here provides a concrete list of data

needed, and points out a form in which data can be reported so that it is possible to combine data across fields of research to make quantitative predictions.

Here, we use eqn (1) as a way to identify specific data that are missing to make a prediction that takes physiology, ecology and evolution into account. In the interests of providing a simple illustration, we limit our ‘to do’ list to identifying specific data relevant to the change in CU in phytoplankton communities to elevated CO₂. Our trait of interest (\bar{z}) is the rate of CU. While many other aspects of the environment will change along with an increase in global CO₂ levels, empirical studies that document responses to many simultaneous environmental changes (elevated CO₂, lowered pH, changes in temperatures, light levels and

Table 2 Breakdown of terms used in sample calculation of change in community carbon uptake attributable to carbon enrichment alone

	Initial frequency a_i	Relative total carbon uptake after acclimation \bar{z}_i'	Relative total carbon uptake for group $a_i \bullet z_i$	
Physiological change				
Picoplankton	0.296296296	1.187652676	0.351897089	
Mixed algae	0.176870748	1.143548559	0.202260289	
Calcifyers	0.235827664	0.924997107	0.218139907	
Silicifyers	0.291005291	2.055555556	0.598177543	
Change in phenotype	0.370474828			
	Initial frequency a_i	Final frequency a_i'	Relative total carbon uptake after acclimation \bar{z}_i'	Relative total carbon uptake for group $(a_i' - a_i)z_i'$
Ecological change				
Picoplankton	0.296296296	Must be measured by well	1.187652676	Must be calculated
Mixed algae	0.176870748	replicated community composition	1.143548559	
Calcifyers	0.235827664	experiments spanning	0.924997107	
Silicifyers	0.291005291	long time scales.	2.055555556	
Change in phenotype	$(a_i' - a_i)z_i'$			
	Initial frequency a_i'	Relative carbon uptake after genetic change \bar{z}_i^*	Relative total carbon uptake after acclimation \bar{z}_i'	Relative total carbon uptake for group $a_i(\bar{z}_i^* - \bar{z}_i')$
Evolutionary change				
Picoplankton	Must be measured	Must be measured by	1.187652676	Must be calculated
Mixed algae	(see Ecological change)	well replicated experimental	1.143548559	
Calcifyers		evolution studies for	0.924997107	
Silicifyers		each phytoplankton group.	2.055555556	
Change in phenotype	$a_i'(z_i^* - z_i')$			

All carbon uptake rates are relative, and expressed as fold differences per individual for each group. Data for physiological responses and initial frequency of groups are calculated from: Burkhardt *et al.* 2001; Clark & Flynn 2000; Fu *et al.* 2007; Hansen *et al.* 2007; Hutchins *et al.* 2007; Langer *et al.* 2006; Leonardos & Geider 2008; Le Quéré *et al.* 2005; Post *et al.* 1984; Smith & Lancelot 2004; Söderberg & Hansen 2007; Riebesell *et al.* 1993; Rost *et al.* 2006; Trimborn *et al.* 2007; S. Trimborn, personal communication, Zondervan *et al.* 2001, 2002, Zondervan 2007.

stratification, to name a few) are rare. In any case, the same framework may be used as data on responses to more complex environmental change become available. In this example we use species rather than functional groups, according to the definition of evolutionary change as change that occurs within species. The concept of the functional group (e.g. silicifiers, calcifiers, green algae and cyanobacteria) is widely used in phytoplankton studies, and so alternatively the community level change could be partitioned into within and between functional group components. Examples of published numerical data that could be used or concise descriptions of missing data can be found in Table 2.

