



An introduction to microevolution: rate, pattern, process

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Abstract

This special issue of *Genetica* brings together a diverse collection of contributions that examine evolution within and among populations (i.e., microevolution), and the role that microevolution plays in the formation of new species and morphological forms (i.e., macroevolution). Many of the papers present evidence of microevolution occurring over contemporary time frames, further validating the near ubiquity of ongoing evolution in the world around us. Several synthetic reviews of empirical work help to define the conditions under which microevolution is or is not likely to occur. Some of the studies speak directly to current controversies in evolutionary biology, such as the relative roles of determinism and contingency, and the nature of the relationship between microevolution and macroevolution. In general, microevolution seems driven largely by deterministic mechanisms, particularly natural selection, but contingency plays a role in (1) determining whether or not suitable conditions are present for evolution to proceed, and (2) guiding the precise manner by which evolution proceeds. Several theoretical treatments and empirical reviews confirm previous research in showing that microevolutionary processes are at least *capable* of generating macroevolutionary trends. Macroevolution may indeed reflect microevolution writ large but the pattern by which it arises is perhaps best characterized as microevolution writ in fits and starts.

Introduction

Evolution is often considered in two categories: microevolution and macroevolution. The former obviously implies a small amount of change and the latter a large amount. The difficulty comes in deciding where the boundary between the two should fall, whether or not they reflect the same processes (acting over different time scales), and whether or not the dichotomy is even useful or valid. The collection of papers in this special issue of *Genetica* is titled 'Microevolution: rate, pattern, process', which begs the question of just what is meant by the term microevolution. A brief historical survey provides some perspective.

The terms appear to have been coined by Filipchenko (1927, 1929): 'Modern genetics doubtless represents the veil of the evolution of Jordanian and Linnaean biotypes (microevolution), contrasted

with the evolution of higher systematic groups (macroevolution), which has long been of central interest. This serves to underline the above-cited consideration of the absence of any intrinsic connection between genetics and the doctrine of evolution, which deals particularly with macroevolution' (from Filipchenko, 1927, p. 93-94, translated by P. Gingerich, pers. comm.). In contrast, Dobzhansky (1937, p. 12) felt that the micro and macro of evolution were inseparable: 'Experience seems to show, however, that there is no way toward an understanding of the mechanisms of macro-evolutionary changes, which require time on a geological scale, other than through a full comprehension of the micro-evolutionary process observable within the span of a human lifetime...'. The opposing argument, that for different mechanisms at the different scales of evolution, was continued most enthusiastically by Goldschmidt (1940, p. 8), for whom

macroevolution was ‘...evolution of the good species and all the higher taxonomic categories’. Mayr (1942, p. 291) described the difference thus: ‘Under the term microevolution such evolutionary processes are understood as occur within short spaces of time and in lower systematic categories, in general within the species... . By the term macroevolution we understand the development of new organic systems – in short, evolutionary processes that require long periods of time and concern the higher systematic categories...’.

In Simpson’s (1944, p. 97) opinion, ‘Microevolution involves mainly changes within potentially continuous populations, and there is little doubt that its materials are those revealed by genetic experimentation. Macro-evolution involves the rise and divergence of discontinuous groups, and it is still debatable whether it differs in kind or only degree from microevolution’. Simpson (1944) also pointed out that the use of macroevolution by some biologists (species level and above) was different from that adopted by others (higher taxonomic levels). He suggested that the latter might more appropriately be called ‘megaevolution’ (Simpson, 1944, p. 98), but later asserted ‘...that all three of these somewhat monstrous terminological innovations have served whatever purpose they may have had and that clarity might now be improved by abandoning them’ (Simpson, 1953, p. 339). Rensch (1954) was also critical of the terms, preferring ‘intraspecific’ and ‘transspecific’. Despite their monstrosity, microevolution and macroevolution persist in the lexicon of biology. Indeed, they are discussed in every major textbook on evolution (although definitions vary).

For the purposes of this special issue, microevolution refers to changes within and among populations. Also considered are the formation and divergence of new species by processes known to act within and among populations (e.g., natural and sexual selection, micromutation, genetic drift, gene flow). Defined in this way, microevolution is conceptually independent of time scale, and so it is also useful to distinguish between contemporary microevolution (over one generation to a few centuries) and microevolution occurring over longer intervals (evident in paleontological series). In the past few decades, studies of microevolution have taken the legacy of the evolutionary synthesis to new levels of refinement, and now represent the flagship for the presence and power of evolution. This expanding interest has come with the development of new techniques (see below) and the realization of microevolution’s relevance to many issues in eco-

logy, evolution, and conservation. This special issue of *Genetica* is intended to provide a timely synthesis of current information, an illustration of exciting new directions, and a springboard for future investigations.

