EDITORIAL
Evolution on ecological time-scales

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Summary

1. Ecologically significant evolutionary change, occurring over tens of generations or fewer, is now widely documented in nature. These findings counter the long-standing assumption that ecological and evolutionary processes occur on different time-scales, and thus that the study of ecological processes can safely assume evolutionary stasis. Recognition that substantial evolution occurs on ecological time-scales dissolves this dichotomy and provides new opportunities for integrative approaches to pressing questions in many fields of biology.

2. The goals of this special feature are twofold: to consider the factors that influence evolution on ecological time-scales – phenotypic plasticity, maternal effects, sexual selection, and gene flow – and to assess the consequences of such evolution – for population persistence, speciation, community dynamics, and ecosystem function.

3. The role of evolution in ecological processes is expected to be largest for traits that change most quickly and for traits that most strongly influence ecological interactions. Understanding this fine-scale interplay of ecological and evolutionary factors will require a new class of eco-evolutionary dynamic modelling.

4. Contemporary evolution occurs in a wide diversity of ecological contexts, but appears to be especially common in response to anthropogenic changes in selection and population structure. Evolutionary biology may thus offer substantial insight to many conservation issues arising from global change.

5. Recent studies suggest that fluctuating selection and associated periods of contemporary evolution are the norm rather than exception throughout the history of life on earth. The consequences of contemporary evolution for population dynamics and ecological interactions are likely ubiquitous in time and space.

Key-words: contemporary evolution, anthropogenic change, modern syntesis, natural selection, rapid evolution

Introduction

> Clearly, our thinking must not exclude the possibility of animals attaining to extremely rapid rates of evolution ...   (Johnston & Selander 1964)

A wave of recent studies has shown that many organisms can undergo adaptive phenotypic evolution over just a few generations. Across a wide range of taxa, this contemporary evolution has been observed in many biological contexts, on fine spatial scales, and in the presence of gene flow (e.g. Hendry & Kinnison 1999; Schluter 2000; Kinnison & Hendry 2001; Palumbi 2001; Gilchrist *et al.* 2004; Hargeby, Johansson & Ahnesjo 2004; Garant *et al.* 2005; Strauss, Lau & Carroll 2006; Hendry *et al.* 2006; Phillips *et al.* 2006). Moreover, strong selection on observable time frames has caused substantial differentiation among populations within species, in some cases enough to represent the early stages of speciation (Hendry *et al.* 2000; Filchak, Roethele & Feder 2000; Schwarz *et al.* 2005; Hendry, Nosil & Rieseberg 2007). Evolution may also occur quickly enough to alter the outcomes of ecological interactions and ecosystem-level processes (Thompson 1998; Agrawal, Lau & Hambäck 2006; Fussmann, Loreau & Abrams 2007), including those that generate selection in the first place (Yoshida *et al.* 2003; Hairston *et al.* 2005). Given all of these effects, ignoring contemporary evolution will likely limit success in many biological disciplines.

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Recognizing the potentially broad influences of contemporary evolution leads to many new questions. Are the high frequencies and rates of evolution observed in modern times unusual, perhaps the result our own increasing impact on the selective environments of other taxa? Or, has evolution always occurred on ecological time-scales, but been largely overlooked until recently? How do rates of evolution measured in ecological time relate to those assessed by macroevolutionary and palaeontological studies? What are the genetic, developmental, behavioural and demographic factors that influence rates of contemporary evolution? And, what are the implications of contemporary evolution for general principles and problems in evolutionary biology, ecology, conservation biology, medicine and agriculture? Empirically, the reality of contemporary evolution means that many evolutionary processes thought approachable only by inferential study, such as speciation, can now be studied directly.

This special feature of *Functional Ecology* starts from the premise that contemporary evolution is a common phenomenon. This recognition allows us to move forward beyond simply documenting the process to examining the factors that influence it and that are influenced by it. We specifically emphasize evolution on ecological time-scales; that is, ecologically significant evolution occurring on a time frame over which ecological studies typically consider populations to be evolutionarily static. Our goal is to synthesize and broadcast what is known about the biology of contemporary evolution, to highlight the opportunities it presents, and to identify current gaps in our understanding.