Physiological change

The part of the total change at the community level that is attributed to physiology is that which is not due to changes in the relative abundance of lineages within species or changes in the relative abundance of species within the community. As before, this is most readily estimated by assuming that physiological effects occur relatively quickly and evolutionary and ecological effects occur relatively slowly, and measured as the change in CU per unit chlorophyll after an acclimation period of hours or days. The physiology effect for lineage i is simply the CU after physiological acclimation has reached steady-state levels minus the original CU: $\bar{z}'_i - \bar{z}_i$. To find the total physiology effect for the community, we simply average this over all the lineages:

$$\Delta_{\text{PHY}}\bar{z} = E_I(E_{J_i}(\Delta z_{ij})) = E_I(E_{J_i}(\bar{z}'_{ij} - \bar{z}_{ij})) \quad (2)$$

Different experiments use different media, methods, dissolved inorganic carbon levels, pH, etc., but the difference in CU in response to carbon enrichment for any given organism is repeatable when expressed as fold increase in net CU or fold increase in carbon fixation per unit chlorophyll. There are sufficient published data to estimate this term at the resolution of functional groups. See Table 2 for how data that could be used to calculate the physiology term. For the moment, community composition data is available at the level of functional groups, even though acclimation data are available for individual species. To properly estimate this term, community composition must be reported at the same taxonomic level that physiological studies are carried out at.

Ecological change

The part of the total change at the community level that is attributed to ecology is that which is due to changes in the relative abundance of species in the community. One way to

measure this would be to carry out experiments similar to those in the toxin tolerance example considered in the previous section, where phytoplankton communities could be exposed to elevated levels of carbon over several months and the change in community composition measured. This has been attempted over short timescales and with very little replication such that only extremely large effects could have been detected. Results have been equivocal so far, and general results that could be extrapolated to longer-term effects on community composition have not yet emerged (see e.g. Riebesell *et al.* 2007; Tortell *et al.* 2008).

Evolutionary change

The part of the community level change that can be ascribed to evolution is that which is due to changes in the relative abundance of lineages within species. In eqn (1) we have defined this as the average (over species) covariance within each species of a lineage's (post-physiological-effect) CU (\bar{z}'_{ij}) and its relative growth factor (w_{ij}). We can re-express this change as:

$$\Delta_{\text{EVO}}\bar{z} = E_I\left(\text{cov}_{J_i}\left(w_{ij}, \bar{z}'_{ij}\right)\right) = E_I\left(w_i(\bar{z}_i^* - \bar{z}'_i)\right). \quad (3)$$

where \bar{z}_i^* is the CU of species i at time t_2 , and hence $\bar{z}_i^* - \bar{z}'_i$ is the change in this species' CU level that can be ascribed to evolution. For each lineage, we have the CU that is reached once physiology has settled down, i.e. \bar{z}'_i . We can also define CU after genetic change has occurred \bar{z}_i^* , which may differ from the nongenetic (physiological) response, \bar{z}'_i . Thus, the change in CU due to evolution in lineage i is simply $\bar{z}_i^* - \bar{z}'_i$. The growth factor w_i must be measured experimentally. Having obtained these quantities, their product $w_i(\bar{z}_i^* - \bar{z}'_i)$ can be calculated and averaged over all species to obtain the total evolutionary change. In trying to calculate the evolution term, we see immediately that different marine phytoplankton species must be used for standard experimental evolution studies where replicate populations are grown for hundreds of generations at rising or elevated dissolved organic carbon (or elevated CO₂) if we are to make better, or indeed any, predictions about evolutionary outcomes. Specifically, we need to know the genetic response in CU to long-term growth at elevated CO₂, as well as how CO₂ uptake correlates with fitness, in different lineages of marine phytoplankton. Until these data are available, we will be unable to estimate the contribution of evolutionary change to changes in CU in future phytoplankton populations.

Discussion

To date, empirical studies of how phytoplankton CU may change in a higher CO₂ world have focused almost

exclusively on physiological responses along with a few qualitative descriptions of changes in community composition. It has been assumed (somewhat optimistically) that micro-evolutionary responses expected over decades or centuries may be somehow inferred from changes in community structure from sediment or other data that reflect patterns of change in community composition over tens or hundreds of thousands of years (Falkowski & Oliver 2007). However, the validity of simply scaling up or down between such different timescales is contentious. For example, effects of differences in the rates/magnitudes of global change cannot be taken into account systematically, nor can any other differences in global change such as the presence of other nutrients/pollutants, or differences in biotic surroundings brought about by human activity or chance. This suggests that empirical measures of evolutionary responses to relevant rates and magnitudes of environmental change over micro-evolutionary timescales (hundreds or thousands of generations of phytoplankton) may be a more conservative and reliable route to take.

