REVIEWS AND SYNTHESES

Rapid evolution and the convergence of ecological and evolutionary time

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Abstract

Recent studies have documented rates of evolution of ecologically important phenotypes sufficiently fast that they have the potential to impact the outcome of ecological interactions while they are underway. Observations of this type go against accepted wisdom that ecological and evolutionary dynamics occur at very different time scales. While some authors have evaluated the rapidity of a measured evolutionary rate by comparing it to the overall distribution of measured evolutionary rates, we believe that ecologists are mainly interested in rapid evolution because of its potential to impinge on ecological processes. We therefore propose that rapid evolution be defined as a genetic change occurring rapidly enough to have a measurable impact on simultaneous ecological change. Using this definition we propose a framework for decomposing rates of ecological change into components driven by simultaneous evolutionary change and by change in a non-evolutionary factor (e.g. density dependent population dynamics, abiotic environmental change). Evolution is judged to be rapid in this ecological context if its contribution to ecological change is large relative to the contribution of other factors. We provide a worked example of this approach based on a theoretical predator–prey interaction [Abrams, P. & Matsuda, H. (1997). *Evolution*, 51, 1740], and find that in this system the impact of prey evolution on predator per capita growth rate is 63% that of internal ecological dynamics. We then propose analytical methods for measuring these contributions in field situations, and apply them to two long-term data sets for which suitable ecological and evolutionary data exist. For both data sets relatively high rates of evolutionary change have been found when measured as character change in standard deviations per generation (haldanes). For Darwin's finches evolving in response to fluctuating rainfall [Grant, P.R. & Grant, B.R. (2002). *Science*, 296, 707], we estimate that evolutionary change has been more rapid than ecological change by a factor of 2.2. For a population of freshwater copepods whose life history evolves in response to fluctuating fish predation [Hairston, N.G. Jr & Dillon, T.A. (1990). *Evolution*, 44, 1796], we find that evolutionary change has been about one quarter the rate of ecological change – less than in the finch example, but nevertheless substantial. These analyses support the view that in order to understand temporal dynamics in ecological processes it is critical to consider the extent to which the attributes of the system under investigation are simultaneously changing as a result of rapid evolution.

Keywords

Adaptation, bill size, Darwin's finches, diapause timing, ecological rate, evolutionary rate, *Geospiza fortis*, haldane, *Onychodiaptomus sanguineus*.

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INTRODUCTION

In his book '*The Growth and Regulation of Animal Populations*', Slobodkin (1961) drew a distinction between 'ecological time' and 'evolutionary time' that has been influential for over 40 years in structuring the way we think about the processes underlying patterns in nature. He defined ecological time as *c.* 10 generations – a period over which he

expected that populations could maintain approximate steady state, and contrasted this with evolutionary time, which he suggested is on the order of half a million years – sufficient for evolutionary change to disrupt ecological steady states. In Slobodkin's terms evolutionary and ecological time differ by orders of magnitude.

Although useful in many ways, the distinction Slobodkin drew has been misleading when interpreted too strictly because it overemphasizes differences between rates of ecological and evolutionary change. Even during the decade of Slobodkin's (1961) publication several studies reported quite rapid evolution in ecologically important phenotypes (Kettlewell 1958; Ford 1964; Johnston & Selander 1964), and in the 1980s and 1990s a flood of such examples was released (reviewed by Thompson 1998; Hendry & Kinnison 1999; Palumbi 2001). Gingerich (2001) working from Dobzhansky's (1937) distinction between micro- and macroevolution suggested three evolutionary time scales: generational, microevolutionary and macroevolutionary. The former two cover the time frame of ecological change envisioned by Slobodkin (1961) and more recently by Thompson (1998). Interestingly, although seemingly high evolutionary rates have often been characterized as rapid, the question of what exactly is meant by 'rapid' has remained undefined, leaving open the question: rapid relative to what? We suggest here that the answer depends upon why we care. Some investigators have been motivated by a desire to establish the upper limit of the rate of phenotypic change (c.f. Gingerich 1983, 2001; Hendry & Kinnison 1999), and Lynch (1990) used the expected rate of neutral evolutionary change as a benchmark against which to judge if observed rates of morphological change for mammals in the fossil record were unusually fast (they were not). In contrast, Thompson (1998) proposed that rapid evolution could be viewed as an ecological process in which genetically based phenotypic change takes place at such a high rate that the trajectory of ecological dynamics is simultaneously altered: in essence a convergence of ecological and evolutionary time. Here we examine the meanings that have been assigned to rapid evolution of ecologically important phenotypes, briefly review several studies where evolutionary change in phenotypes has altered on-going ecological dynamics, and propose a method for quantifying evolutionary and ecological rates that, when applied to field data, provides an ecological context in which to evaluate the rate of evolutionary change.

Two studies that in the past decade have synthesized the literature on rapid evolution from different perspectives came to rather different conclusions about its biological significance. Thompson (1998) provided an explicitly ecological reference for rapid evolution, defining it as genetic changes taking place at the time scale of a century or less – the time frame typical of research on the dynamics of ecological communities. In so doing, he accepted that evolution in some systems was exceptionally fast. In contrast, Hendry & Kinnison (1999) proposed that rates described as rapid by investigators of microevolution in extant populations were not in fact particularly exceptional, but rather part of a general pattern, previously documented by Gingerich (1983; see also Gingerich 2001), in which the greatest rates of evolutionary change are typically found when measured over short time periods or few generations.

In light of these differing perspectives, we evaluated the papers included in the reviews by Thompson (1998) and Hendry & Kinnison (1999) in order to discover how the original authors had characterized the rates of change in the populations they studied. In particular, we were curious if they had used the term 'rapid evolution' or similar phrasing and if so, what, if any, meaning they had intended. Of the 38 papers included in the two reviews (five were the same between the two compilations), 21 described their results as rapid evolution with 12 providing no rationale for their use of this term, six compared their data explicitly or implicitly with previously published evolutionary rates, and three gave a definition that was in some sense ecological. Although none of the latter three actually defined rapid evolution in terms of ecological rates, each noted that evolutionary change was observable within a single season (Via & Shaw 1996), a single generation (Grant & Grant 1995), or several generations (Singer *et al.* 1993). The remaining 17 papers covered in the two reviews did not actually characterize the rates they observed as either especially fast or slow. Thus neither explicit comparisons among evolutionary rates as adopted by Gingerich (1983, 1993, 2001) and Hendry & Kinnison (1999), nor Thompson's (1998) implicit use of ecological rates of change as a reference against which to assess evolutionary rates, appears to have become widely accepted standards for judging whether a particular generational or microevolutionary rate is rapid.

IS SHORT-TERM EVOLUTION RAPID?

