

# How Universal Is Natural Selection?

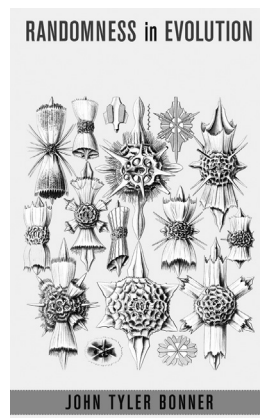
**Randomness in Evolution.** John Tyler Bonner. Princeton University Press, 2013. 148 pp., illus. \$27.95 (ISBN 9780691157016 cloth).

**Relentless Evolution.** John N. Thompson. University of Chicago Press, 2013. 512 pp., illus. \$35.00 (ISBN 9780226018751 paper).

**A**mong evolutionary biologists, there has been considerable argument about how universal and powerful natural selection is. Is every phenotypic and genetic characteristic of every species an adaptation, honed by a history of selection? Many biologists, especially those who study organisms, are prone to an affirmative, “adaptationist” answer (e.g., Reeve and Sherman 1993). Others have objected. After lengthy controversy, Kimura’s (1983) neutral theory of molecular evolution was accepted as accounting for some evolution of DNA sequences; Gould and Lewontin’s (1979) famous critique of adaptationism, especially in the morphological realm, remains controversial; Lynch (2007) proposed that much of genome evolution has resulted from random processes (e.g., genetic drift). *Randomness in Evolution* and *Relentless Evolution* are a study in contrast between the neutralist and adaptationist positions.

In *Randomness in Evolution*, John Tyler Bonner, who has contributed to developmental and evolutionary biology for more than six decades, builds on two of his previous books, *Size and Cycle* (1965) and *The Evolution of Complexity* (1988). He argues that the evolution of larger size necessitates increased complexity, which entails prolonged development, during which “internal selection” operates to expunge most mutations. Therefore, the morphology of “large” (apparently meaning multicellular) organisms is governed by natural selection. In contrast, he proposes that “small” organisms

(specifically, unicellular eukaryotes) are largely free of such internal selection, because they do not undergo such development, and so their morphologies evolve nonadaptively—by mutation and random genetic drift.



Bonner cheerfully agrees that this is his “just-so” story, complementing similarly speculative adaptationist stories, and that his hypothesis is difficult to test. Although his short essay is largely free of data—or indeed of evidence—he cites two major observations that he interprets as support for his idea. One is that many species of related, morphologically diverse protists (e.g., radiolarians, diatoms) coexist, and he cannot imagine that their morphologies are adaptations to different niches or natural enemies; that is, they are “neutral” with respect to one another. The other observation, based largely on the fossil record, is that some of these morphologies are very old, and he interprets the lack of change in such cases as “consistent with the idea that they might be neutral phenotypes” (p. 46).

As far as I know (i.e., not far), little research has been done on the functional morphology of protists such as radiolarians or on their adaptations or their ecology. Nevertheless, although Bonner’s thesis is intriguing, I am highly skeptical of it. Consider

his argument from the coexistence of morphologically different species, in view of model studies on large organisms. When studied in detail, species of such organisms often prove to differ subtly in their ecology (as MacArthur famously showed in 1958 for species of warblers), and slight morphological differences are often shown to be affected by selection. Do any comparable studies of protists bear on Bonner’s proposition? Some ecologists are prepared to accept Hubbell’s (2001) neutral model for the coexistence of hundreds of species of trees in tropical rainforests, but few botanists would argue that their diverse morphologies have evolved entirely by genetic drift. A critical point, moreover, is that selection operates through fitness differences between ancestral and derived characters *within* species lineages; whether it produces competitively equal species does not bear on the question. Hubbell (2006), in fact, developed a model in which large numbers of coexisting species evolve to be ecologically equivalent!

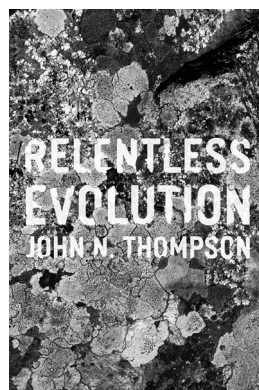
Bonner’s argument from long-term stasis is even weaker, I believe, because stasis actually contradicts his hypothesis. Population genetic theory tells us that if mutation generates neutral variation in a character, the mean will vary (drift) over time; it cannot remain fixed in a finite population. Indeed, fossil lineages of radiolarians show phenotypic variance within populations and change in the mean over time (Kellogg 1975, Lazarus 1983). If a character is capable of varying (as it clearly is, if it varies among related species), stasis requires a stabilizing factor, and some form of selection must be the leading hypothesis. (Of course, selection may act through pleiotropic effects of genes, not necessarily on the observed character itself; see Dobzhansky 1956.) Although I think Bonner’s hypothesis is wrong, if he stimulates research on the causes of the exquisite—and

exquisitely diverse—morphologies of diatoms or of the radiolarians that he reproduces from Haeckel's (1887) monograph, his provocative proposition will have been very useful.

The slightly odd title of John N. Thompson's *Relentless Evolution* conveys his conviction that many or most species undergo almost unceasing evolution—specifically, evolution by natural selection. Thompson has been a major figure in evolutionary ecology for more than three decades and is a leading authority on the coevolution of interacting species. He has become especially well known for his geographic mosaic theory (GMT) of coevolution, which holds that different geographic populations of a species interact with different sets of other species and consequently experience different sources and directions of selection. The dynamics of gene flow and divergent selection among the populations has important effects: Some populations may be suboptimally adapted (as in generalized population genetic models of selection opposed by gene flow); some may frequently evolve as their biotic environment changes; and the species, as a whole, seldom evolves in any one direction, because its constituent populations have different optima. Appearing 8 years after Thompson's (2005) book on that theme, this new—and I think his best—book is a grand synthesis with a majestic sweep, drawing on about 1800 literature references that range from population genetics and genome evolution to community and ecosystem ecology.