This exercise has shown that we are currently unable to make even a rough calculation for how phytoplankton communities will respond to even a single component of global change. However, it reveals that relatively few additional experiments need be performed to remedy this. In terms of ecology, more and longer replicate experiments are needed to detect any general patterns that may exist, and changes in community composition must be quantified. In terms of evolution, only a single published study documenting the evolutionary response to elevated CO₂ exists, and uses *Chlamydomonas reinhardtii*, a common freshwater model system (Collins & Bell 2004; Collins *et al.* 2006). At present, it is not possible to calculate the evolution term unless many untested assumptions are made to apply the Collins & Bell (2004) results to different marine phytoplankton. In a freshwater model system, the contribution of evolutionary change to the end population CU was important (Collins *et al.* 2006), demonstrating that there is no *a priori* reason to suppose that this term can continue to be ignored. We suggest that gathering data for calculating this term should be a priority in research that aims to assess how future phytoplankton may take up carbon. This can be performed using standard microbial experimental evolution studies using marine phytoplankton. A second problem is that while physiological and micro-evolutionary studies report results at the level of species, ecological (community composition) studies report data at the level of larger groups (such as diatoms, coccolithophores, etc.). To combine data from these three levels, an effort must be made to report community composition data in terms of species. This is possible using sequence-based methods.

DISCUSSION

Community-level characters are ultimately determined by who is there and what they are doing. For example, in phytoplankton communities the presence and abundance of different functional groups affects the total primary production of the community. While many functional groups are capable of photosynthesis, they may do so at very different rates and produce different amounts of biomass for a given amount of photosynthesis. The species or lineage composition of the functional groups themselves may affect how rapidly or efficiently these processes are carried out by the functional group. We expect that many environmental changes will alter the composition of communities by changing the relative fitnesses of types either between functional groups, within functional groups, or both. Additionally, selection may differ in intensity and even direction between and within functional groups, requiring that selection within and between functional groups be treated separately in experiments and explanations. However, evolutionary ecologists have lacked a general quantitative framework for combining data on how the composition of communities changes between environments (or over time) that explicitly allows incorporation of changes in the relative abundance of functional groups along with evolutionary change within functional groups. This may not be a problem when one of the processes can be legitimately ignored over the time or spatial scale of interest, but may pose an important barrier to quantitative predictions or clear explanations when the effect of selection between functional groups and within functional groups is of similar magnitude, as seen in our first worked example.

We have reiterated throughout this article that our use of the Price equation to partition physiological, evolutionary and ecological causes of community-level changes is intended to be applicable wherever these three causes of change are likely to co-occur over the time scale of interest. Microbial communities are assemblages where ecological and evolutionary change will occur on human timescales, since microbial communities are generally composed of several distinct functional groups, each of which may contain large, genetically diverse populations with fast generation times. Our partition could also be used for macrobes, especially if two distinct populations separated in space instead of time were being considered, so long as information at all three levels of biological organization can be gathered. Our worked examples use microbes because physiological, ecological and evolutionary responses can all be measured in the same replicated experiment (as in the diuron example), which makes it simple to combine the different measurements and allows us to focus on the framework itself. We have shown that the Price equation may be used to better understand how the characters of