What should we make of Hendry & Kinnison's (1999) review of the literature showing that rates of evolution reported for studies covering only a few generations are typically significantly faster than for those covering more generations (see small filled circles in Fig. 1), and in particular of their conclusion that therefore it is incorrect to conclude that any particular contemporary rate is unusually rapid? While their review was restricted to rates calculated over periods on the order of a century or less (≤ 140 generations), they pointed out that Gingerich (1983; see also Gingerich 2001) found a similar relationship for time periods ranging between tens of months and tens of
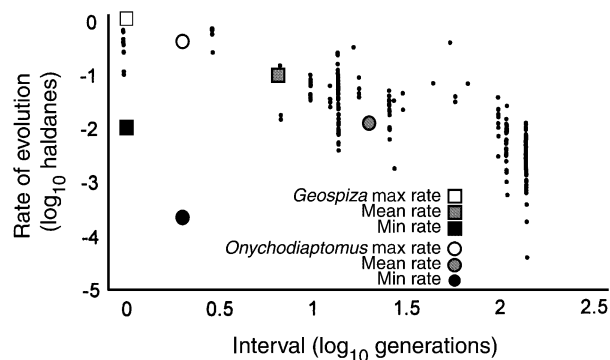
Figure 1 Relationship between rate of phenotypic evolution and the number of generations over which measurements were made. Original figure (small dots) from Hendry & Kinnison (1999) with new calculations added for *Geospiza fortis* (Grant & Grant 1995, 2002) and *Onychodiaptomus sanguineus* (Hairston & Dillon 1990; Ellner *et al.* 1999) showing the slowest, the most rapid, and the average rates of evolution (on a per-generation basis) over the 30- and 10-year (respectively) periods of study. The range of observed per-generation rates for *Geospiza* and *Onychodiaptomus* shows that short-term evolution can be either rapid or slow, suggesting that the reported general pattern of rapid short-term evolution reflects, at least in part, a publication bias against findings of stasis.

millions of years (1–10^7 generations). In addition, for very short-time intervals, Hoekstra *et al.* (2001) reviewing the recent literature on the strength of selection reached a similar conclusion: measurements made over short-time periods (days) tend to be greater than those made over longer intervals (years). Gingerich (1983), Hendry & Kinnison (1999), and Hoekstra *et al.* (2001) all concluded that rates studied over short periods only seem rapid because (among other reasons) average rates over longer periods include not only short bursts of rapid directional evolution but also reversals and periods of stasis. There is, however, a bias implicit in the rates summarized by Hendry & Kinnison (1999) and subsequently used by Gingerich (2001): rates studied over short periods will especially appear to be more rapid on microevolutionary time scales if findings of stasis (i.e. little or no short-term directional change) are rarely or never reported [Gould (1984), mentions the possibility of this bias in his discussion of Gingerich's (1983) analysis]. This bias is not only plausible, but documentable: Hendry & Kinnison (1999) cited as an example the rapid and reversible evolution of beak dimensions in one of the Galápagos finches, *Geospiza fortis*, (Grant & Grant 1995) which experienced two periods of extreme climate, one (1976–1978) that favoured large birds with relatively large bills, and another several years later (1984–1987) that favoured small birds with small beaks. Hendry & Kinnison (1999) calculated rates of beak-size evolution for these two time periods of +0.66 and −0.37

haldanes respectively (where a haldane is the per generation change relative to character variance; Gingerich 1993). Whereas the Grants and their colleagues have understandably focused on years of marked directional evolution (e.g. Boag & Grant 1981; Grant & Grant 1993, 1995; Grant *et al.* 2000), Grant & Grant (2002) have also reported values for selection differentials in other years where evolution was less dramatic. Using their data for beak size ('PC1 beak size' values digitized from Fig. 1 in Grant & Grant 2002) we calculate that between 1972 and 2001 the maximum rate of evolution was indeed high at 1.08 haldanes. However, the overall rate of beak size evolution over this 30-year period (6.4 generations) was quite low at −0.095 haldanes, and the minimum rate of change for any 2-year interval (1981–1983) is even lower at 0.010 haldanes.

Another example of reversals and stasis is our study of diapause phenology in a population of the freshwater copepod, *Onychodiaptomus sanguineus*, in Bullhead Pond, Rhode Island (Hairston & Dillon 1990; Ellner *et al.* 1999). The copepods are active in the water column during winter, but each spring switch from producing immediately hatching eggs to producing diapausing eggs. As summer progresses, the active copepod population dies out because of predation by sunfish. Because diapausing eggs are immune to predation but represent a cost in reproductive potential during the current year, year-to-year variation in the intensity and timing of the spring onset of fish predation has resulted in fluctuating selection on the optimal switch-to-diapause date (switch date). Using data on the mean and variance of switch date for the years 1979–1989 (Hairston & Dillon 1990; Ellner *et al.* 1999), we calculate that the maximum rate of change in switch date was −0.406 haldanes, the minimum rate was 0.0002 haldanes, and the mean rate over the entire 10-year period (20 generations) of study was 0.012 haldanes.

When the rates of evolution calculated for *O. sanguineus* and those for *G. fortis* are plotted on the graph of rates reported by Hendry & Kinnison (1999) (Fig. 1), we see that the minima, although calculated for very short time periods, are well below the relatively high rates included in Hendry & Kinnison's (1999) review, and most similar to the rates calculated for evolutionary change over the longest time periods they summarized [i.e. where the effect of the large denominator (time) combined with a long-term average stasis come to dominate the relationship between evolutionary rate and interval of measurement]. Consistent with Gingerich's (1983, 2001) and Hendry & Kinnison's (1999) suggestions about the effects of reversals and periods of stasis, the rates of evolution calculated for these systems depend upon which years are included in the calculation: they indicate that there are bouts of very fast evolution that result from responses to intense natural selection, and that can legitimately be characterized as

'rapid' in comparison with other measured short-term evolutionary rates.

RAPID EVOLUTION IN AN ECOLOGICAL CONTEXT

Even if the evolutionary rates that have been called rapid are simply at the high end of a continuum of possible rates, it may be useful to consider a meaning for 'rapid' that focuses on the relative rates of evolutionary change and ecological dynamics. Thompson (1998) pointed out that when evolution is rapid, the changing phenotypes of organisms can alter simultaneous ecological change. We propose to turn this relationship around, and say that evolution should be considered rapid when it occurs at the same time as, and results in, alterations to ecological dynamics.

It is important to make clear that it is not sufficient that an evolved trait influence ecological processes for its evolution to be considered rapid. Rather, evolution is rapid in this ecological context only if the heritable phenotypic change occurs sufficiently quickly to alter the trajectory of an ecological process while it is still in progress. An example is our research on predator–prey dynamics between rotifers, *Brachionus calyciflorus*, and algae, *Chlorella vulgaris*, in continuous-flow laboratory chemostat cultures. Predator–prey dynamics are typically studied in mathematical models, laboratory experiments and in the field with the assumption that the phenotypes of the players are fixed (but see Abrams & Matsuda 1997). However, in our apparently simple microcosms, the period of oscillations and the phase relations between predator and prey were dramatically affected by whether or not the prey could evolve (Yoshida *et al.* 2003, 2004). Microcosms containing multiple prey genotypes, and therefore with the possibility of prey evolution, had predator–prey oscillations that were three to four times longer and exactly out of phase (instead of the standard 25% phase offset) compared with microcosms containing a single algal genotype and therefore with no possibility for prey evolution.