We invited active evolutionary biologists to contribute theoretical developments and statistical methods, synthetic reviews and perspectives, and empirical demonstrations in natural systems. The resulting papers are concerned to varying degrees with the rate at which microevolution proceeds (rate), variation in evolution over space and time (pattern), and mechanisms causing evolutionary change (process). Several major themes emerged: descriptions of microevolution within and among populations, evidence for contingency versus determinism in microevolution, considerations of how microevolution contributes to macroevolution, and the development and assessment of theoretical models and statistical methods.

Microevolution

It now seems almost quaint that microevolution was ever seriously questioned as a prevalent and important phenomenon. At present, evolutionary biologists have illuminated so many concrete examples of evolutionary change within populations that even the staunchest critics tend to concede the reality of microevolution. Classic demonstrations include industrial melanism in peppered moths (Kettlewell, 1973; Majerus, 1998), adaptation of plants to different soil conditions (Snaydon, 1970; Antonovics, Bradshaw & Turner, 1971), divergence of mosquitofish introduced to Hawaii (Stearns, 1983a,b), adaptation of guppies to different predation regimes in Trinidad (Endler, 1980; Reznick et al., 1997), evolution of resistance to pesticides (Tabashnik, 1994) and antibiotics (Baquero & Blazquez, 1997), and changes in the size and shape of finch beaks in the Galápagos Islands (Grant & Grant, 1995).

Model systems for investigating microevolution continue to be developed. This special issue includes research in several such systems, including soapberry bugs on introduced host plants (Carroll et al., 2001), *Drosophila subobscura* introduced to North America (Gilchrist, Huey & Serra, 2001), mosquitoes adapting to pesticides (Raymond et al., 2001), riparian and aridland spiders (Riechert, Singer & Jones, 2001), marine snails exposed to an introduced predator (Trussell & Etter, 2001), European shrews (Polly, 2001), Darwin’s finches (Grant, Grant & Petren, 2001), rainforest vertebrates (Smith, Schneider & Holder, 2001), *Anolis*

lizards introduced to Bahamian Islands (Losos et al., 2001), side-blotched lizards (Sinervo, 2001), African cichlids (Lande, Seehausen & van Alphen, 2001), threespine stickleback (Bell, 2001), Trinidadian guppies (Magurran, 2001), grayling introduced to new sites in Norway (Haugen & Vøllestad, 2001), chinook salmon introduced to New Zealand (Quinn, Kinnison & Unwin, 2001), and sockeye salmon introduced to Lake Washington (Hendry, 2001).

One benefit of multiple systems is that the data can be combined into reviews that address general questions about evolution. Examples include analyses of heritability (Mousseau & Roff, 1987), genetic variance (Houle, 1992), and natural selection (Endler, 1986; Kingsolver et al., 2001). Several papers in the present volume provide reviews and syntheses of contemporary microevolution. Pergams and Ashley (2001) perform a meta-analysis on morphological data over the last century in four widely-separated island rodent populations. They conclude that the observed changes are best explained by natural selection, and that rates of evolution are higher on smaller and more remote islands. Bone and Farres (2001) review rates of microevolution in plants, concluding that evolution can be sustained under artificial selection but slows with time in natural populations, and that physiological traits evolve more rapidly than morphological traits. Kinnison and Hendry (2001) build on Hendry and Kinnison's (1999) earlier review of rates of contemporary microevolution in animals. We find that natural selection is strong enough to explain observed microevolution but that selection is probably rarely sustained over many generations, that life history traits evolve as fast as (or faster than) morphological traits, and that evolutionary diversification increases with time but at a decreasing rate.

What conditions favor adaptation and what conditions do not? Reznick and Ghalambor (2001) review studies of contemporary microevolution and conclude that a general condition favoring adaptive evolution is colonization followed by an opportunity for population growth. Colonization opportunities may include novel host or food resources, new biophysical environments, new predator communities, or human-modified environments. The opportunity for population expansion is important because it reduces the probability of extinction before adaptation is successful (see also Gomulkiewicz & Holt, 1995). Merilä, Sheldon and Kruuk (2001), however, point out that when natural populations are monitored for extended periods, they often appear to be under sustained directional

selection without any net change in the expected direction. They argue that this paradox may be explained by biased estimates of heritability, varying selection in time or space, selection on environmental deviations, selection on correlated traits, or low statistical power. Furthermore, microevolution may go undetected with traditional approaches if changes taking place at the genetic level are counteracted by simultaneous and opposing environmental influences (see also Conover & Schlutz, 1995; Merila, Kruuk & Sheldon, 2001).