communities change over time by: (1) providing a way to quantitatively combine data from physiology, ecology and experimental evolution studies and (2) reducing unnecessary speculation in the interpretation of evolutionary ecology experiments by explicitly partitioning effects. There are numerous studies in both the experimental evolution (MacLean 2005; Benmayor *et al.* 2007; Brockhurst *et al.* 2007; Venail *et al.* 2008) and ecology (Urban 2006; Loeuille & Leibold 2008) literature on how ecological interactions such as predation, infection and competition affect community-level properties, usually diversity or primary productivity. Our framework would allow studies (or meta analyses) to quantitatively compare the relative contributions of physiological (termed 'acclimation' or 'plastic responses' in most studies), ecological and evolutionary processes to either diversity or primary productivity between studies. This would be a significant improvement on qualitative agreement or disagreement between studies, especially since whether or not results agree is often a subjective judgement based on the presence of similar enough qualitative patterns. For example, recent metacommunity models of dispersal in patchy environments have taken adaptation into account (Urban 2006; Fussmann *et al.* 2007), and experimental tests of how migration rates in structured environments affect diversity and adaptation exist (for recent examples see Habets *et al.* 2006; Venail *et al.* 2008). Here, our framework could be used as a way to compare studies and test models in community ecology and experimental evolution, two fields that often investigate many of the same problems, such as determination and maintenance of diversity or of community function, using different experimental and theoretical frameworks. In cases where it is not possible to test models with existing experimental data, our framework could be used as a tool for identifying what specific information is missing, as shown in our worked example.

We have taken a Price equation approach to partition phenotypic change so that the contributions of processes operating at three levels of biological organization – physiology, evolution and ecology – can be included in a single quantitative framework. Price's equation was developed by a population geneticist to study evolutionary change (Price 1970), and now provides the formal basis for topics such as kin selection and levels of selection in social evolution (Frank 1998; Okasha 2006). However, the equation has since been generalized to describe any transformative process, and has been applied to problems elsewhere in the biological sciences, and beyond (Price 1972, 1995; Frank 1995, 1998; Loreau & Hector 2001; Andersen 2004; Day & Gandon 2005, 2007; Fox 2006; Fox & Harpole 2008; Gardner 2008; Jäger 2008).

The Price equation is unlike most other mathematical modelling approaches used in the biological sciences. In

particular, it makes no mechanistic assumptions. Instead, it emerges as a logical consequence of notational definitions. The benefit of this is that it achieves far greater generality and exactness than more conventional models of biological transformation. Thus, it can be used to solve conceptual problems in a more decisive, complete and convincing way than would be possible using – and attempting to generalize from – specific 'demonstrations' that require particular and restrictive assumptions. The cost of this generality is that it does not provide the kind of concrete results that biologists typically expect from a mathematical modelling exercise.

Thus, it could be said that Price's equation is a tool for understanding rather than for making predictions. This is certainly the case for our worked example concerning the evolution of diuron tolerance in microbial communities, in which the overall transformation was already known but where the relative contributions of physiology, evolution and ecology were unknown and, indeed, a matter of controversy. However, this view may be too simplistic, as Price's equation can be used in conjunction with mechanistic assumptions to make predictions about future changes in important community-level characters, as illustrated by our worked example on changes in CU in phytoplankton communities as a response to elevated CO₂ levels. Here, the Price equation acts as an organizational tool, which allows the knowledge and understanding of physiologists, ecologists and evolutionary biologists to be applied simultaneously to a problem of global importance. This approach is not limited to microbial communities. The same analysis could be performed on, for example, studies investigating the effects of CO₂ enrichment on terrestrial plant communities.

Our partition of community transformation into its separate ecological, evolutionary and physiological effects echoes a similar partition provided by Fox (2006; see also Fox & Harpole 2008) in an effort to understand the impact of species loss on community productivity. We now outline some similarities and differences with this earlier partition, which also arose out of a Price equation analysis. First, as outlined in the Appendix 1, our partition of effects contributing to change in the community-average value of some character of interest ($\Delta\bar{x}$; e.g. per unit biomass photosynthetic rate) is readily extended to describe the change in the community-total value of this character (ΔT ; e.g. the total photosynthetic rate), when the size of the community changes over time. This leads to a separate 'biomass' effect ($\Delta N\bar{x}$) which is the product of the total change in biomass (ΔN) and the initial average character value (\bar{x}) and which is simply the change in the total character value that would be expected if the community were to change in size but the average character value were to stay the same. Fox's (2006) partition – given in his

equation (4) – begins with an analogous ‘size’ effect, which is due to change in the species richness of the community (i.e. number of species) rather than to change in biomass. In particular, his ‘species richness’ effect is also defined as the product of change in community ‘size’ (species richness; Δs) and the initial average value of the character (\bar{z}). Hence, our community ‘biomass’ effect is mathematically analogous to Fox’s (2006) species richness effect.

