

The dynamics of evolutionary stasis

Niles Eldredge, John N. Thompson, Paul M. Brakefield, Sergey Gavrillets,
David Jablonski, Jeremy B. C. Jackson, Richard E. Lenski, Bruce S. Lieberman,
Mark A. McPeck, and William Miller III

Abstract.—The fossil record displays remarkable stasis in many species over long time periods, yet studies of extant populations often reveal rapid phenotypic evolution and genetic differentiation among populations. Recent advances in our understanding of the fossil record and in population genetics and evolutionary ecology point to the complex geographic structure of species being fundamental to resolution of how taxa can commonly exhibit both short-term evolutionary dynamics and long-term stasis.

Niles Eldredge. Division of Paleontology, American Museum of Natural History, Central Park West at Seventy-ninth Street, New York, New York 10024. E-mail: epunkeek@amnh.org

John N. Thompson. Department of Ecology and Evolutionary Biology, A316 Earth and Marine Sciences Building, University of California, Santa Cruz, California 95060. E-mail: thompson@biology.ucsc.edu

Paul M. Brakefield. Institute of Biology, Leiden University, Post Office Box 9516, 2300 RA Leiden, The Netherlands. E-mail: brakefield@rulsfb.leidenuniv.nl

Sergey Gavrillets. Department of Ecology and Evolutionary Biology and Department of Mathematics, University of Tennessee, Knoxville, Tennessee 37996. E-mail: gavril@tiem.utk.edu

David Jablonski. Department of Geophysical Sciences, 5734 South Ellis Avenue, University of Chicago, Chicago, Illinois 60637. E-mail: djablons@midway.uchicago.edu

Jeremy B. C. Jackson. Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92039. E-mail: jbjackson@ucsd.edu

Richard E. Lenski. Center for Microbial Ecology, Michigan State University, East Lansing, Michigan 48824. E-mail: lenski@pilot.msu.edu

Bruce S. Lieberman. Departments of Geology and Ecology and Evolutionary Biology, University of Kansas, 120 Lindley Hall, Lawrence, Kansas 66045. E-mail: blieber@ku.edu

Mark A. McPeck. Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755. E-mail: mark.mcpeek@dartmouth.edu

William Miller III. Department of Geology, Humboldt State University, 1 Harpst Street, Arcata, California 95521. E-mail: wm1@axe.humboldt.edu

Accepted: 17 April 2004

Introduction

The pronounced morphological stability displayed by many fossil species (Eldredge 1971; Eldredge and Gould 1972; Gould and Eldredge 1977; Stanley and Yang 1987; Jackson and Cheetham 1999; Jablonski 2000), often for millions of years, contrasts sharply with the rapid, often adaptive, evolutionary changes documented in many extant species (Reznick et al. 1997; Thompson 1998; Huey et al. 2000; Thomas et al. 2001). If evolutionary change occurs frequently within populations, why is it that in some species so little of it is conserved and translated through time as net change? In this paper we examine what paleobiologists, population geneticists, and evolutionary ecologists have learned about stasis and rapid evolution over the past decade as new approaches

have been adopted and results obtained in all these fields. Our basic conclusion—that stasis derives from the geographic structure and partitioning of genetic information within widespread species—is derived from a consideration of all known population genetic processes that promote (or conversely hinder) genetic change, as well as from analysis of data from the fossil record.

Stasis is generally defined as little or no net accrued species-wide morphological change during a species-lineage's existence up to millions of years—instantly begging the question of the precise meaning of “little or no” net evolutionary change. All well-analyzed fossil species lineages, as would be expected, display variation within and among populations, but the distribution of this variation typically remains much the same even in samples sep-

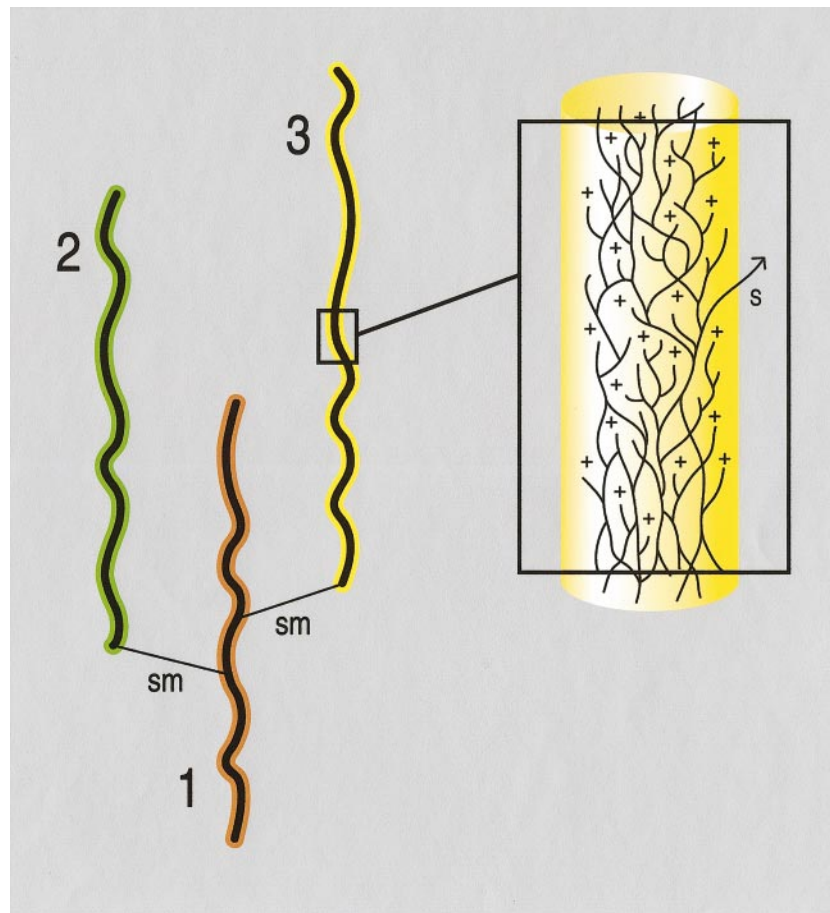


FIGURE 1. Species stasis in the face of ongoing population-level evolution. Species (lineages 1, 2, and 3 on the left) exhibit negligible net phenotypic changes, while their component population systems (on the right) continually differentiate, fuse, or go extinct. Stasis is occasionally broken by establishment and spread of novel phenotypes (*s*); when this is matched with ecological opportunity, highly differentiated new lineages (*sm*) may be formed that eventually develop internal (population) dynamics and geographic structure resulting, again, in stasis. (In this view, species-lineages consist of anastomosing population systems and, at the same time, belong to clades composed of similar lineages).

arated by millions of years (Fig. 1). This view of fossil variation has been reinforced over the past decade as paleontological studies have applied higher sampling intensities in time and space, improvements in both relative and absolute stratigraphic dating, more comprehensive use of multivariate statistical analysis, and better controls for sampling biases.