In this introductory essay, we review the history of thought on the pace of evolution and its importance in ecological pattern and process. This introduction is followed by seven papers – each a general review of conceptual ideas and empirical support for them – examining emerging topics in this field. Four of these papers treat factors that influence evolution on ecological time-scales – phenotypic plasticity, maternal effects, sexual selection, and gene flow. The remaining papers examine the ecological consequences of contemporary evolution for population persistence, speciation, and community/ecosystem dynamics.

Natural selection and the pace of evolution

Darwin's impeccable logic allowed him to infer the primary mechanism of evolution without being able to observe it directly. Despite knowing that artificial selection could produce phenotypic change very quickly, his intuition about the rate of evolution in nature appears conservative: 'We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages' (1859, p. 84). Elsewhere, however, he seems to have considered a contemporary and reciprocal interplay between ecology and evolution: 'But it is difficult to tell ... whether habitats generally change first and structure [morphology] afterwards;

or whether slight modifications of structure lead to changed habitats; both probably often change almost simultaneously' (1859, p. 183). His experiences in the Southern Hemisphere as naturalist on the *Beagle* sensitized him to the fact that environments do in fact sometimes change swiftly and suddenly (1860, e.g. pp. 120, 311). Yet, the perception that evolutionary change can really only be documented through palaeontological study remained dominant for more than a century.

With the exception of a few examples documenting that natural selection occurs in nature (e.g. Bumpus 1899), little progress was made towards understanding the causes and consequences of natural selection until the rise of population genetics in the 1920s. Bridging the gap, Turreson (1922, 1930) proposed the study of 'genecology' – adaptive properties of populations in relation to the environment, which include the concept of 'ecotypes'. The first thorough experimental field studies of selection appeared during the Modern Synthesis. Clausen, Keck & Heisey (1940) conducted transplantation/common garden experiments that documented the genetic basis of adaptive morphological differences across an elevational gradient in the western North American herb, *Potentilla glandulosa*. During the same period, Dobzhansky (1948) conducted myriad studies of adaptation in *Drosophila*, including the demonstration of cyclical annual evolution in relation to habitat seasonality. These studies showed that natural selection is a decipherable, quantifiable phenomenon, subject to hypothesis testing. Under the influence of these pioneers, biologists came to recognize the value of spatial and temporal comparisons for inferring the role of selection in nature.

The 1950s marked the emergence of the British School of Ecological Genetics, and Ford's first book with that title was published in 1964. Like Clausen's work, these were not studies of 'evolution in action' per se, but rather inferential analyses of colour variation in relation to predation (e.g. Brower 1958; Sheppard 1959; Clarke & Murray 1962). Of all such examples, that of 'industrial melanism' in the peppered moth (*Biston betularia* Linnaeus), became most well known (e.g. Kettlewell 1956). Along with studies of heavy metal tolerance evolving in plants on mine tailings (Antonovics, Bradshaw & Turner 1971), and adaptation to fertilizer treatment in the Park Grass Experiment (Snaydon 1970, reviewed in Silvertown *et al.* 2006), this 'smoking gun' of the industrial revolution was widely taught in biology courses as the principal heuristic exposition of evolution by natural selection. What set these last examples apart from earlier work was that adaptation had occurred in contemporary time.

Despite this burgeoning literature on natural selection, it proved difficult to shake the perception that evolution and ecology happened on very different time-scales. Slobodkin (1961) formalized this perspective by arguing that 'ecological time' was the ten-or-so generation period over which a population might, on average, maintain a steady state. 'Evolutionary time', in contrast,

was considered the approximately half-a-million-year period sufficient for evolutionary change to disrupt ecological steady states. Bucking this inertia, Johnston & Selander (1964) and Berry (1964) found convincing evidence of something quite different. In the first case, house sparrows (*Passer domesticus*) introduced to North America diversified phenotypically as they colonized different habitats. In the second, house mice introduced to the Welsh island of Skokholm changed dramatically in skeletal measurements over only 70 years. This was soon followed by other examples, such as the evolution in < 100 generations of host races of *Rhagoletis pomonella* (apple maggot fly) in response to introduced apples (Bush 1969). A few scattered studies in the 1970s added to the pantheon of contemporary evolution.