Second, as outlined in the Appendix 1, the remaining change unaccounted by this community size effect is given by the $(N'\Delta\bar{z})$, i.e. it is the product of the final size of the community (N') and the change in the average value of the character of interest ($\Delta\bar{z}$). We have partitioned the change in the average character value into three separate effects: ecological, evolutionary and physiological change. In contrast, Fox (2006) discriminates two separate effects, termed ‘species composition’ and ‘context dependence’ effects). Fox’s (2006) species composition effect describes the impact of any propensity for species with high or low character values *before* the species-loss event to be those that survive or are lost, and is given by $\text{cov}(w, z)$ [in our notation, this could be expressed as $\text{cov}_f(w, z)$]. This is somewhat – but not exactly – analogous to our ecological effect, which describes the impact of any propensity for species with high or low character values *after* the physiology-changing event to wax or wane in the community, and is given by $\text{cov}_f(w, z')$. The rationale for this difference is that the species richness effect in Fox’s (2006) analysis is expected to be causally mediated by the initial character of each species, whereas the ecological effect in our analysis is expected to be causally mediated by each species’ character value post-physiological change. Thus, the remaining terms – the combined effect of evolution and physiology in our analysis, and the context dependence effect in Fox’s analysis – are somewhat, but not exactly, analogous. It is important to emphasize that neither Fox’s nor our own partition is ‘more correct’; they are both mathematically exact and full characterizations of community change.

CONCLUSIONS

Here, we have shown how the Price equation can be used to partition physiological, evolutionary and ecological contributions to changes in the properties of an assemblage, and argued that this approach could be widely applicable as a framework for thinking about changes in community function whenever changes at all three levels of biological organization are likely to co-occur. The worked examples provided demonstrate how explicitly partitioning these contributions can help to evaluate mechanistic hypotheses and provide direction for future research.

The exercise we have performed here is largely a proof of principle showing that a single quantitative framework can be used to integrate information from several different levels of biological organization to make a prediction about an end phenotype. The Price equation approach that we have used is very pragmatic, in that it allows us to estimate or partition the causes of a phenotype without requiring that we know anything about the underlying mechanisms. More generally, we suggest that this may provide a quantitative framework for integrating information across disciplines that study changes in community function and take different approaches to very similar questions, particularly community ecology and experimental evolution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Calculations for community tolerance to diuron.

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APPENDIX 1

We consider the changes in a biological community between time t_1 and time t_2 . At each time point we assign each species a unique index $i \in I$, and within each species i we assign each lineage a unique index $j \in J_i$. We assume asexual reproduction, and identify the same species or lineage at each time point by matching the indices. The fraction of the total community biomass at time t_1 that is due to lineage j in species i is denoted q_{ij} and hence the fraction of community biomass at time t_1 due to species i is $q_i = \sum_{j \in J_i} q_{ij}$. Similarly, the fraction of community biomass at time t_2 that is because of lineage j in species i is denoted q'_{ij} and the fraction because of species i is $q'_i = \sum_{j \in J_i} q'_{ij}$. Hence, the relative growth factor of lineage j in species i between times t_1 and t_2 is given by $w_{ij} = q'_{ij}/q_{ij}$, and the relative growth factor of species i during this period is $w_i = q'_i/q_i$. Finally, we denote the value of the character of interest for lineage j in species i at time t_1 as z_{ij} and at time t_2 as $z'_{ij} = z_{ij} + \Delta z_{ij}$, and the initial and final averages of the character of interest for species i are $z_i = \sum_{j \in J_i} (q_{ij}/q_i) z_{ij}$ and $z'_i = \sum_{j \in J_i} (q'_{ij}/q'_i) z'_{ij}$ at times t_1 and t_2 respectively. (Note that the final character value is an average taken over lineages, weighted according to their initial, rather than final, relative abundances within the species; this separates the effects of changes within lineages from effects that are due to changes in the relative abundances of lineages).