Although it is now clear that some fossil species lineages do indeed accrue morphological change through time (Geary 1995), it is also now evident that many do not. Well-documented examples of stasis range from Paleozoic brachiopods (Lieberman et al. 1995) to late Cenozoic bivalves (Stanley and Yang

1987) and bryozoans (Jackson and Cheetham 1999). Inventories of evolutionary tempo and mode across entire clades are sparse, but Jackson and Cheetham's (1999) survey of well-documented case studies in the Neogene fossil record found 52 instances of stasis and only two instances of anagenesis in nine benthic macroinvertebrate clades, and eight instances of stasis as opposed to 10–12 instances of anagenesis in marine microplankton. Anagenesis occurs in only eight of 88 trilobite lineages in the Ordovician of Spitsbergen, and in but one of 34 scallop lineages in the northern European Jurassic (Jablonski 2000).

Studies of extant taxa with rich fossil rec-

ords provide mounting evidence that morphologically defined species-level lineages recognized in fossil sequences often correspond to genetically defined species in the modern biota (Jablonski 2000). Such studies are crucial to the demonstration that patterns of stasis in the fossil record constitute a genuine problem for evolutionary theory. Perhaps the most rigorous and detailed of such studies (and one that has proven compelling to population geneticists) are those on tropical American Neogene cheilostome bryozoans (Jackson and Cheetham 1999). Cheilostomes are small, clonal marine animals that grow in plantlike shapes by budding modules (zooids) to form a colony. They are abundant in Recent seas and in the fossil record. In the tropical American genera *Metrarabdotos* and *Stylopoma*, all long-ranging species (11 in each genus) persisted essentially morphologically unchanged for 2–16 Myr. New species appear abruptly in the fossil record, with morphological change occurring within the limits of stratigraphic resolution of sampling (approximately 150,000 years). Studies of extant species in these genera indicate that morphological stasis also reflects stasis in key life history traits, with occasional rapid change. For example, the size of larval brood chambers, which is correlated with larval size, differs by up to twofold among closely related species, and entirely arborescent species have given rise to entirely encrusting species. Such examples show that stasis can include reproductive and behavioral characteristics in addition to pure morphology. We find this example and other such case studies compelling evidence that morphological stasis is a common pattern in the fossil record, which thus requires an examination of how evolutionary and ecological processes can account for it.

If many, perhaps even most, species accrue little morphological change during their lifetimes, then a corollary is immediately raised: the possibility that much of the morphological change accrued within evolutionary lineages over time is concentrated in relatively brief episodes of speciation. Mayr (1954) suggested a link between speciation and evolutionary change, and stasis+morphological change concentrated at speciation events is the core of

punctuated equilibria (Eldredge 1971; Eldredge and Gould 1972). Recently, Webster, Payne, and Pagel (2003), in their analysis of speciation events and underlying genetic change in 56 phylogenies, concluded that “rapid genetic evolution frequently attends speciation,” and that their results provide a “genetic component” to the pattern of stasis and change of morphological traits seen so commonly in the fossil record.

Our purpose here is to explore further the dynamics generating such patterns, particularly insofar as stasis itself is concerned. Given patterns of changes in heritable phenotypic variation and genetic variation commonly seen in local populations, what factors prevent such change from becoming species-wide? Do novelties arise only at speciation, or do they arise but are typically not conserved throughout the history of species—perhaps further suggesting that speciation conserves rather than prompts the generation of novelty? Previous authors (Darwin 1871; Ohta 1972; Futuyma 1987; Eldredge 1989; Lieberman et al. 1995) have discussed the difficulties inherent in conserving evolutionary novelties arising in local populations and their spread over the entire range of a far-flung, heterogeneous species. Futuyma (1987) in particular has discussed the closely related corollary that speciation may be the key to the phylogenetic conservation of such novelties. More recently, the geographic mosaic of ongoing local adaptation has become the very foundation for new views of how coevolving interactions between species persist over long periods of time in a constantly changing world (Thompson 1994, 1999a,b).

What, then, constrains the species-wide spread of evolutionary change when experimental and field data clearly show that the potential for rapid change within populations is nearly always present? We divide the question into three stages related to the establishment of evolutionary change in a geographically heterogeneous world: origin, local population establishment, and species-wide spread. Our analysis of studies from the past decade, including examples drawn from our own work, suggests that patterns and processes related to

geographic structure contribute importantly to the maintenance of stasis.

Origin, Local Population Establishment, and Species-wide Spread

To be preserved in the fossil record with any reasonable likelihood, a novel genotype must originate, become established in a local population, and then spread and increase in numbers across a large geographic area. Failure to complete all three of these stages will result in stasis in the fossil record. Consequently, if we are to understand the evolutionary dynamics of stasis, we need to understand where most failures occur along this sequence of origin and spread of novelty. Many earlier attempts to reconcile our understanding of the evolutionary dynamics of extant species with the paleobiological evidence for stasis focused on the role of genetic constraints and stabilizing selection in preventing the origin and establishment of novelty within local populations (Charlesworth et al. 1982; Van Valen 1982; Levinton 1983; Maynard Smith 1983; Wake et al. 1983; Williamson 1987). More recent mathematical and empirical studies have refined our understanding of the roles of these evolutionary forces, and they have shown that the spatial structure of species strongly influences the pattern of establishment of novel types.

Constraints on the Origin and Local Establishment of Novelty.—From a theoretical perspective, the origin of novel genotypes involves a set of processes (mutation and recombination) distinct from those processes that determine the local fate of the variants that are produced (drift and selection). From an empirical perspective, however, the actual rate of production of novel variants is very rarely observed directly. Instead, the failure to produce novelty, on the one hand, versus the failure of novelties to become locally established, on the other hand, must often be inferred indirectly from the dynamics of experimental systems. Therefore, we combine our analysis of these two dynamical stages in the section that follows.