Potential examples of evolutionary impacts on ecological dynamics in the wild were reviewed by Thompson (1998), who identified four categories of interactions in which evolution had been shown to be potentially important: trophic specialization, defence against natural enemies, interaction outcome, and trait reduction following loss of an ecological interaction. Of course, other types of ecological interactions may also be impacted. In the area of consumer–resource dynamics, Hairston *et al.* (1999, 2001) studied the impact of evolutionary change in a grazer's resistance to unpalatable algae. They demonstrated that *Daphnia galeata*, in Lake Constance, Europe, evolved within a decade greater ability to grow with low food-quality cyanobacteria in its diet while cyanobacteria became increasingly abundant during eutrophication. Kümmerlin

(1998) observed independently that in Lake Constance the well-known positive relationship in lakes between phytoplankton biomass and water-column phosphorus became less strong in the period after cyanobacteria became abundant. He suggested that grazer-control might have become more important at this time. While one explanation may be that the *Daphnia* became more abundant during the period of eutrophication, Hairston *et al.* (1999) noted that this was also the period when *Daphnia* became increasingly resistant to dietary cyanobacteria. They suggested that grazer evolution may have altered the strength of the link between nutrient concentration and phytoplankton biomass. If this interpretation is correct, then trait evolution altered an interaction that is commonly viewed as a non-evolving trophic–dynamic interaction.

Daphnia evolution may also alter ecosystem dynamics (Elser *et al.* 2000). Based upon substantial earlier work establishing links between the levels of phosphorus-rich RNA required to support population growth of grazers and the amount of phosphorus that they release back to the environment in excretion and feces (reviewed by Sterner & Elser 2002), these investigators proposed that natural selection acting on *Daphnia* growth rate could influence nutrient limitation of phytoplankton production, biomass and species composition. They documented differences between closely related species of *Daphnia* in which the one with the higher growth rate also had a higher %P of body mass, and excreted P at a much lower rate than the population with the lower growth rate. In a separate laboratory study, Gorokhova *et al.* (2002) found that under divergent selection regimes mean *Daphnia* growth rates, RNA content and P content evolved to differ significantly within five generations (35 days).

Thus, from an ecological perspective, three studies suggest that rates of character evolution can be considered rapid because of their potential ecological effects on population dynamics (Yoshida *et al.* 2003, 2004), community interactions (Hairston *et al.* 1999) and ecosystem processes (Elser *et al.* 2000; Gorokhova *et al.* 2002).

DEFINING RAPID EVOLUTION IN TERMS OF ECOLOGICAL CHANGE

Judging whether a particular estimate of evolutionary rate is fast relative to the distribution of other measured rates is possible, although not without limitations (Gingerich 1983, 1993, 2001; Gould 1984; Hendry & Kinnison 1999). Making such an evaluation in the context of ecological change is, however, less straightforward since the environment is never static and the components of any ecological system vary temporally at dramatically different rates, from extremely rapid biogeochemical fluxes to the statelier pace of global climate change. For this reason, assessing whether

evolutionary and ecological changes occur on similar time scales is an empirical question that can only be answered with data. One of our goals is to clarify the nature of the data that will be needed to answer this question in any particular instance. Evolutionary and ecological dynamics have both been studied intensively, but there are very few data available that can be used to make meaningful quantitative comparisons of ecological and evolutionary rates.

We emphasize the need for *meaningful* quantitative comparisons of evolutionary and ecological rates of change, because measures of change are hard to interpret without information about their consequences. Consider a hypothetical zooplankton-eating fish population that fluctuates in abundance and during the same period has heritable changes in gill-raker spacing (critical to size-dependent prey capture). Over 5 years we might observe a 50% decrease in abundance and a 10% increase in linear gill-raker dimensions, and conclude that evolution was slow compared with the ecological change. Now add the information that the evolution of gill-raker dimension allowed a near-total shift in the species composition of the fish's diet, leading to major changes in the composition of the annual zooplankton community. Because of its consequences, gill-raker evolution would then be regarded as very rapid and significant. Moreover, whether or not an evolutionary rate is rapid can be specific to the particular ecological variable that is considered. For example, evolutionary change may be rapid with respect to one ecological process (e.g. population dynamics), in that evolution has a measurable impact on ecological change, whereas the same rate of phenotypic change may be slow with regard to its effect (or lack thereof) on another ecological process (e.g. species turnover).

Comparisons of rates of change are even more difficult when changes are fluctuating rather than directional. Constant weak selection may be pervasive in theoretical models of evolution, but selection in the field can be strong, at least for short periods, and is often variable in both magnitude and direction, because of ecological changes that may be random or cyclic. Such temporal variations underlie the patterns of declining evolutionary rate as a function of the interval of measurement described by Gingerich (1983) and illustrated here in Fig. 1. We take the evolution of copepod diapause timing discussed above as an example of fluctuating selection. Figure 2 shows estimated changes over time in an ecological factor – the intensity of fish predation (Hairston 1988) – and in two variables that characterize the prey evolutionary response, the mean and standard deviation of the switch-to-diapause date. All of these variables change from year to year, but without any information on the consequences of those changes we cannot decide whether the evolutionary changes are rapid evolution of a significant trait on the same time scale as ecological changes,
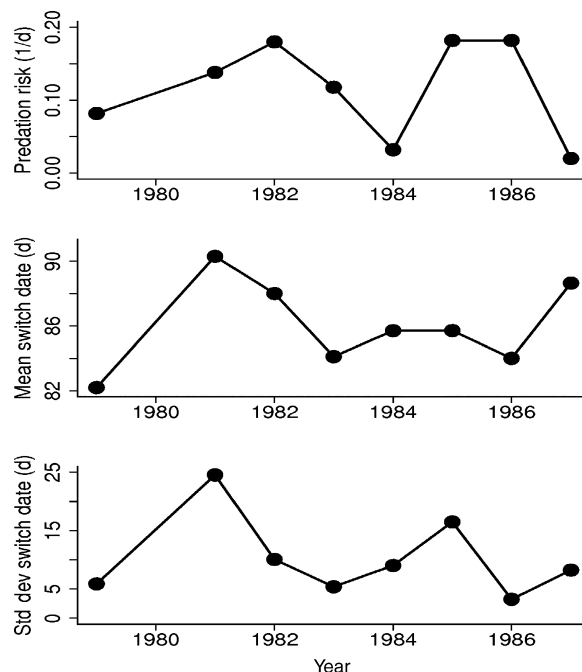
Figure 2 Changes over time in an ecological factor (top: the risk of fish predation on female copepods *Onychodiaptomus sanguineus* in Bullhead Pond, RI), and two traits that evolve in response to variation in this selective factor, the mean (middle) and variance (bottom) of the day of year when females switch to producing diapausing eggs rather than immediately hatching eggs. An early switch date is advantageous in years when predation risk is high, because offspring from immediately hatching eggs face intense predation and have little chance of surviving to reproduce. Trait distributions in the population are also affected by hatching of eggs from long-term diapause, which have not experienced recent selection. Are these temporal trait variations so small that we should regard them as stasis, or large enough that they should be regarded as rapid evolution? We argue that this question can only be answered by reference to the ecological impacts of the trait variations.

or just noise from an ecological perspective that we can ignore.