The above papers demonstrate that microevolution is a frequent phenomenon in nature, particularly when populations are exposed to new conditions. In general, altered selection pressures lead to adaptive changes, many of which have a genetic basis. Adaptive microevolution may also be influenced by phenotypic plasticity (Losos et al., 2001; Trussell & Etter, 2001). In contrast, microevolution appears to be constrained in some situations, either because investigators cannot correctly measure the relevant parameters or because specific conditions hamper adaptive divergence. The reported instances of little or no adaptive change within populations are not in conflict with neo-Darwinian theory because stasis or maladaptation can be explained by selection, micromutation, gene flow, and genetic drift (see also Barton & Partridge, 2000).

Contingency versus determinism

Are patterns of evolutionary diversification repeatable? The remarkable convergence of independent faunas into similar sets of niches on different continents or islands provides a classic argument for the deterministic nature of evolution (i.e., similar selective pressures lead to similar adaptive solutions; Simpson, 1944, 1953; Lack, 1947; Schluter, 2000). Conversely, based on the 'Cambrian Explosion' and the Burgess Shale fauna, Gould (1989) argued that contingency (chance events) is so important that if the 'tape of life' were replayed, a similar outcome would be unlikely. This conclusion has been disputed by one of the prominent Burgess Shale researchers (Conway Morris, 1998). Unfortunately, the Cambrian Explosion and other such historical events are not replicated, leaving them of limited use in dissecting the relative roles of contingency versus determinism. Such is not the case with microevolution, where independently-derived replicate populations are often exposed to similar environmental conditions.

Microevolutionary studies reveal that similar selective pressures acting on replicate populations tend to result in remarkably convergent (from different starting conditions) or parallel (from similar starting conditions) adaptations. In guppies, for example, numerous low-predation populations have evolved similar characteristics despite being derived independently from different high-predation populations (Endler, 1980, 1995; Reznick et al., 1997). In *Anolis* lizards, similar sets of ecologically-specialized forms have evolved independently from different ancestral forms on multiple islands (Losos et al., 1998; Losos et al., 2001). In threespine stickleback, independent freshwater populations have predictably evolved fewer lateral plates than their marine or anadromous ancestors (Bell, 2001). In sockeye salmon, similar beach and stream ecotypes have evolved independently in many different lake systems (Hendry et al., 2000; Hendry, 2001). In chinook salmon introduced to New Zealand, juvenile life history and reproductive investment have evolved in response to growth conditions and migration distance, respectively, in patterns remarkably similar to those observed within the species' native range (Kinnison et al., 2001; Quinn et al., 2001).

Nested within the overall deterministic nature of microevolution is an element of unpredictable contingency that can cause adaptation to vary in interesting ways. In threespine stickleback, sympatric benthic and limnetic pairs have evolved in only six geographically-proximate lakes, suggesting specific geological conditions are necessary for their divergence (i.e., 'double invasions', Taylor & McPhail, 2000). In *Drosophila subobscura*, latitudinal clines in wing size have evolved independently in both native and introduced populations but the particular wing segment causing the cline can vary (Huey et al., 2000; Gilchrist, Huey & Serra, 2001). In greenish warblers, parallel increases in song complexity to the north around the Tibetan plateau have been achieved through divergent changes in song structure (Irwin, Bensch & Price, 2001; Irwin, Irwin & Price, 2001). In mosquitoes, resistance to pesticides frequently evolves but the specific genes responsible may vary, at least early in the process of adaptation (Raymond et al., 2001).