The simplest potential explanations for stasis are exhaustion of standing genetic variation or the limited production of useful novelties within populations. Even when genetic

variation is present, however, evolutionary potential is not equal in all traits, and the origination of useful novelties may depend upon mutations appearing in a particular sequence (Mani and Clarke 1990). Antagonistic pleiotropy (leading to negative genetic correlations), epistasis, and linkage disequilibrium can all constrain the generation of novel genotypes, even when standing genetic variation is not limited by population size or the previous history of selection (Barton and Partridge 2000). Some artificial-selection experiments have shown that rates of phenotypic change may decelerate during prolonged directional selection (Falconer and Mackay 1996). This pattern has often been attributed to the depletion of the genetic variation for the selected trait that was present in the founding population or, alternatively, depletion of variation in fitness more generally, such as when selection on some other aspect of organismal performance opposes the response to artificial selection (Barton and Partridge 2000; Falconer and Mackay 1996). Consistent with these explanations, response to selection can be accelerated by increasing population size, which both increases the overall level of genetic variation and opens new permissible directions (“ridges”) available to selection in the multi-dimensional adaptive landscape (Weber 1996).

Pronounced decelerations in rates of phenotypic evolution have also been observed over thousands of generations in asexual populations of *Escherichia coli* founded from a single cell (Cooper and Lenski 2000). In these populations, new mutations provide the only source of genetic variation, and this mutational source continues indefinitely. In this case, stasis cannot derive from depletion of preexisting variation, nor from exhaustion of genetic variation more generally. In fact, the amount of genetic variation increased in these populations even as the rate of phenotypic evolution declined (Sniegowski et al. 1997). Instead, these populations evidently approached a local adaptive peak or plateau, at which point most potential (i.e., genetically accessible) beneficial mutations were fixed. Consistent with this explanation, the rate of adaptive evolution was re-accelerated by per-

turbing populations from their proximity to an adaptive peak, either by changing the environment (Travisano et al. 1995) or by introducing deleterious mutations (Moore et al. 2000).

These studies show that relative stasis can arise fairly quickly following periods of rapid adaptive evolution. They also indicate that the exhaustion of beneficial variants—whether preexisting or potentially accessible by mutation—can contribute to stasis. However, the depletion of standing variation is relevant only in small populations, which contribute very little to the fossil record. Species-wide depletion of accessible beneficial mutations requires a degree of environmental constancy that is not typical of the earth's history (Lambeck and Chappell 2001; Zachos et al. 2001).

More likely, genetic and developmental correlations among traits can also influence both the direction and extent of change in local populations, and advances in evolutionary developmental biology are suggesting the extent to which these genetic interactions may influence stasis. For example, some experiments on butterfly wing patterns show that multiple eyespots are made by the same developmental pathway and, consequently, there exist strong genetic correlations among them. Selection to increase the size of the posterior eyespot on the forewing of *Bicyclus anynana*, in the absence of any selection on the anterior eyespot (Beldade et al. 2002), will typically increase the size of both eyespots. Nonetheless, selection can readily uncouple the two eyespots to produce highly divergent morphologies in all directions of morphological space (Fig. 2). Indeed, novel patterns not seen in any related species can be obtained after 25 or so generations. These results indicate that genetic and developmental processes can produce genetic correlations and favor evolution along paths of least resistance, but they need not absolutely constrain the process of adaptive radiation (Brakefield et al. 2003).

In fact, recent studies have revealed a variety of genetic mechanisms that may overcome constraints imposed by gene interaction. Epistatic components of genetic variance may be converted into additive variance, promoting evolutionary change in small, perturbed pop-

ulations (Wade and Goodnight 1998). Environmental stress may disrupt developmental stability sufficiently to uncover latent genetic variance that can promote evolvability (Rutherford and Lindquist 1998). Yet other processes—including gene or genome duplication, polyploidy, hybridization, and horizontal gene transfer—can further promote novel paths of evolution (Rieseberg 1997; Soltis and Soltis 1999; Lynch and Force 2000; Sandstrom et al. 2001). Consequently, it increasingly seems that neither an absence of genetic variation nor genetic constraints are sufficient to account for long-term stasis.

Expression of advantageous genetic variation in highly variable environments, however, may constrain the breaking of stasis within local populations. Recent theoretical studies of multidimensional genotype space have demonstrated the possibility of prolonged phenotypic change within local populations by a chain of substitutions that are nearly neutral with respect to overall fitness in the absence of a highly variable environment (Gavrilets 1997). Only a small proportion of mutations with significant phenotypic effects are expected to be advantageous or even neutral. The more variable the environment over time, the more restricted the range of these genotypes with equal or higher fitness, because each genotype must function under a wide range of environmental conditions.

When stasis breaks down, it may do so either in large or in small populations. Considering both the production of mutations and their subsequent fate, advantageous mutations will become established more often in larger than in smaller populations. An environmental change, by redefining the "optimum" phenotype, may result in increasing the probability of mutations being conditionally advantageous or neutral, thereby promoting evolutionary change. On the other hand, decreasing population size will increase the role of stochastic fluctuations, creating an opportunity to overcome stabilizing selection or incumbency effects (Barton and Charlesworth 1984) and facilitating evolution along an adaptive ridge of genotypes that are nearly equal in fitness (Gavrilets 1999). Strong competition for a resource may potentially lead to sympatric or-