Without convergence of their time scales, ecological and evolutionary dynamics will have relatively minor effects on each other. Ecological dynamics would proceed as if evolution were not occurring, because the changes are imperceptible on the relevant time scale. Conversely, the rapid fluctuations in ecological variables would 'average out' over evolutionary time – like the flickering of a fluorescent lamp, they happen so fast (relative to evolution) that only their average value is relevant on the longer time scale. Therefore, we argue, the most meaningful way to compare ecological and evolutionary rates is through their mutual impact. We describe below an approach to making this type of comparison, and give an example based on a predator–

prey model in which the prey can evolve. We then propose three quantitative methods for this approach and apply two of them to data on beak size evolution in Galápagos finches and on diapause timing in the copepod *O. sanguineus*.

A GENERAL CONCEPTUAL FRAMEWORK FOR COMPARING EVOLUTIONARY AND ECOLOGICAL DYNAMICS

Evolutionary change is generally thought of as genetic change in the mean (and variance) of an attribute of individuals within a population, while ecological change involves change in attributes of populations, communities or ecosystems. The relevant attributes of an individual could be any heritable trait, or the genetic variance-covariance structure of multiple traits. At the population level, one might be interested in demographic rates (e.g. mean fecundity, natal dispersal distance) or emergent properties of those rates (e.g. the rate of population increase or the steady-state density). Changes in species composition, richness or evenness, the strength of food web links, etc. would qualify as community attributes. Changes in the standing pools of major nutrients, nutrient limitation, the rate of primary production, etc. are ecosystem properties potentially covarying with evolutionary change in the biota.

As a concrete example, one might be interested in the reciprocal influence of ecological changes in population growth rate, r, and evolutionary change in a morphological trait, z, of individuals in the population. The rate of change in r over time is likely to be a function of population dynamics (e.g. the effect of density, n, on population growth rate) and of evolutionary changes in z. This can be formalized by assuming that $r(t) = r[z(t),\ n(t)]$, and then by the chain rule we have

$$\frac{\mathrm{d}r}{\mathrm{d}t} = \frac{\partial r}{\partial z}\frac{\mathrm{d}z}{\mathrm{d}t} + \frac{\partial r}{\partial n}\frac{\mathrm{d}n}{\mathrm{d}t}. \tag{1}$$

$\partial r/\partial z$ is the unit change in r that results from a unit change in z independent of changes because of population dynamics (i.e. influence of n), and $\frac{\partial r}{\partial z}\frac{\mathrm{d}z}{\mathrm{d}t}$ is the actual rate of change in r resulting from the changes in z. The second term decomposes in the same way the effect on r of changes in n.

The relative importance of ecological vs. evolutionary dynamics for change in r depends on the relative magnitudes of the two terms on the right side of eqn 1 The relative influence of evolutionary dynamics increases with increasing $\left|\frac{\partial r}{\partial z}\right|$, with increasing $\left|\frac{\mathrm{d}z}{\mathrm{d}t}\right|$, or both. This same idea can be applied to any attribute X, either ecological or evolutionary, that is affected by ecological attributes $k_1, k_2, \ldots, k_n$ and evolutionary attributes $z_1, z_2, \ldots, z_m$. If we have correctly identified the variables influencing the dynamics of X then we can write (in principle)

$$X = X(z_1, z_2, \ldots, z_m, k_1, k_2, \ldots, k_n), \tag{2}$$

and therefore

$$\frac{\mathrm{d}X}{\mathrm{d}t} = \sum_{j=1}^{m} \frac{\partial X}{\partial z_j}\frac{\mathrm{d}z_j}{\mathrm{d}t} + \sum_{i=1}^{n} \frac{\partial X}{\partial k_i}\frac{\mathrm{d}k_i}{\mathrm{d}t}. \tag{3}$$

The relative importance of each factor, evolutionary or ecological, is then measured by the absolute value of the corresponding term in eqn 3, $\left|\frac{\partial X}{\partial *}\frac{\mathrm{d}*}{\mathrm{d}t}\right|$. Because this is a relative comparison, the result does not depend on the choice of units for time (e.g. years or generations), the response variable, or the evolutionary and ecological factors.

We have so far assumed that there is no environmental component to the expression of evolving traits. However, a phenotypically plastic trait can be analysed in the same way by using as traits a set of parameters that describe the reaction norm relating the sensitivity of expressed trait values to environment state. For example, for our study described above of the evolution of *Daphnia* tolerance to cyanobacteria (Hairston *et al.* 2001), the reaction norm could be characterized by the juvenile growth rates in both the presence and absence of cyanobacteria in their diet.

Worked example: a model for rapid prey evolution

To illustrate the conceptual framework we consider an idealized application: a model for prey evolution during predator–prey cycles. The model is a simplified version of one used by Abrams & Matsuda (1997) to show how prey evolution can modify the dynamics of predator–prey interactions. In their model, prey can evolve along a tradeoff curve between their intrinsic rate of reproduction and their vulnerability to attack by predators. The model's state variables are the abundances of prey (N) and predators (P), and a heritable quantitative trait z that represents prey vulnerability:

$$\begin{aligned}
\frac{\mathrm{d}N}{\mathrm{d}t} &= N[(r + Qz) - mN] - zNP/(1 + hzN) \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= P[BzN/(1 + hzN) - d] \\
\frac{\mathrm{d}z}{\mathrm{d}t} &= V_0[Q - P/(1 + hzN)].
\end{aligned} \tag{4}$$

Here r, Q, m, h, B, d and V_0 are positive parameters. If prey vulnerability is held fixed, the first two lines in eqn 4 are the standard Rosenzweig–MacArthur model for predator–prey dynamics: prey follow the logistic differential equation, and predators have a type-II functional response. Evolution occurs because a higher value of z gives prey a higher intrinsic growth rate $r + Qz$, and a higher vulnerability to attack. The third line in eqn 4 says that the rate of change of z is the product of the additive trait variance V_0, and the

fitness gradient (Abrams & Matsuda 1997). So z will increase when predator density is low or prey are so abundant that predators are satiated, and z will decrease when predators are abundant and hungry.

As the response variable X in our general framework, we choose the instantaneous predator growth rate:

$$X = \frac{1}{P}\frac{dP}{dt} = BzN/(1 + hzN) - d. \qquad (5)$$

The ecological variable k is the prey abundance N, and the evolving trait is prey vulnerability z. Writing

$$\frac{dX}{dt} = \frac{\partial X}{\partial k}\frac{dk}{dt} + \frac{\partial X}{\partial z}\frac{dz}{dt}, \qquad (6)$$

the terms on the right hand side are the ecological and evolutionary contributions, respectively, to change in X.

Figure 3 shows the results from a model simulation with the parameter values such that the system would converge to a stable steady state in the absence of prey evolution (Abrams & Matsuda 1997, Fig. 3a). When predators are scarce (e.g. around day 540 in Fig. 3a), prey increase in vulnerability and therefore in abundance. Eventually these changes allow the predators to rebound. The prey, under intense grazing pressure, decline in abundance and evolve to be less vulnerable, leading to collapse of the predator population – and the cycle then repeats.