The 1980s, however, ushered in an important innovation in the study of contemporary evolution: the use of common garden or experimental methods to determine the genetic basis for phenotypic differences that have evolved in contemporary time. Chief examples include Endler's (1980) and Reznick & Bryga's (1987; Reznick, Bryga & Endler 1990) work on colour patterns and life-history traits in guppies introduced to new predator environments, Stearns' (1983) work on life-history traits in mosquitofish introduced to Hawaii, and Williams & Moore's (1989) work on phenotypic traits in rabbits introduced to New Zealand. These and other studies confirmed that substantial genetically based adaptive genetic change can indeed occur in contemporary time.

Drawing on examples such at these, Endler's (1986) book *Natural Selection in the Wild* clearly established for the first time that evolution by natural selection was a potent ongoing phenomenon. He reviewed enough cases to show that measurable responses to contemporary natural selection, if not common, were at least not exceedingly rare or aberrant. Simultaneously, modern 'selection thinking' (e.g. Charnov 1982) was making broad incursions into ecology, yielding progressively more evidence of precise specialization and fine-scale adaptive population differentiation in nature.

The field seemed to explode in the late 1990s, probably spurred by the publication of high-profile papers that compared rates of phenotypic change in the fossil record to those observed in experimental introductions of guppies (Reznick *et al*. 1997) and *Anolis* lizards (Losos, Warheit & Schoener 1997). These empirical examples were followed by the influential reviews of Thompson (1998) and Hendry & Kinnison (1999), both showing that many studies have found substantive phenotypic changes occurring on ecological (contemporary) time-scales: '... claims of rapid microevolution should not necessarily be considered exceptional, and perhaps represent typical rates of microevolution in contemporary populations facing environmental change' (Hendry & Kinnison 1999, p. 1650).

This emerging shift in mindset brought into sharper relief a paradox earlier elucidated by Gingerich (1983):

short-term studies often find dramatic and rapid rates of phenotypic change, whereas long-term studies seem to manifest much slower rates of change (see also Estes & Arnold 2007). Fortunately, long-term studies of selection and evolution had, by the late 1990s, continued for long enough to provide some resolution. Specifically, selection and evolution often fluctuate dramatically in direction through time, presumably tracking fluctuating environments, so that rapid short term changes rarely accumulate into long-term directional trends (Gibbs & Grant 1987; Hairston & Dillon 1990; Ellner *et al*. 1999; Grant & Grant 2002, 2006).

A related concern was the realization that many examples of contemporary evolution result from anthropogenic disturbances (Palumbi 2001; Rice & Emery 2003, Carroll *et al*. 2005; Strauss *et al*. 2006; Hendry *et al*. 2006). Since humans are reshaping selective environments across the globe, contemporary evolution may be more frequent, and directional selection may be less ephemeral, in the present than under more 'natural' conditions prevailing in the past (Strauss *et al*. 2006). Although the global scale of environment change caused by human disturbance is largely unprecedented in evolutionary history, the magnitude of the resulting genetic change does not seem abnormally high. Instead, observed rates of contemporary evolution may mirror historical processes, and what currently appears 'rapid' may have been common throughout the history of life, though less contemporaneous among such a wide diversity of organisms.

If contemporary evolution is often reversible and rarely accumulates into long-term changes, how do larger changes in taxa ultimately arise. Comparing various genetic models, Estes & Arnold (2007) found that the distribution of observed evolutionary rates is best explained by a model that assumes a fitness optimum that can move but within fixed limits (i.e. an 'adaptive zone'). Under this scenario, most of evolutionary time is characterized by stabilizing selection at the level of an adaptive zone, within which populations can move to new local adaptive peaks. Indeed, Darwin's finches, which show such dramatic change on short time-scales (Grant & Grant 2002, 2006), continue to appear much as they did millions of years ago (Carroll 1997). Macroevolution may thus require progressive change in the environment that takes evolution consistently in one direction (such as increased body size). It is important to note, however, that this may sometimes be a gradual process, interspersed with many temporary reversals of direction. Macroevolution may thus be nothing more than an aggregate of many small events, and is entirely explainable by events that we can observe and quantify over the course of our lives as investigators. The frequency with which evolution stemming from ongoing human disturbance will likewise show a highly iterated or reversible nature, versus consistent and enduring shifts, remains to be discovered.