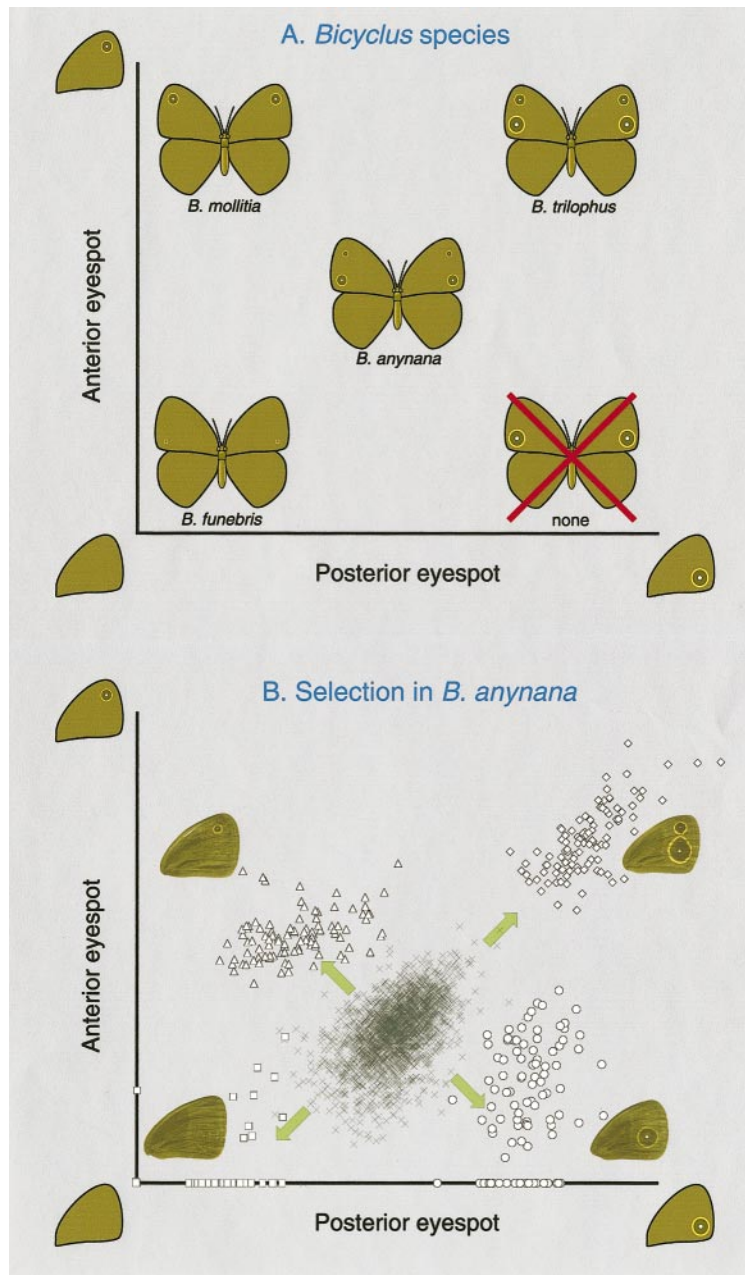


FIGURE 2. Analysis of a potential evolutionary constraint. A, Occupation by species of the butterfly genus *Bicyclus* of morphological space for the pattern of the forewing eyespot size. Names of representatives from among the 80 or so species are given. B, Responses obtained over 25 generations of artificial selection in replicate lines of *B. anynana*. Results show that butterflies similar to each corner pattern were produced from standing genetic variation in a single laboratory stock, including one morphology not seen in any extant species. Crosses indicate butterflies from the base population, and open symbols show samples from generation 25 in each direction of selection (green arrow) together with a representative forewing. Redrawn from Beldade et al. 2002.

igin and within-deme establishment of genetic novelties (Kawata 2002). More complete cessation of gene flow can result in rapid evolutionary change in a population experiencing a novel environment (Garcia-Ramos and Kirkpatrick 1997).

These theoretical expectations on the conditions allowing occasional breakdown of stasis receive support from experimental studies during the past decade. Besides the deceleration in phenotypic evolution found during the long-term experiments in *E. coli* (Lenski and Travisano 1994), both performance and morphology show a stair-step dynamic over shorter periods. Most of the changes in the first 3000 generations were concentrated in a few episodes that appeared instantaneous at a 100-generation sampling interval. These episodes have a simple explanation: each step in performance reflects a selective fixation of a beneficial mutation, and the morphological changes are pleiotropic effects of these mutations.

Rapid diversification of a lineage may therefore often involve the invasion of a new selective environment by one or a few local populations. The breakdown of stasis occurs as a local population adapts rapidly to an initially inhospitable habitat before it would otherwise be driven extinct (Gomulkiewicz and Holt 1995). Rapid, pulsed diversification of some phytophagous insects as they colonize new host taxa in local populations has long been a working model for studies of plant-insect interactions (Ehrlich and Raven 1964). Molecular phylogenetic analyses of insect taxa during the past decade have provided evidence for such bouts of rapid diversification at the bases of clades, as species colonize new host lineages (Pellmyr et al. 1998). Similarly, the occasional invasion by *E. coli* of thermally stressful environments, beyond the tolerance limits of ancestral populations, fits this model (Mongold et al. 2001).

One well-studied example of invasion of a novel environment leading to the breakdown of stasis—and the generation of evolutionary novelty correlated with speciation—is found in the diversification of damselflies. *Enallagma* damselflies have diversified in North America into permanent ponds and lakes with either

fish or large dragonflies as the top predators (McPeck and Brown 2000). *Enallagma* species differ in their vulnerability to these predators and are thus capable of living with only one of them. Species that coexist with fish use crypsis to avoid predators, whereas species that coexist with large dragonflies are more active and swim away from attacking predators (McPeck 1998). Moreover, several *Enallagma* species are found in each lake type, and co-occurring species are phenotypically very similar (McPeck 2000). Lakes with fish are the ancestral habitat for the genus, and at least two independent invasions by damselflies into the dragonfly lake environment have occurred (McPeck and Brown 2000). These habitat shifts have been accompanied by rapid evolution in a number of morphological, behavioral, and biochemical characters that enhance burst swimming speed because of selection imposed by dragonfly predators in the new environment (McPeck 2000; McPeck and Brown 2000). It may have taken the invading lineages only a few hundred years to gain a high degree of local adaptation to their new environment (McPeck 1997).

Such rapid evolutionary change would appear saltatory in the fossil record. In contrast, rates of evolution in these characters within the fish lake environment are very slow. Millions of years of evolution within the fish lake environment have produced few or no differences among species in many other characters that are important in determining their ecological performance (McPeck 2000; McPeck and Brown 2000). Importantly, shifts to dragonfly lakes and accompanying rapid evolution have been rare events, occurring in only one of the two primary clades of *Enallagma*. That clade has a number of phenotypic characters that are already similar to phenotypes favored by selection in dragonfly lakes (McPeck 2000). Hence, there appears to be a fundamental niche conservatism that dooms shifts by most populations to failure, thereby contributing to stasis within many *Enallagma*.