From the predator's perspective, the ecological and evolutionary changes are usually acting in concert: while prey are becoming scarcer they are also evolving to evade attack better. The ecological and evolutionary terms are therefore positively correlated (correlation coefficient $r = 0.63$). The sharp peak in the ecological term occurs because increases in prey abundance have a larger impact when the prey are less vulnerable. To compare the overall importance of the ecological and evolutionary terms in eqn 6 we averaged their absolute values over a long simulation. Omitting the initial transient, the values are 0.023 (ecological) and 0.015 (evolutionary): measured by the impact on predator per-capita growth, the evolutionary dynamics of the prey is on average 63% as fast as the ecological dynamics.

Applying the framework

Applying our framework to real-world systems presents some challenges. First, data must be collected on ecological and evolutionary changes that are strongly coupled, either through their impacts on each other or through their joint impacts on another relevant attribute. In terms of eqn 3, we need first to identify the driving variables (the k's and z's) that are of primary importance for the focal attribute X, and then quantify their changes over time.
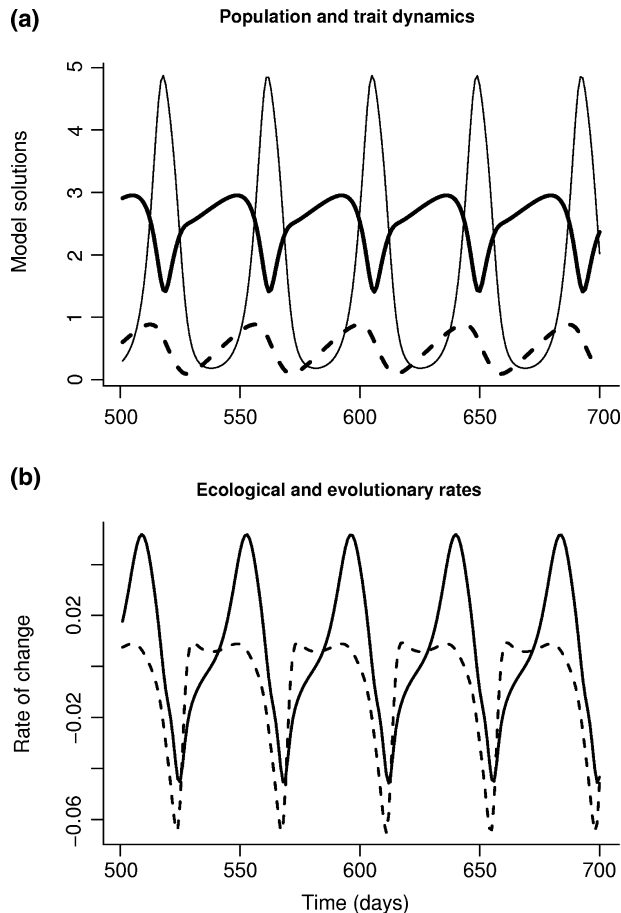
Figure 3 Comparison of ecological and evolutionary rates in a model for predator–prey dynamics with prey evolution (Abrams & Matsuda 1997). (a) Population dynamics of predators (solid thin line), total prey (solid bold line), and prey vulnerability (dashed bold line). (b) The ecological (solid line) and evolutionary (dashed line) contributions to the total rate of change (per day) in predator per-capita growth rate, given by the two terms on the right-hand side of eqn 6.

Second, we need to know the independent effect of each driving variable – the partial derivatives of X with respect to each driving variable. This can be approached in three different ways: statistical analysis of observational data, process-based modelling, or experimental manipulations.

(1) In principle, the independent effects of the driving variables can be estimated statistically from observational data on the variables in (2) or (3). Equation 3 is written as a multiple linear regression of dX/dt on dz_i/dt and dk_i/dt, but the regression coefficients $\partial X/\partial *$ are actually functions of the driving variables rather than constants. With non-constant coefficients, (2) and (3) become multivariate non-linear regressions, which is a very data-hungry enterprise. Also, in many cases the driving variables will be dynamically coupled, so their

observed values will covary too tightly for their separate effects to be disentangled statistically. A purely statistical approach would then be infeasible unless the form of the relationships between driving and response variables is already known. Despite these constraints, we can demonstrate this approach using the well-known example of Darwin's finches on the Galápagos Islands.

(2) Process-based modelling will often be the most reliable approach because the form of the relationship (2) is based on the causal mechanisms. Moreover, because parameters are biologically meaningful, many of them can be estimated through experiments that manipulate a single variable rather than the full set of ecological and environmental variables. We demonstrate this approach using our data for copepod diapause in a Rhode Island lake.

(3) Experimental manipulations can 'break' the dynamic couplings between driving variables, and generate data for estimating (2) by descriptive statistical modelling. The limitations to this approach are the practical difficulty of creating selected lines differing in z values, and then evaluating the response variable across a range of values for the ecological variables. There is no study we know of that has all the data necessary for such an analysis, however, we will describe below the essential components.

Another complication is that the simplicity of eqns 1 and 3 reflects their formulation in terms of instantaneous rates and the tacit assumption of an unchanging, non-seasonal environment. In practice, we measure discrete changes $X(t + h) - X(t)$ where h is the time interval between samples, and the between-sample dynamics may be closer to discrete than continuous (e.g. a discrete birth pulse). Then starting from (2), instead of (3) we get a Taylor series

$$X(t + h) - X(t) = \sum_{j=1}^{m} \frac{\partial X}{\partial z_j} \Delta z_j + \sum_{i=1}^{n} \frac{\partial X}{\partial k_i} \Delta k_i + \cdots$$

(7)

in which '$\cdots$' are higher order terms including interactions between the changes in the driving variables [$\Delta k_i = k_i(t + h) - k_i(t)$, etc.].

We then want to estimate the independent *main effects* of evolutionary and ecological changes, and perhaps also estimate their interaction. This can be carried out in a linear-models or ANOVA framework. Because our interest centres on temporal dynamics the most appropriate analysis is based on the observed temporal sequence of changes. In the simplest case, with only one evolutionary and one ecological driving variable, the estimated relationship (2) can be used to compute the X values in Table 1. The top right and bottom left cells in Table 1 are the estimated consequences of a change in only the ecological variable, or in only the evolutionary variable.

Table 1 An attribute of interest X is affected by simultaneous discrete changes in an ecological variable k and an evolutionary variable z (diagonal terms $X_{t,\,t}$ vs. $X_{t+1,\,t+1}$)

	z_t	z_{t+1}
k_t	$X_{t,t} = X(z_t, k_t)$	$X_{t+1,t} = X(z_{t+1}, k_t)$
k_{t+1}	$X_{t,t+1} = X(z_t, k_{t+1})$	$X_{t+1,t+1} = X(z_{t+1}, k_{t+1})$

The hypothetical values $X_{t+1,\,t}$ and $X_{t,\,t+1}$ allow a partitioning into the independent effects of the ecological and evolutionary changes, as explained in the text.

Thus they correspond to the (unobserved) 'independent effects' of each change on their own.