It thus seems that microevolution is often driven by deterministic mechanisms, particularly natural selection, but that contingency can play a role in determining whether or not suitable conditions present themselves (e.g., double invasions of freshwater by

sticklebacks) and the manner by which adaptation proceeds (e.g., proximate or distal wing segment in *Drosophila*). The role of contingency in determining the course of evolution presumably increases when the starting populations are more divergent (phylogenetic constraints become increasingly important) or smaller (founder effects become increasingly important). The role of contingency may also decrease with time along a temporal sequence of adaptation. Determinism and contingency also influence the evolution of reproductive isolation and may thus contribute to macroevolution. In sticklebacks, benthic females prefer to mate with benthic males and limnetic females with limnetic males regardless of their lake of origin, providing strong evidence that parallel evolution in response to natural selection has led to 'parallel speciation' (Rundle et al., 2000). In greenish warblers, however, parallel evolution of increased song complexity has initiated reproductive isolation because changes in song complexity along different geographical paths were caused by different modifications to song structure (Irwin, Bensch & Price, 2001; Irwin, Irwin & Price, 2001).

Micro to macro

Are macroevolutionary events (large morphological changes or speciation) simply the cumulative outcome of microevolutionary mechanisms (micromutation, selection, gene flow, genetic drift), or does macroevolution require some qualitatively different mechanism? The history of this debate is long, convoluted, and sometimes acrimonious. Many of the disagreements before the evolutionary synthesis, such as the battle between Biometricians and Mendelians, ultimately proved illusory (Provine, 1971). Accordingly, architects of the evolutionary synthesis favored the equivalency of micro and macro (Fisher, 1930; Dobzhansky, 1937; Huxley, 1942; Mayr, 1942; Simpson, 1944, 1953), although some contemporaries disagreed (e.g., Goldschmidt, 1940). Elements of the debate have changed to the present but differences of opinion remain strong.

For example, the history of life as recorded in the fossil record tends toward long periods of relative stasis interrupted by short bursts of diversification, with the geologically-instantaneous appearance of new species. Some biologists have argued that this pattern conflicts with neo-Darwinian theory (Gould & Eldredge, 1977; Stanley, 1979; Bennett, 1997 but see

Charlesworth, Lande & Slatkin, 1980), which supposedly considers evolution to be slow and gradual (e.g., 'she can never take a leap, but must advance by the shortest and slowest steps', Darwin 1859, p. 194). Rarely acknowledged, however, is that the 'slow' evolution of neo-Darwinists would appear 'instantaneous' in the fossil record: for example, Darwin (1859, p. 120–123) discussed the origin of new species after only 10,000–14,000 generations. Other current arguments center on the possible role of developmental mechanisms that may or may not fall outside the purview of microevolution (Schwartz, 1999; Jablonski, 2000; Stern, 2000). The current state of the controversy can be illustrated by juxtaposing the opinions of two recent authors: 'A microevolutionary focus amounts to the study of "macroevolution in action"' (Schluter, 2000, p. 8) and '...large-scale evolutionary phenomena cannot be understood solely on the basis of extrapolation from process observed at the level of modern populations and species' (Carroll, 2000).

How might modern evolutionary biologists attempt to reconcile microevolution and macroevolution? One approach is to use theoretical models for asking how microevolutionary processes can generate large morphological changes (e.g., Kirkpatrick, 1982; Lynch, 1990; Hansen & Martins, 1996) or reproductive isolation (e.g., Orr & Orr, 1996; Kondrashov & Kondrashov, 1999; Gavrilets, 2000). Another approach is to ask whether rates of evolution in contemporary populations are consistent with rates in the fossil record (e.g., Losos, Warheit & Schoener, 1997; Reznick et al., 1997). One can also test whether divergence between species is consistent with patterns of genetic variation within species (e.g., Schluter, 1996), and whether microevolutionary processes are responsible for reproductive isolation in natural systems (Schluter, 2000). For example, divergent selection seems the best explanation for reproductive isolation between sympatric threespine sticklebacks (e.g., Rundle et al., 2000) and insect host races (e.g., Filchak, Roethele & Feder, 2000; Via, Bouck & Skillman, 2000).

Several papers in this special issue adopt these approaches. Arnold, Pfrender and Jones (2001) show how neo-Darwinian theory and Simpson's (1944, 1953) concept of the adaptive landscape can be used as a bridge between microevolution and macroevolution. Johnson and Porter (2001) discuss how the gap can be bridged by linking quantitative genetics with the evolution of development. Gingerich (2001) examines evolutionary rates on different time scales and concludes that evolution can be very rapid when stability

is perturbed but that rapid changes will be interspersed by long periods of relative stasis. Kinnison and Hendry (2001) reach a similar conclusion based on rates of contemporary microevolution, suggesting that macroevolution may often accrue as microevolution 'in fits and starts'. Irwin, Irwin and Price (2001) review research on ring species that demonstrates how small sequential changes along geographical clines can lead to species-level differences. Hendry (2001) argues that divergent natural selection has led to the rapid evolution of reproductive isolation between two ecotypes of sockeye salmon. Smith, Schneider and Holder (2001) review work on rainforest vertebrates that suggests natural selection leads to morphological divergence on par with that observed among congeneric species.