Recent studies therefore suggest that the absence of useful novelties, or their failure to become established within local populations, may contribute to stasis in certain limited cases. But more generally, the field of evolution-

ary ecology has clearly shown the ability of local populations to evolve rapidly under changing conditions. Consequently, species-wide stasis would seem to require additional constraints acting above the level of local populations.

Species-wide Spread.—A key change in population genetic theory and evolutionary ecology over the past decade has been the increasing incorporation of geographic structure into our understanding of the evolutionary dynamics of species. We now know from various genetic modeling approaches that spatial structure can decrease the likelihood of regional extinction, maintain genetic polymorphisms across populations, and shape evolutionary and coevolutionary trajectories (Gandon et al. 1996; Thrall and Burdon 1997; Gomulkiewicz et al. 2000; Nuismer et al. 2000). At the same time, a burgeoning number of studies in molecular ecology and evolutionary ecology reveal even more widespread genetic differentiation among populations than was apparent from earlier studies that often underestimated spatial genetic structure. These modeling and empirical results together suggest that the geographic genetic structure of species must be a central component of any overall theory resolving the discrepancy between short-term dynamics and long-term stasis.

Novel forms must spread beyond their site of origin if they are to have a reasonable chance of being preserved in the fossil record. If a local population is already reproductively isolated from its neighbors, then novel forms must successfully expand beyond their initial geographic limits. Alternatively, if the local population is still genetically connected to other populations, then a novel form must be able to spread across those other populations if it is to become sufficiently widespread to leave a record of the change. In both cases the key problem is expansion of geographic range (Kirkpatrick and Barton 1997; Thomas et al. 2001). We now know that, even once established locally, novel forms may face large hurdles in spreading beyond their site of origin.

These spatially induced hurdles may be the most potent evolutionary forces maintaining stasis. Established species often have an in-

trinsic advantage over invaders because they occur at high relative frequency or density (Gomulkiewicz and Holt 1995; McPeck 2000). The incumbency of established species can be further maintained through effects on hybrids. Recent mathematical models show that if hybrids between the novel and incumbent forms have reduced fitness, then the chance of spread of the novel form is further reduced (Gavrilets 1996; Coyne et al. 1997). Moreover, through asymmetric gene flow most hybrids are likely to occur within the population where the novel genotype originated, because the absolute numbers will often be less than surrounding populations. This asymmetric gene flow will therefore minimize the chance that a novel form will rise to high frequencies elsewhere.

The development of metapopulation theory (Hanski and Gilpin 1997) has provided yet additional insights into the problem of spread in novel forms (Lande 1985; Tachida and Ilizuka 1991). Some current models suggest that high population turnover rates can reduce the chances of establishment and spread of novel genotypes, unless those genotypes are favored by their very rarity through negative frequency-dependent selection as occurs in gene-for-gene coevolution between some plants and pathogens (Burdon and Thrall 1999; Gandon et al. 1996). This kind of negative frequency-dependent selection, which maintains polymorphisms by favoring rare genotypes within and among populations, may also maintain stasis within a species rather than lead to diversification. When metapopulation structure is coupled with heterogeneous selection across landscapes, it may become even more difficult for novel genotypes to spread.

Paleobiologists have argued that widespread species are expected to exhibit slower rates of species-wide evolution than species with small ranges, because natural selection will not be consistently directional across space and time (Eldredge 2003; Jablonski 2000; Lieberman et al. 1995)—e.g., ecological conditions acting on local populations of American robins in the southwestern United States are clearly different from those present in the deep woodlands of the Northeast. That

overall expectation is supported by population genetic theory, which suggests that it is difficult for a mutant to be advantageous under all conditions required by a highly heterogeneous environment (Ohta 1972). Consistent with the expectation that most mutations that are locally adaptive would not be globally advantageous, lines of *E. coli* adapted to a glucose-containing environment for 20,000 generations tend to have reduced performance on a range of other substrates (Cooper and Lenski 2000).

The developing mathematical theory of species ranges provides additional indications that the spatial structure of habitats and heterogeneous selection may be important sources of stasis. Gene flow from the center of a species range can impede novel adaptation at the periphery and prevent the range from expanding outward (Kirkpatrick and Barton 1997). The problems of spatial structure and heterogeneous selection may therefore contribute to the kind of sustained habitat tracking found in the fossil record (Eldredge 2003). Data from several paleontological studies on Pleistocene plants (Davis 1983), beetles (Coope 1979), foraminifera (Bennett 1990), and mollusks (Valentine and Jablonski 1993) have demonstrated little morphological response to protracted climate change. Instead, geographic distributions changed. Species tended to survive, usually with little or no discernible morphological change, as long as recognizable habitats could be tracked. That does not mean that natural selection is not acting (Davis and Shaw 2001; Hoekstra et al. 2001), as the data from population and evolutionary genetics show that populations are constantly under selection. Rather, it means that selection often acts in ways that favor populations that are evolutionarily conservative at the species level.

The geographic mosaic of coevolution may also contribute to species-wide stasis, even though coevolution is one of the evolutionary forces most commonly thought to generate novelty. Studies over the past decade have indicated that selection mosaics, coevolutionary hotspots, and gene flow can combine to create extensive coevolutionary dynamics (Thompson 1994, 1997, 1999a). This ongoing coevolution creates local novelty and is undoubt-

edly important to the ecological dynamics of species. Moreover, it may be crucial for keeping coevolving species in the evolutionary game as one species or the other temporarily gains the upper hand in different environments. But most of these dynamics may not result in much net change at the species level. Recent mathematical models have indicated that geographically structured coevolution can actually constrain the escalation of antagonistic arms races. These interactions may continually recycle defenses and counterdefenses through frequency-dependent selection, because geographic structure may maintain the polymorphisms on which frequency-dependent selection depends (Gandon et al. 1996; Gomulkiewicz et al. 2000; Nuismer et al. 2000). Long-term studies of gene-for-gene coevolution within natural populations support this mathematical prediction (Burdon and Thrall 2000). Similarly, geographic structure may stabilize some kinds of coevolved mutualisms, by maintaining previously fixed traits in the face of moderate gene flow (Nuismer et al. 2000). As a result, the geographic mosaic of coevolution may often create ongoing genetic dynamics embedded within longer-term stasis, with populations only rarely breaking through in fundamentally novel directions.