To quantify the relative contributions of z and k we treat Table 1 as a two-way ANOVA with row and column as factors. The main effects measure the relative impacts of evolutionary and ecological change between times t and $t + 1$. This is equivalent to the following: the sequence of actual observations goes from top left to bottom right cells in Table 1. That can be carried out by going across then down (evolution first, ecology second), or by going down then across (ecology first, evolution second). Either way the net change is decomposed into separate evolutionary and ecological effects. Averaging the two paths, we get

Effect of evolutionary change:

$$\Delta_V(t, t + 1) = [(X_{t+1,\,t} - X_{t,\,t}) + (X_{t+1,\,t+1} - X_{t,\,t+1})]/2.$$

(8)

Effect of ecological change:

$$\Delta_C(t, t+1) = [(X_{t,\,t+1} - X_{t,\,t}) + (X_{t+1,\,t+1} - X_{t+1,\,t})]/2.$$

These are the main effects estimated by a two-way ANOVA without interaction, or equivalently the coefficients in a linear model where values 0 and 1 are assigned to years t and $t + 1$ [$X_{t+1,\,t} = X(1, 0)$, etc.] and the model does not have an interaction term. If the inter-sample interval is uneven, the between-sample effects can be standardized into rates by dividing each by the inter-sample interval.

In general, there is no reason to assume that interactions are absent: the effect of a particular environmental or ecological change will usually depend on the value of the evolving trait, and the effect of evolution depends on the environment in which it occurs. In other words, the 'main effects' of ecological and evolutionary changes are situation-specific and should be evaluated in the situations experienced by the population. Equation 8 actually does this, averaging over the beginning and end of each observation period: by the fundamental theorem of calculus

$$\Delta_C = \frac{1}{2}\left(\left\langle\frac{\partial X}{\partial k}(k, z_t)\right\rangle + \left\langle\frac{\partial X}{\partial k}(k, z_{t+1})\right\rangle\right)\left\langle\frac{dk}{dt}\right\rangle,$$

where $\langle\bullet\rangle$ denotes the average over $k_t \leq k \leq k_{t+1}$, and similarly for Δ_V. We therefore recommend using (8) to

estimate the main effects of ecological and evolutionary changes, even when an interaction may be present.

Example of method 1: Darwin's finches

We apply the statistical approach of method 1 to analyse data on the medium ground finch, *Geospiza fortis*, part of Grant and Grant's extensive ongoing studies of evolution in Darwin's finches. Our chosen response variable is the rate of population growth $r_t = \log(N_{t+1}/N_t)$. The evolving traits are individual size and beak shape, which affect the birds' ability to consume seeds of different size and hardness. The ecological driving variables are the total seed density and the fraction of large seeds. There is also a large effect of rainfall on population growth. The data plotted in Fig. 4 are all years for which there is a complete (or nearly complete) set of measurements of all variables.

The abrupt change in seed size in the early 1980s caused selection for smaller finches, but the evolutionary response was gradual. We hypothesized that a population of 'right-size' birds (for current seeds) would have a higher r than a population of 'wrong-size' birds, all else being equal. To explore this hypothesis we took the 'before' (1978–1982) and 'after' (1988–1991) phases to represent finch sizes

adapted to the initial and final seed size distributions, based on the observation that finch size and the fraction of large seeds both remained essentially constant from the late 1980s to 2001 (Grant & Grant 2002). As 'before' and 'after' are really two points we fitted a line $\hat{\theta} = -0.09 + 0.72f$ where $\hat{\theta}$ is the estimated optimal finch size and f is the fraction of large seeds. Figure 5a confirms that deviations from optimal size are accompanied by a lower population growth rate at a given level of rainfall. The effect of suboptimal size is reasonably fitted by a quadratic curve, with deviations below the optimum penalized more heavily and resulting in stronger selection pressure. This makes biological sense in that small birds cannot consume larger seeds, which is more problematic than being a bit larger than absolutely necessary.

Based on this exploratory analysis we fit a Generalized Additive Model with quadratic terms for the effects of body size,

$$\hat{r}_t = F[\log(R_t)] + \sum_{0 \le i+j \le 2} a_{ij} f_t^i z_t^j, \tag{9}$$

where R is rainfall, F is a fitted spline function, and z is finch size [model fitted using the mgcv package (Wood 2004) in R (R Development Core Team 2004)]. Both conventional (analysis of deviance) and AIC-based model selection
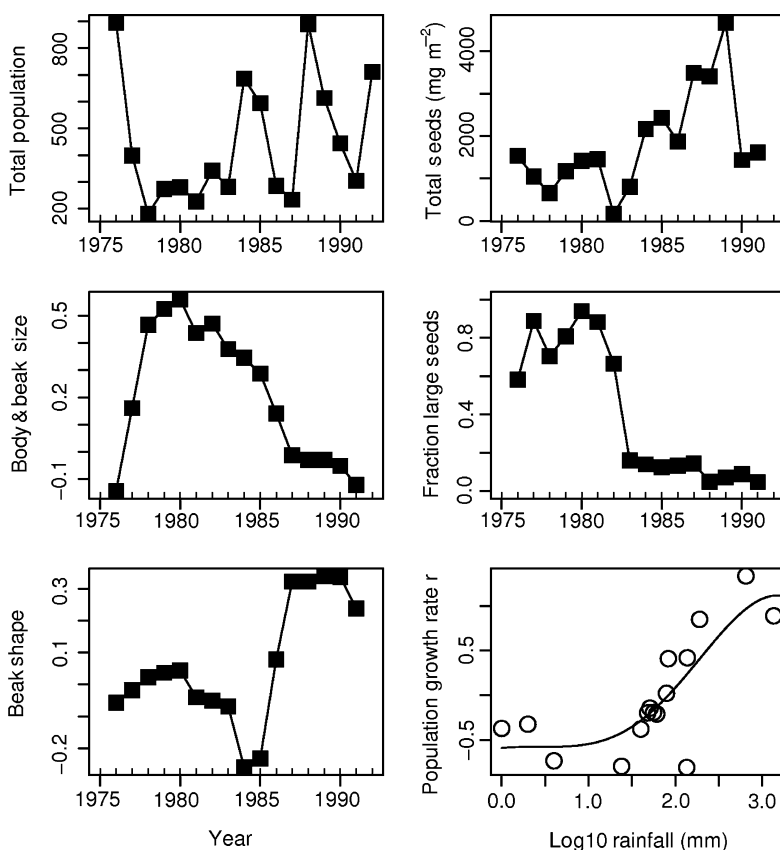
Figure 4 Ecological and evolutionary dynamics in the medium ground finch *Geospiza fortis* on Daphne Major island, which we use to compare the ecological and evolutionary rates in this system. Rainfall data provided by Peter Grant (*personal communication*); other values obtained by digitizing graphs in Grant & Grant (1993, 2002). 'Body and beak size' is the average of two strongly correlated size measures (PC1 beak size and PC1 body size), 'beak shape' is PC2 beak shape (from Fig. 1 of Grant & Grant 2002). No size or shape values were recorded for 1977, so we interpolated a value from the adjacent years, based on the fact that size changes in *G. fortis* over this time period were closely correlated with size changes in *G. scandens*, which showed a nearly linear trend in body size from 1975 to 1978. Population growth rate r and trait changes are both strongly affected by rainfall [the fitted curve for r as a function of $\log_{10}$(rainfall) is a penalized regression spline constrained to be monotonic, with smoothing parameter selected by generalized cross validation].
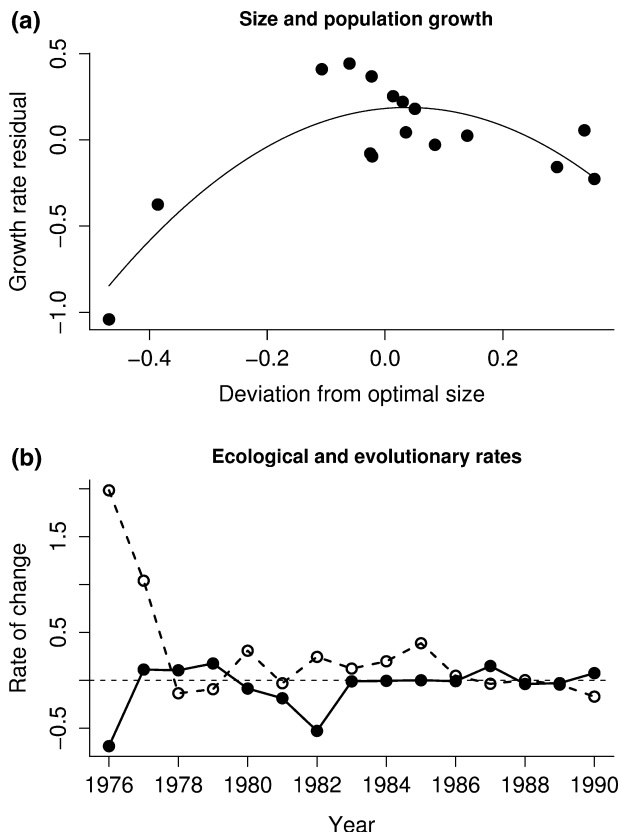
Figure 5 Ecological and evolutionary rates in the medium ground finch *Geospiza fortis* on Daphne Major island. (a) An estimated fitness function, analogous to Fig. 6, showing how deviations from optimal finch size affect population growth rate. 'Growth rate residual' is the deviation between the observed population growth rate r, and the expected population growth rate for the amount of rainfall that year based on the regression spline in Fig. 5. The curve is a fitted quadratic function. (b) The annual ecological (solid line) and evolutionary (dashed bold line) contributions to the total rate of change (per year) in population growth rate.