The change in the average character value across the whole community between times t_1 and t_2 is then:

$$\begin{aligned}
 \Delta \bar{z} &= \bar{z}' - \bar{z} \\
 &= \sum_{I, J_i} q'_{ij} z'_{ij} - \sum_{I, J_i} q_{ij} z_{ij} \\
 &= \sum_{I, J_i} q_{ij} w_{ij} z'_{ij} - \sum_{I, J_i} q_{ij} (z'_{ij} - \Delta z_{ij}) \\
 &= \sum_{I, J_i} q_{ij} w_{ij} z'_{ij} - \sum_{I, J_i} q_{ij} z'_{ij} + \sum_{I, J_i} q_{ij} \Delta z_{ij} \\
 &= \text{cov}_{I, J_i} (w_{ij}, z'_{ij}) + E_{I, J_i} (\Delta z_{ij}).
 \end{aligned} \tag{A1}$$

This is the sum of combined evolution and ecology (first term) and physiology (second term), and is formally equivalent to a levels-of-selection application of Price's equation, in particular of the form outlined by Okasha

(2006, p. 26). This can be expanded for any number of levels of 'selection': making explicit the separate ecology and evolution effects, we can write $\text{cov}_{I,J_i}(w_{ij}, z'_{ij}) = \text{cov}_I(w_i, z'_i) + E_I(\text{cov}_{J_i}(w_{ij}, z'_{ij}))$; substituting this into eqn (A1) yields eqn (1) of the main text. We do not explicitly consider uncertainty (randomness) in future outcomes in this article, but uncertainty is readily incorporated into a levels-of-selection approach, in which case the LHS of the Price equation may take the form of an expected (arithmetic average) change (Gardner & Grafen 2009). Finally, we do not explicitly consider migration of individuals in or out of the community. We may define the community at the level of closed system, such that migration is incorporated implicitly, or alternatively we may allow for an open community, in which case migration could be explicitly incorporated following the approach of Kerr & Godfrey-Smith (2009).

Here we have described the change in the average value of the character across the community. For some biological problems, it may be more useful to know the change in the total value of the character (for example, total CO₂ uptake, rather than simply the average value per unit biomass). If the total biomass of the community does not change then we may multiply the change in the average character value ($\Delta\bar{z}$) by the total biomass to recover the change in total character

value. However, if biomass of the community does change over the focal time interval, then we must also calculate its impact upon the change in total character value. We may denote the overall community biomass as N at time t_1 and N' at time t_2 , and the total character value as $T = N\bar{z}$ at t_1 and $T' = N'\bar{z}'$ at t_2 , and hence the change in the total character value over this interval is:

$$\begin{aligned}\Delta T &= T' - T \\ &= N'\bar{z}' - N\bar{z} \\ &= N'(\bar{z} + \Delta\bar{z}) - N\bar{z} \\ &= (N' - N)\bar{z} + N'\Delta\bar{z} \\ &= \Delta N\bar{z} + N'\Delta\bar{z},\end{aligned}\tag{A2}$$

where $\Delta N = N' - N$ is the change in the total biomass of the community over the time interval. Thus, the change in total character value is equal to: the sum of the three effects described in eqn (1) of the main text, scaled by the new total biomass N' ; plus the product of the change in total biomass (ΔN) and the original average character value (\bar{z}). If total biomass (N') is known, and the change in total biomass (ΔN) can be estimated, then these data can be combined with our calculation of $\Delta\bar{z}$ in the main text to estimate the total change in character value (ΔT), using eqn (A2).