Several papers evaluate conditions that might hamper evolutionary diversification. Day (2001) shows how finite interaction groups and population viscosity (i.e., related individuals cluster together) can inhibit diversification otherwise mediated by resource competition. Bell (2001) describes how morphologically divergent and partially reproductively-isolated stickleback populations can evolve within decades but do not persist or become widespread because they are confined to small, ephemeral habitats. Magurran (2001) argues that sexual conflict inhibits the formation of strong reproductive isolation between guppy populations exposed to different predation regimes. Riechert, Singer and Jones (2001) show how high levels of gene flow between riparian and arid-land spider populations ultimately limits genetic divergence in response to natural selection.

Although not everyone would agree, microevolutionary studies generally show that micromutation, genetic drift, and selection are at least *capable* of contributing to macroevolutionary trends. Whether or not microevolution is the major determinant of evolutionary diversification will likely remain a matter of debate because it is unlikely that many (or perhaps even any) clear-cut macroevolutionary events will be observed in real time. The above papers are particularly useful in delineating the conditions under which microevolution is or is not likely to cause large evolutionary changes and reproductive isolation.

Theory and methods

Advances in evolutionary biology are often precipitated by new theoretical developments or methodologies. For example, microevolutionary research has

long been guided by the theoretical population genetics of Fisher (1930), Haldane (1932), Wright (1968), and others. More recently, the conceptual integration of quantitative genetics and natural selection revitalized the study of quantitative traits (Lande & Arnold, 1983). Other examples of influential developments include game theory (Maynard Smith, 1982), phylogenetic comparative methods (Felsenstein, 1985), allozyme electrophoresis (Lewontin, 1974), and molecular genetics (Avisé, 1994).

This issue of *Genetica* includes several theoretical treatments. Arnold, Pfrender and Jones (2001) summarize evolutionary quantitative genetics theory. Agrawal, Brodie and Rieseberg (2001) discuss how genes-of-major-effect can have dramatic transient effects on the genetic variance-covariance matrix. Day (2001) shows how population structure influences evolutionary diversification initiated by resource competition. Lande, Seehausen and van Alphen (2001) examine how sex reversal and sexual selection may lead to sympatric speciation in cichlid fishes. Sinervo (2001) shows how frequency- and density-dependent selection in lizards can drive cycles of female morphs (*r*- vs. *K*-strategists) and male morphs (rock-paper-scissors mating game). Wade (2001) shows how variation in genetic background influences the expression of allelic effects through epistasis. Because genes that function well in conspecific backgrounds but poorly in heterospecific backgrounds are important for post-zygotic reproductive isolation, understanding how epistasis can change the sign of a gene's effect on fitness may help our understanding of speciation. Johnson and Porter (2001) argue for an integration of population genetics and developmental biology into a new evolutionary synthesis.

Several emerging methodologies are examined. Merilä, Sheldon and Kruuk (2001) discuss the 'animal model' approach for quantifying heredity, selection, and evolution in natural populations. Kingsolver, Gomulkiewicz and Carter (2001) describe how to quantify selection and evolution for traits that are functions, 'function-valued traits'. Sheets and Mitchell (2001) review and assess the performance of methods for inferring directional or stabilizing selection from evolutionary time series. Polly (2001) describes the use of morphological variation for examining phylogeographic patterns in extant and extinct organisms.

Despite improvements in our ability to predict and assess evolutionary rate, pattern, and process, we have little reason for complacency. Additional model systems are sorely needed before we can begin to deter-

mine the frequency with which different evolutionary mechanisms have contributed to the diversification of life. Theoretical models have been extremely useful in demonstrating what is and what is not possible through the action of specific evolutionary mechanisms. Future models will continue to be informative as they investigate additional interacting factors, incorporate more realistic biological foundations, and assess the consequences of violating assumptions. New methodologies will allow biologists to answer long-standing questions, as well as questions that have yet to be asked. The study of microevolution is long past its infancy but certainly not long-of-tooth. Many new and exciting systems and ideas have yet to be advanced. Hopefully this volume provides some inspiration for those who might contribute to such advances.

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