methods led to a reduced model without an f^2 term. The fitted interaction term is positive, $\hat{a}_{11} = 5.35$, confirming that population growth is favoured by a correspondence between finch size and seed size.

The changes over time in f and z are smooth enough to be treated as continuous, so we used eqn 3 with df/dt and dz/dt estimated by finite differences. The results (Fig. 5b) show a pattern of fluctuating selection and response. Negative impacts of ecological change (increase in mean seed size 1976–1977, decreases in seed size from 1981 to 1982 and 1982 to 1983) are followed by positive impacts of evolutionary change as the population adapts to the new conditions. To compare the average rates we again used the average absolute values of the ecological and evolutionary contributions to $\partial r / \partial z$. By this measure, the evolutionary

change in body and beak size was even faster than the ecological dynamics, and by a factor of 2.2.

Beak shape is a different story. We were unable to find any statistically significant (or even marginally significant) effect of beak shape on population growth, either alone or in combination with size. Direct studies have shown that beak shape underwent natural selection during at least 2 years (1980 and 1985, Grant & Grant 2002), but the impact on population growth may have been too small to detect despite the length and quality of the data series. Alternatively, changes in beak shape may be driven by some environmental factor not included in our data. The most rapid changes in beak shape came shortly after a major El Niño event, and the change in mean seed size is only one aspect of the resulting changes in plant community composition (Grant & Grant 1989).

Finally, we remind readers that for the sake of illustration we have deliberately used a small fraction of the available data on this system. A careful analysis of the complete data record could easily give a different picture.

Example of method 2: diapause dynamics in a freshwater copepod

As described above, we studied a population of *O. sanguineus* in a small permanent lake in Rhode Island. During winter the population is actively swimming, feeding and reproducing via immediately hatching eggs. Each spring all females, responding to photoperiod and temperature cues, switch from producing immediately hatching eggs to producing diapausing eggs that stay dormant throughout summer (Hairston & Munns 1984; Hairston & Kearns 1995). This summer diapause is an adaptation to survive the annual springtime increase in predation by fish (Hairston & Munns 1984; Hairston 1987; Hairston & Dillon 1990). Unlike immediately hatching eggs, diapausing eggs survive gut passage if consumed while still attached to the female that laid them, and within a few days of being laid are dropped to the sediment where they are impossible for the fish to find. Females do not switch to diapause synchronously because they vary genetically for photoperiod and temperature response (Hairston & Dillon 1990). During 8 of 9 years between 1979 and 1987, the distribution of the switch-to-diapause date (hereafter 'switch date') was documented by weekly sampling (Hairston & Dillon 1990), as was the onset of fish predation (hereafter 'catastrophe date') (Hairston 1988; Hairston & Dillon 1990).

For this example, we choose as our response variable X the average per-capita production of diapausing eggs in a given year, which we can think of as *mean realized fitness*. We estimated the entries in Table 1 using a stage-structured demographic model (Ellner *et al.* 1999). The model allows us to compute individual fitness w (total lifetime production of
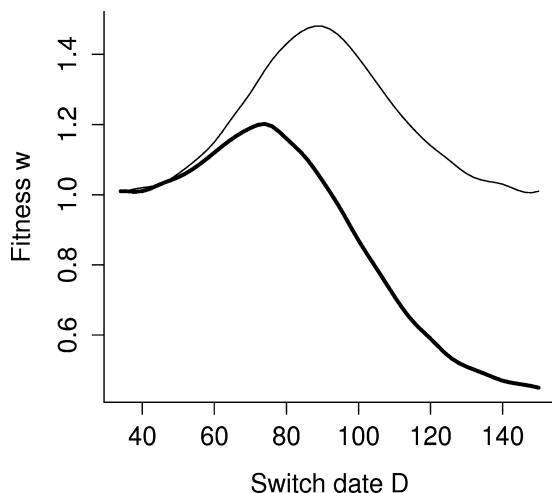
Figure 6 Individual fitness (female per-capita production of diapausing eggs) as a function of switch date (day of year) for female *O. sanguineus* in Bullhead Pond, Rhode Island, calculated from the demographic model described in the text. Fitness curves are scaled relative to the fitness for a very early switch date, which is not affected by fish predation. The heavy curve represents a year with early onset of intense fish predation, the light curve a year with a late onset of mild fish predation. The optimal switch date is approximately one copepod generation prior to the onset of predation (Hairston & Munns 1984). The curves illustrate how evolutionary (switch date) and ecological (fish predation) variables jointly determine fitness, which we use as the basis for comparing ecological and evolutionary rates of change in this population.

diapausing eggs by a female and her current-year offspring since individuals survive at most 1 or 2 months) as a function of the female's switch date D, the catastrophe date C in that year, and the intensity of fish predation after the catastrophe date, μ. Figure 6 shows the model's main features. In any given year there is an optimal switch date that maximizes reproductive success. In a year when predation is intense and begins early (bold curve) the optimal date is early; when fish predation is late and mild (light curve) the optimal date is later and the potential maximum fitness is higher. The mean realized fitness X is the average of $w(D, C, \mu)$ over the distribution of D values in that year (the 'switch date distribution'). In terms of eqn 2, z is the distribution of switch date D (characterized by its mean and variance) and k is the temporal pattern of fish predation characterized by (C, μ). From our studies of this system (Hairston 1988; Hairston & Dillon 1990; Ellner *et al.* 1999) we have the necessary information – C, μ, and switch date distribution – to compute X values for 1979 and 1981–1987. We constructed Table 1 for each pair of successive years, fit a linear model with interaction, and thus estimated the effects of ecological and evolutionary changes on X.