Increasingly detailed paleontological studies corroborate the potential importance of spatial structure in maintaining stasis. Moreover, the great strength of paleontological data is that within-population variation can be compared over time as well as space, allowing analysis of the importance of the spatial structuring of species throughout a species' history. Analysis of two broadly distributed species lineages of Devonian brachiopods highlights the significance of spatial structuring within species to the generation of patterns of stasis and change (Lieberman et al. 1995). Statistical analysis revealed no discernible net change in the morphology of either species over their respective five-million-year histories. However, within any single environment, large morphological shifts did occur—larger, in fact, than the net morphological change across the entire environmental distribution of the species over the same time period (Fig. 3). As these changes were in different directions in different en-

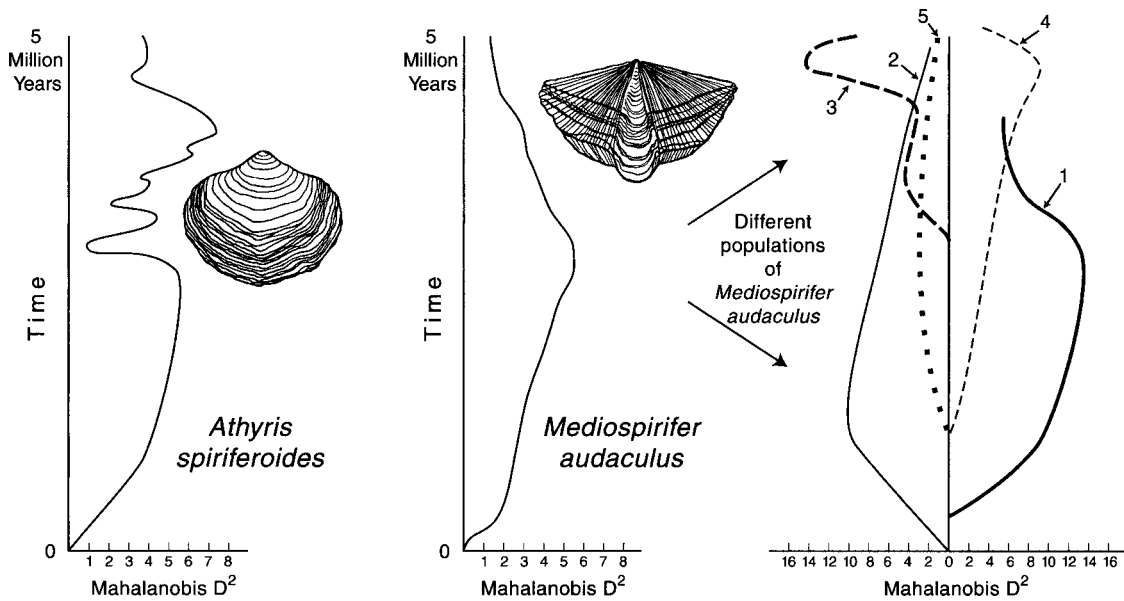


FIGURE 3. Schematic diagram showing temporal and environmental (spatial) patterns of morphological change in two species of Middle Devonian brachiopods, measured as Mahalanobis D^2 values from canonical discriminant analysis of morphometric data. Each of these species occurred in five distinct environments over a period of 5 Myr. Note the oscillatory nature of morphological change in each species (left and middle panels). The morphological changes of *Mediospirifer audaculus* sampled from the five distinct environments (far right panel) are also oscillatory, but have larger D^2 distance excursions than when samples of the species are lumped as a whole (see middle panel). Moreover, changes within individual environments tend to cancel out, leading to negligible net change for the species as a whole.

vironments, they tended to cancel out, resulting in no net change: stasis resulted at least in part from a species' presence in several distinct environments (Lieberman et al. 1995; Lieberman and Dudgeon 1996).

These results agree with the expectation that spatial structuring of widespread species will, as a rule, lead to stasis—but that local populations, under certain conditions, can be expected to develop more substantial amounts of morphological change in the short term. They further suggest that the patterns of generally fluctuating change documented by Gingerich (1976) in Eocene mammals and Sheldon (1987) in Ordovician trilobites reflect the evolutionary histories of geographically localized populations of these species. Gingerich's data involved meticulously collected time series from the Bighorn Basin of Wyoming, a localized subset of the regions over which the *Hyopsodus* and other species have been documented to have lived. Likewise, Sheldon's study of eight trilobite lineages from the Builth Inlier of Wales did not include sub-

stantial geographic sampling. Both of these data sets contain examples of short-term evolutionary change that is repeatedly reversed over longer timescales (Gingerich 1983)—much like the fluctuations in beak morphology in Galapagos finches (Grant 1986) and in floral color of desert plants (Schemske and Bierzychudek 2001). Thus, the entire spatio-temporal history of a species can reveal less net change than what is documented in temporal or geographic subsets of a species lineage.

Conclusions

Both theoretical and empirical studies of the past decade suggest that the complex pattern of selection imposed on geographically structured populations by heterogeneous environments and coevolution can paradoxically maintain stasis at the species level over long periods of time. By contrast, neither lack of genetic variation nor genetic and developmental constraint is probably sufficient in and of itself to account for species-wide stasis.

Further resolution of our understanding of the dynamics of evolutionary stasis will require novel integration of modeling and empirical analyses. Comparison of rates of gradual change in widespread versus endemic species will help us better test our conclusion that geographic range shapes stasis. Such analyses of the genetic and geographic structure of species when placed within a phylogenetic context will help us further test the relative contributions of geographic structure, underlying genetic variation, and development to the ongoing dynamics of stasis.

Remaining issues include finer resolution of the issue of conservation versus generation of novelty in short bursts of speciation, and the possibility that many such bursts of speciation are spatiotemporally correlated among sympatric lineages in regional ecological settings. Such bursts could reflect "turnovers" (Vrba 1985) or the events between episodes of "coordinated stasis" (Brett and Baird 1995), reflecting spatiotemporal scales intermediate to local ecological succession, on the one hand, and the well-documented evolutionary responses to episodes of global mass extinctions on the other (Eldredge 2003). And what dynamic processes underlie the emergence of stable species (Miller 2003)? The solution to these and related problems will demand further integration of the fields of evolutionary ecology and evolutionary developmental biology into evolutionary genetic and paleontological approaches.