Historically, macroevolution has been equated with substantive adaptive change, and rapid and fluctuating evolution has been regarded as evolutionary noise. Thus, debate continues over what constitutes trivial versus important evolution. We argue that the real distinction between macro- and microevolution may lie only in the degree to which the factors causing evolution are fluctuating or are gradually and persistently directional, and not in the ecological significance of that evolution.

The ecological significance of evolution

Recognition of the rate and ecological significance of adaptive evolution is heralding a new epoch where the dichotomy between ecological and evolutionary time and, more importantly, between ecological and evolutionary processes is breaking down. Here, again, Thompson (1998) was formative in noting that high rates of evolution, even when transient, are 'constantly reshaping populations and interspecific interactions through frequency-dependent selection, seasonal fluctuations in allele frequencies, selective death of genotypes within and among cohorts, and the constantly shifting genetic configuration of populations and interspecific interactions across broad geographic landscapes' (p. 331). In other words, the continuously evolving face of the biotic environment, including simultaneously co-evolving relationships among (and likely within) populations, drives dynamic variation in selective environments that are linked to adaptation.

A general prediction is that the importance of contemporary evolution to ecological interactions will increase with (i) increasing changes in traits under selection, and (ii) increasing links between that trait variation and ecological interactions (Hairston *et al.* 2005). Hairston *et al.* 2005 propose a quantitative approach to assessing concurrent rates of evolutionary and ecological change in populations, and to modelling the direct contribution of evolution to ecological change. Using comprehensive and long-term data for Darwin's finches and freshwater copepods, they conclude that population growth rate can sometimes be at least twice as sensitive to evolutionary changes as to important ecological changes in abiotic factors, such as rainfall. In other words, evolutionary change can have substantial effects on ecological dynamics.

Thus, while it has long been recognized that adaptive evolution occurs in an ecological context, it is now clear that evolutionary change feeds back directly and indirectly to demographic and community processes, and that ecological studies should consider this reciprocal interplay between ecology and evolution. Because we are now in a period of accelerated environmental change, evolutionary biologists have an unprecedented opportunity to study evolutionary processes and their influence on ecological processes. Likewise, evolutionary biology has an unprecedented opportunity

to contribute to other areas of basic and applied biology (e.g. Palumbi 2001; Stockwell, Hendry & Kinnison 2003; Strauss *et al.* 2006; Carroll in press).

What is explored in this special feature?

The foregoing sections illustrate that contemporary evolution is common and is likely important to ecological pattern and process. We can thus turn to the main goal of this special feature, which is to move beyond simple demonstrations of evolution on ecological time-scales to a more complete and nuanced consideration of (i) factors influencing contemporary evolution, and (ii) the effects of contemporary evolution on specific aspects of ecology. Here we provide an introduction to what the reader will encounter in the other contributions to this special feature.

Genetic and phenotypic interactions within and among populations and species may strongly influence the interplay of ecological and evolutionary change, and thereby determine our ability to predict the impact of environmental alteration on individual and population characters of interest ('eco-evolutionary dynamics', e.g. Kinnison & Hairston 2007; Fussmann *et al.* 2007). To broaden the applicability of eco-evolutionary models, a next step will be incorporating even more complex variables and scenarios during simultaneous ecological and evolutionary change. For example, in determining the phenotypic and fitness values of traits under selection, the interaction between genes, development and ongoing evolution itself should be a fundamental source of variation (*sensu* Coulson *et al.* 2006, Carroll in press). Two such interactions include phenotypic plasticity and maternal effects.

Phenotypic plasticity results from the developmental and behavioral responses of genotypes to environmental influences, and operates both within and across generations (Ghalambor *et al.* 2007). Plasticity may have a variety of influences on contemporary evolution, ranging from being a constraint on adaptive evolution (owing to reduced selection) all the way to being a promoter of adaptive evolution (by bringing populations into the domain of attraction of new fitness peaks) (Price, Qvarnström & Irwin 2003). Plasticity may also serve to buffer populations from environmental change, thus reducing the risk of extinction and making adaptive evolution possible. Maternal effects are like phenotypic plasticity in that they can change fitness in the absence of genetic change, and can thereby alter the frequencies of phenotypes (Rasanen & Kruuk 2007). Moreover, reaction norms (patterns of plasticity) and maternal effects may both evolve substantially across just a few generations (e.g. Hairston *et al.* 2001; Ghalambor *et al.* 2007; Rasanen & Kruuk 2007), thus changing the response of organisms to environmental heterogeneity.