Table 2 Results of applying the decomposition in Table 1 to changes in mean realized fitness of *Onychodiaptomus sanguineus* in Bullhead Pond, RI

Time interval	Ecological change rate	Evolutionary change rate
1979–1981	−2.5	−1.1
1981–1982	3.7	1.3
1982–1983	2.7	0.6
1983–1984	0.5	−0.2
1984–1985	−1.4	−0.9
1985–1986	−4.5	1.3
1986–1987	6.3	−0.5
Mean absolute rate	3.1	0.8

For each pair of successive years the three columns give the main effects of the ecological and evolutionary changes. Because changes in each variable can have either positive or negative effects on fitness, we average the absolute values of the annual effects to compare the overall relative importance of ecological and evolutionary changes. The unit for both rates is fitness (eggs per female) per year.

The results (Table 2) show that the variation in mean realized copepod fitness is largely driven by the ecological variable, fish predation. Measured in terms of its impact on fitness, ecological change was faster (on average) than evolutionary change, but the effect of evolution was nevertheless substantial at a quarter that of ecology. Evolution in this population was driven by the variation in fish predation and its effects on the relative reproductive payoffs for different switch dates. The maximum evolutionary rate over the period of study was high at 0.405 haldanes (Fig. 1), and these evolutionary changes had a quantifiable reciprocal impact on the overall fitness of the population. The result that relative rate of ecological change was four times that of evolutionary change makes sense since ecological change (predation risk) in this system varied between years by as much as an order of magnitude (9.1-fold) and the timing of the onset of fish predation varied between years by as much as 28.2 days, whereas the timing of diapause only changed at most by 2.4 days.

Experimental design required for method 3

The ideal experimental design would be factorial. For simplicity consider a single trait z and ecological variable k. The first step is to create a set of selected lines having known and different values of the trait z, spanning the range of values observed in the study system. Then for each of these lines, a series of experiments would be performed to measure the response variable X across the relevant range of values for the ecological variable k. The measured values X_{ij} (for the *i*th selected line, under the *j*th set of ecological

conditions) would then be used to fit a response surface model $X = \hat{F}(z, k)$, that would be used to estimate $\mathrm{d}F/\mathrm{d}k$ and $\mathrm{d}F/\mathrm{d}z$. The dynamics of the driving variables, $\mathrm{d}z/\mathrm{d}t$ and $\mathrm{d}k/\mathrm{d}t$, would be estimated from repeated measurements of z and k over time in the unmanipulated study system.

Although no study that we know of has measured all of these components, some have parts complete. For example Agrawal (2000) demonstrated that lines of spider mites adapted to different host plants exhibit heritable differences in host choice and in population growth rate, when fed host plants induced by herbivory. Similarly, Yoshida *et al.* (2004) showed that algal lines grown in the presence or absence of grazing rotifers became heritably distinct in their food value to rotifers and in their competitive ability under nitrogen limitation. In both of these cases, to complete method 3 it would be necessary to measure system response, and to construct a model of how response depends on changes in phenotype and environment.

CONCLUSIONS

The expanding number of reports of rapid evolution in natural populations has generated interest for two distinct reasons. First, calculated rates of change seem very fast relative to what has, until recently, been considered typical rates of evolution (e.g. Losos *et al.* 1997; Reznick *et al.* 1997; Kinnison *et al.* 1998). Second, rapid trait changes have the potential to affect the outcome of simultaneous ecological change (Geber & Dawson 1993; Thompson 1998; Hairston *et al.* 1999).

Recent studies of short-term evolutionary change have tended to focus on rates that exceed by orders of magnitude the average rates measured over geological time scales (Thompson 1998; Hendry & Kinnison 1999). However, studies of annual patterns of selection and response followed over multiple years (Grant 1986; Hairston & Dillon 1990; Ellner *et al.* 1999; Grant & Grant 2002) show that even in systems where evolutionary change can be rapid, average rates over periods as short as a decade may be quite low (Fig. 1). The reason, as previously noted by Gingerich (1983, 2001), is that the direction and magnitude of selection can vary over time intervals as short as a single generation. It may be that instances of rapid evolution have received disproportionate attention because studies of adaptive change are more likely to be carried out in systems where intense natural selection is expected. In addition, findings of unusually rapid evolution are more likely to be the subject of separate publication than results showing no change: exceptionally high rates are interesting on their own, whereas stasis is only interesting in the broader context of temporally varying rates. The studies we have discussed above of Galápagos finches and Rhode Island copepods found periods of both rapid evolution and relative stasis, but only the former were the subject of separate publications (Boag & Grant 1981; Hairston & Walton 1986; Grant & Grant 1995).

If estimates of evolutionary rates that encompass long periods of time are low because they average periods of rapid evolution with reversals and intervals of slow evolution or stasis, then rapid evolution has probably not been rare in the history of life (Gingerich 1983, 2001; Hendry & Kinnison 1999). Thus, although anthropogenic forcing underlies many recent discoveries of rapid evolution (Palumbi 2001), including many of those reviewed by Thompson (1998) and Hendry & Kinnison (1999), natural events can also produce intense natural selection and rapid response. The changes in rainfall that have driven evolution in both the Galápagos finches and Rhode Island copepods are only very indirectly related to human activity, if at all. Environmental changes that evoke evolutionary responses and altered ecological dynamics may thus be a natural part of the history of life, perhaps only accelerated by recent human activity.

If we wish to understand ecological responses to environmental change [a major objective of 'ecological forecasting' (e.g. Clark *et al.* 2001)], then it may be necessary to consider whether evolutionary change in organismal phenotypes alters the outcome of concurrent population, community or ecosystem processes. Whether evolutionary change is considered rapid or not is then a relative assessment that requires a comparison between concurrent rates of evolutionary and ecological change and an evaluation of the direct contribution of evolutionary change to ecological change. Where ecological change is slow, even low absolute rates of evolutionary change may be considered rapid if they are fast enough to alter the outcome of ecological interactions. Several authors have suggested that as the climate warmed at the end of the Pleistocene some plant species evolved to be successful in the new conditions, while others experienced changes in geographic range or simply went extinct (Geber & Dawson 1993; Davis & Shaw 2001; Davis *et al.* 2005). Those evolutionary changes must have included adaptation to new interspecfic interactions leading to altered dynamics, not only at the level of organism physiology but at the community and ecosystem levels as well.

We have provided here an approach for evaluating, by this ecological standard, whether evolution is rapid. Where there is a significant effect of a change in a species' trait on a measure of ecological performance, evolution is ecologically rapid and, in contrast to Slobodkin's (1961) distinction, evolutionary time becomes inseparable from ecological time. Where evolutionary time converges with ecological time, our analysis of ecological dynamics becomes dependent upon also understanding ecologically rapid evolutionary change.

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