Acknowledgments

This work was conducted as part of the Ecological Processes and Evolutionary Rates Working Group supported by National Center for Ecological Analysis and Synthesis at University of California, Santa Barbara (NSF DEB-94-21535); and by National Science Foundation support to J.N.T., D.J., R.E.L., B.S.L., M.A.M., S.G.; Human Frontiers Science Program support to P.M.B.; and National Institutes of Health support to S.G. We thank D. J. Futuyma for discussion, and C. Thomas, J. Valentine, and anonymous reviewers for comments on the manuscript.

Literature Cited

- Barton, N. H., and B. Charlesworth. 1984. Genetic revolutions, founder effects, and speciation. *Annual Review of Ecology and Systematics* 15:133–164.
- Barton, N. H., and L. Partridge. 2000. Limits to natural selection. *BioEssays* 22:1075–1084.
- Beldade, P., K. Koops, and P. M. Brakefield. 2002. Developmental constraints versus flexibility in morphological evolution. *Nature* 416:844–847.
- Bennett, K. D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16:11–21.
- Brakefield, P. M., V. French, and B. J. Zwaan. 2003. Development and the genetics of evolutionary change within insect species. *Annual Review of Ecology, Evolution and Systematics* 34:633–660.
- Brett, C. E., and G. Baird. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. Pp. 285–315 in R. Anstey and D. H. Erwin, eds. *Speciation in the fossil record*. Columbia University Press, New York.
- Burdon, J. J., and P. H. Thrall. 1999. Spatial and temporal patterns in coevolving plant and pathogen associations. *American Naturalist* 153:S15–S33.
- . 2000. Coevolution at multiple spatial scales: *Linum marginale-Melampsora lini*—from the individual to the species. *Evolutionary Ecology* 14:261–281.
- Charlesworth, B., R. Lande, and M. Slatkin. 1982. A neo-Darwinian commentary on macroevolution. *Evolution* 36:474–498.
- Coope, G. R. 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography and ecology. *Annual Review of Ecology and Systematics* 10:247–267.
- Cooper, V. S., and R. E. Lenski. 2000. The population genetics of ecological specialization in evolving *E. coli* populations. *Nature* 407:736–739.
- Coyne, J. A., N. H. Barton, and M. Turelli. 1997. A critique of Sewall Wright's shifting balance theory of evolution. *Evolution* 51:643–671.
- Darwin, C. D. 1871. *The descent of man, and selection in relation to sex*. John Murray, London.
- Davis, M. 1983. Quaternary history of deciduous forests of eastern North America and Europe. *Annals of the Missouri Botanical Garden* 20:550–563.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673–679.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608.
- Eldredge, N. 1971. The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156–167.
- . 1989. *Macroevolutionary dynamics: species, niches and adaptive peaks*. McGraw-Hill, New York.
- . 2003. The sloshing bucket: how the physical realm controls evolution. Pp. 3–32 in J. Crutchfield and P. Schuster, eds. *Evolutionary dynamics: exploring the interplay of selection, accident, neutrality, and function* (SFI Studies in the Sciences of Complexity Series). Oxford University Press, New York.
- Eldredge, N., and S. J. Gould. 1972. Punctuated equilibrium: an alternative to phyletic gradualism. Pp. 82–115 in T. J. M. Schopf, ed. *Models in paleobiology*. Freeman, Cooper, San Francisco.
- Falconer, D. S., and T. Mackay. 1996. *Introduction to quantitative genetics*, 4th ed. Longman, London.
- Futuyma, D. J. 1987. On the role of species in anagenesis. *American Naturalist* 130:465–473.
- Gandon, S., Y. Capowiez, Y. Dubois, Y. Michalakis, and I. Olivieri. 1996. Local adaptation and gene-for-gene coevolution in