Sexual selection is another factor that may influence contemporary evolution, and this process can be thought of as co-evolutionary dynamics within and

between the sexes within a species. The tight cycling of sexual selection in models of mate choice, for example, suggests that contemporary evolution should be especially apparent in such systems. Surprisingly, despite the high volume of scientific activity aimed at sexual selection in general, few studies have considered its role in contemporary evolution, although the few examples include some classics (e.g. Endler 1980). Svennson & Gosden (2007) conclude that the apparent rarity of contemporary evolution in secondary sexual traits may simply result from an absence of long-term studies of sexual selection within a population biology framework. It is also possible that inherent peculiarities of the traits themselves may somehow limit rapid responses to altered selection pressures (Svennson & Gosden 2007; Karim *et al.* in press).

Contemporary evolution will be strongly influenced by rates and patterns of gene flow and dispersal. For example, gene flow may hinder adaptive differentiation by reducing the genetic independence of populations inhabiting different selective environments, but may sometimes promote adaptive differentiation by supplementing the genetic variation on which selection can act. Gene flow can thus variously promote or retard adaptive divergence between populations, and may thus act to structure adaptation across the geographic range of a species. Garant, Ford & Hendry (2007) highlight the important differences between traits adapting to relatively static environmental conditions versus those caught up in co-evolutionary dynamics, with the latter likely benefiting more from the genetic variation brought by gene flow. One of the main implications of this perspective is that environmental change will alter the complex, dynamic relationships between adaptation and gene flow, and will therefore influence adaptive divergence and speciation (Hendry *et al.* 2007). Gene flow may have similar complicated and dynamic influences on population persistence (Kinnison & Hairston 2007).

Lastly, the eco-evolutionary dynamics of interspecific interactions may strongly influence community dynamics, food web structure and ecosystem function. Fussmann *et al.* (2007) review a series of simple theoretical models that have long shown important feedbacks from evolution to ecology – if only empiricists had paid more attention! The main theoretical hurdle is moving beyond the current simple models to ones that more accurately assess the complexities of ecological communities and ecosystems. Empirical work in natural populations has lagged behind theoretical developments, but we now at least have a number of intriguing examples of how genetic variation in populations can influence community dynamics and ecosystems function (Whitham *et al.* 2006). The next step is to document how contemporary *changes* in genetic variation influence these same dynamics and functions. Some of the best examples here come from interactions between hosts and pathogens in introduced species (Fussmann *et al.* 2007).

The frequency, magnitude and importance of evolution on ecological time-scales are likely to grow as human environmental impacts increase and their effects ramify. The dialogue in evolutionary biology will soon be dominated by discussions of systems in which evolution is ongoing, directional and in many cases non-reversing because environments are changed so substantially. Community and conservation ecology will necessarily become microevolutionary disciplines, and other disciplines will follow. As part of this transformation, discussions of evolutionary rates and their significance will broaden as we progress from more unified perspectives about the challenges and prospects to be addressed. One such perspective has given birth to the nascent field of evolutionary conservation management, in which genotypes and population processes may be manipulated to promote the resilience of threatened populations, combat invasive species, or promote coexistence (e.g. Ashley *et al.* 2003; Stockwell *et al.* 2003; Carroll & Watters in press). Evolution on ecological time-scales makes conservation efforts more complex, as taxa become ecological moving targets. Yet many conservation goals will only be met with the assistance of adapting taxa, even if prior phenotypic and genotypic states disappear as a result (e.g. Carroll *et al.* 2005). Theoretical advances are bringing us closer to applied fields of evolutionary demography and community ecology (Kinnison & Hairston 2007; Fussmann *et al.* 2007, respectively). To the extent that contemporary evolution is inevitable, predictable, and central to the generation of biodiversity, we must harness its power to ameliorate damage and reconstitute species and ecosystem functions. Doing so may be the chief path towards sustainable conservation practice.

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