- a metapopulation model. *Proceedings of the Royal Society of London B* 263:1003–1009.
- Garcia-Ramos, G., and M. Kirkpatrick. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51:21–28.
- Gavrilets, S. 1996. On phase three of the shifting-balance theory. *Evolution* 50:1034–1041.
- . 1997. Evolution and speciation on holey adaptive landscapes. *Trends in Ecology and Evolution* 13:307–312.
- . 1999. A dynamical theory of speciation on holey adaptive landscapes. *American Naturalist* 154:1–22.
- Geary, D. H. 1995. The importance of gradual change in species-level transitions. Pp. 67–86 in D. H. Erwin and R. L. Anstey, eds. *New approaches to speciation in the fossil record*. Columbia University Press, New York.
- Gingerich, P. D. 1976. Paleontology and phylogeny: patterns of evolution at the species level in Early Tertiary mammals. *American Journal of Science* 276:1–28.
- . 1983. Rates of evolution: effects of time and temporal scaling. *Science* 222:159–161.
- Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? *Evolution* 49:201–207.
- Gomulkiewicz, R., J. N. Thompson, R. D. Holt, S. L. Nuismer, and M. E. Hochberg. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. *American Naturalist* 156:156–174.
- Gould, S. J., and N. Eldredge. 1977. Punctuated equilibrium: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115–151.
- Grant, P. R. 1986. *Ecology and evolution of Darwin's finches*. Princeton University Press, Princeton, N.J.
- Hanski, I., and M. E. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego.
- Hoekstra, H. E., J. M. Hoekstra, D. Berrigan, S. N. Vignieri, A. Hoang, C. E. Hill, P. Beerli, et al. 2001. Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences USA* 98:9157–9160.
- Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287:308–309.
- Jablonski, D. 2000. Micro- and macroevolution scale and hierarchy in evolutionary biology and paleobiology. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):15–52.
- Jackson, J. B. C., and A. H. Cheetham. 1999. Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* 14: 72–77.
- Kawata, M. 2002. Invasion of vacant niches and subsequent sympatric speciation. *Proceedings of the Royal Society of London B* 269:55–63.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *American Naturalist* 150:1–23.
- Lambeck, K., and J. Chappell. 2001. Sea level change through the last glacial cycle. *Science* 292:679–686.
- Lande, R. 1985. The fixation of chromosomal rearrangements in a subdivided population with local extinction and colonization. *Heredity* 54:323–332.
- Lenski, R. E., and M. Travisano. 1994. Dynamics of adaptation and diversification: a 10,000-generation experiment with bacterial populations. *Proceedings of the National Academy of Sciences USA* 91:6808–6814.
- Levinton, J. S. 1983. Stasis in progress: the empirical basis of macroevolution. *Annual Review of Ecology and Systematics* 14: 103–137.
- Lieberman, B. S., and S. Dudgeon. 1996. An evaluation of stabilizing selection as a mechanism for stasis. *Palaeogeography, Palaeoclimatology and Palaeoecology* 127:229–238.
- Lieberman, B. S., C. E. Brett, and N. Eldredge. 1995. A study of stasis and change in two species lineages from the Middle Devonian of New York State. *Paleobiology* 21:15–27.
- Lynch, M., and A. Force. 2000. The probability of duplicate gene preservation by subfunctionalization. *Genetics* 154:459–473.
- Mani, G. S., and B. C. C. Clarke. 1990. Mutational order: a major stochastic process in evolution. *Proceedings of the Royal Society of London B* 240:29–37.
- Maynard Smith, J. 1983. The genetics of stasis and punctuation. *Annual Review of Genetics* 17:11–25.
- Mayr, E. 1954. Change of genetic environment and evolution. Pp. 157–180 in J. Huxley, A. C. Hardy, and E. B. Ford, eds. *Evolution as a process*. Allen and Unwin, London.
- McPeck, M. A. 1997. Measuring phenotypic selection on an adaptation: lamellae of damselflies experiencing dragonfly predation. *Evolution* 51:459–466.
- . 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* 68:1–23.
- . 2000. Predisposed to adapt: clade-level differences in characters affecting swimming performance in damselflies. *Evolution* 54:2072–2080.
- McPeck, M. A., and J. M. Brown. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies of eastern North American waters. *Ecology* 81:904–920.
- Miller, W., III. 2003. A place for phyletic evolution within the theory of punctuated equilibria: Eldredge pathways. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 2003: 463–476.
- Mongold, J. A., A. F. Bennett, and R. E. Lenski. 2001. Evolutionary adaptation to temperature. VII. Extension of the upper thermal limit of *Escherichia coli*. *Evolution* 53:386–394.
- Moore, F. B.-G., D. E. Rozen, and R. E. Lenski. 2000. Pervasive compensatory adaptation in *Escherichia coli*. *Proceedings of the Royal Society of London B* 267:515–522.
- Nuismer, S. L., J. N. Thompson, and R. Gomulkiewicz. 2000. Coevolutionary clines across selection mosaics. *Evolution* 54: 1102–1115.
- Ohta, T. 1972. Population size and rate of evolution. *Journal of Molecular Evolution* 1:305–314.
- Pellmyr, O., J. Leebens-Mack, and J. N. Thompson. 1998. Herbivores and molecular clocks as tools in plant biogeography. *Biological Journal of the Linnean Society* 63:367–378.
- Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1936.
- Rieseberg, L. H. 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics* 28:359–389.
- Rutherford, S. L., and S. Lindquist. 1998. Hsp90 as a capacitor for morphological evolution. *Nature* 396:336–342.
- Sandstrom, J. P., J. A. Russell, J. P. White, and N. A. Moran. 2001. Independent origins and horizontal transfer of bacterial symbionts of aphids. *Molecular Ecology* 10:217–228.
- Schemske, D. W., and P. Bierzychudek. 2001. Evolution of flower color in the desert annual *Linanthus parryae*: Wright revisited. *Evolution* 55:1269–1282.
- Sheldon, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. *Nature* 330:561–563.
- Sniegowski, P. D., P. J. Gerrish, and R. E. Lenski. 1997. Evolution of high mutation rates in experimental populations of *Escherichia coli*. *Nature* 387:703–705.
- Soltis, D. E., and P. S. Soltis. 1999. Polyploidy: recurrent formation and genome evolution. *Trends in Ecology and Evolution* 14:348–352.
- Stanley, S. M., and X. Yang. 1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. *Paleobiology* 13:113–1119.
- Tachida, H., and M. Ilizuka. 1991. Fixation probability in spatially changing environments. *Genetical Research* 58:243–251.

- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581.
- Thompson, J. N. 1994. *The coevolutionary process*. University of Chicago Press, Chicago.
- . 1997. Evaluating the dynamics of coevolution among geographically structured populations. *Ecology* 78:1619–1623.
- . 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13:329–332.
- . 1999a. The evolution of species interactions. *Science* 284: 2116–2118.
- . 1999b. Coevolution and escalation: are ongoing coevolutionary meanderings important? *American Naturalist* 153: S92–S93.
- Thrall, P. H., and J. J. Burdon. 1997. Host-pathogen dynamics in a metapopulation context: the ecological and evolutionary consequences of being spatial. *Journal of Ecology* 85:743–753.
- Travisano, M., J. A. Mongold, A. F. Bennet, and R. E. Lenski. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution. *Science* 267:87–90.
- Valentine, J. W., and D. Jablonski. 1993. Fossil communities: compositional variation at many time scales. Pp. 341–349 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Van Valen, L. M. 1982. Integration of species: stasis and biogeography. *Evolutionary Theory* 6:99–112.
- Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* 81:229–236.
- Wade, M. J., and C. J. Goodnight. 1998. The theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. *Evolution* 52:1537–1553.
- Wake, D. B., G. Roth, and M. H. Wake. 1983. On the problem of stasis in organismal evolution. *Journal of Theoretical Biology* 101:211–224.
- Weber, K. E. 1996. Large genetic change at small fitness cost in large populations of *Drosophila melanogaster* selection for wind tunnel flight: rethinking fitness surfaces. *Genetics* 144:205–213.
- Webster, A. J., R. J. H. Payne, and M. Pagel. 2003. Molecular phylogenies link rates of evolution and speciation. *Science* 301: 478.
- Williamson, P. G. 1987. Selection or constraint? A proposal on the mechanism for stasis. Pp. 129–142 in K. S. W. Campbell and M. F. Day, eds. *Rates of evolution*. Allen and Unwin, London.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trend, rhythms, and aberrations in global climates 65 Ma to present. *Science* 292:686–693.