Thompson's arguments rest on the GMT and on the great and growing body of evidence that many characteristics evolve rapidly within populations, on the basis of a combination of strong selection and abundant genetic variation. He proposes that natural selection is strong and ubiquitous, largely because of interactions with other species; that most populations are evolving almost constantly but that selection fluctuates, so that sustained directional evolution is rare; and that continuing evolution is necessary for

populations to persist. Moving to longer-term evolution, he ventures that *ecological speciation* (i.e., the evolution of reproductive isolation driven by divergent natural selection on populations in different environments) is the most frequent mode of speciation and is often very rapid, that adaptive radiations are caused by adaptation to diverse interspecific interactions and can emerge from the selection mosaic, and that certain processes of coevolution can lead to the formation of larger networks—or *webs*—of interaction among species. For example, he suggests, mutualisms among free-living species (e.g., plants and their pollinators) may act as “vortices” as more and more species become adapted, often convergently, to interact with a given species or set of similar species. Predators and prey may undergo “coevolutionary alternation,” a frequency-dependent process at the species level, in which predators shift and become adapted to new, less well-defended prey species as their primary prey evolve more-effective defenses—a process that may continue indefinitely as predators shift in their specialization from one prey species to another. Large webs foster the evolution of new ways of life, taking advantage of the resources constituted by sets of similar species.



Some of these conclusions recast familiar propositions in evolutionary theory. It is well known, for example, that maladaptation may result from gene flow between divergently selected populations, and a consumer or mutualist is likely to specialize on a resource

that is abundant or poses little defensive barrier to exploitation. The idea that different populations may adapt to different interacting species—and give rise to an adaptive radiation if they speciate—sounds more novel than it is. As a supporting example, Thompson writes that “the radiation of prodoxid moths has been driven to a large extent by shifts onto novel host plant species” (p. 332), but this is one of the best known patterns in the evolution of phytophagous insects, which are poster children for ecological speciation.

There are a few topics that I think Thompson might profitably have explored further. One is his reconciliation of “relentless” evolution with the stasis in fossil lineages that Eldredge and Gould (1972) so usefully brought to our attention. Thompson describes the remarkable discovery by Uyeda and colleagues (2011) that divergence (in body size) among lineages accumulates only after the lineages have been separated for a million years or so, but he does not suggest why divergence should increase only then. I offer that this pattern may be related to his conclusion that species, as a whole, are likely to display stasis if their constituent populations, knitted together by gene flow, are adapting to different biotic environments (such as different hosts or prey). Consider what would occur if one such population, adapted to a specific host or prey, were to evolve reproductive isolation from the other populations. The adaptations of the newborn species would no longer be compromised by gene flow from divergently adapted populations; they could be perfected, and the refined, divergent character could be retained for the life of the species, which could indeed spread geographically to wherever its resources occur without losing its distinctive character by interbreeding. This process is inherent in Thompson's suggestion that a widespread species could be the progenitor of an adaptive radiation. Because evidence suggests that, in many groups of animals, speciation is completed only after a million years or more (Coyne and Orr 2004), it is

plausible that the “million-year wait for evolutionary bursts” (Uyeda et al. 2011) marks the role of speciation in enabling long-lasting divergence to occur (see Futuyma 1987, 2010).

In treating limitations on adaptations, Thompson acknowledges the existence of internal (genetic or developmental) constraints but tends to favor trade-offs, such as the allocation of resources and the conflicting selection pressures that may arise, especially from interacting with different species. His emphasis, consistent with his cheerful optimism, is therefore on standing genetic variation, ubiquitous and effective selection, and the ready capacity of populations to adapt rapidly to fluctuating circumstances. He does not discuss the gloomy fact that almost every species that has ever existed is extinct, nor, in general, does he treat the question of when populations can avert extinction by adapting to large or sustained environmental changes.

A large change that is abrupt or rapid may be met only if genetic variation in critical characteristics is great enough (Gomulkiewicz and Holt 1995). Adaptation to sustained change eventually exhausts genetic variation, after which the rate of adaptation depends on the rate at which variation is generated by mutation (Lynch and Lande 1993). The geographic distribution, ecological distribution, and persistence of a species often depend on whether a key character is readily evolvable. For instance, the range and abundance of the Kirtland's warbler (*Setophaga kirtlandii*) and the golden-cheeked warbler (*Setophaga chrysoparia*) have declined with the availability of special resources that each bird species requires for nesting: mature jack pines in one case, the bark of a certain species of juniper in the other. Neither species has shown any hint of changing its nesting habits as its habitat has dwindled. If the inflexibility in behavior, apparent for a single feature, might doom a species, what fraction of species can we expect to adapt to rapid, sustained global warming when changes not only in the thermal regime but also in rainfall, in the seasonal

match of species' phenology to their resources, and in the constellation of predators, pathogens, and competitors may require concurrent evolution of a host of characteristics? When is relentless evolution not enough?

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The rich content of this book, however, more than compensates for any omissions. Thompson incarnates theory and hypothesis with substantive reviews of the evidence on countless points. Variation in pathogen resistance among temporal samples of *Daphnia* resurrected from resting eggs illustrates ongoing, relentless coevolution. Polyploidy can affect diverse traits and, consequently, interactions with other species. Genes involved in detecting and enhancing immunity to pathogens show some of the strongest selection in human history. The microbial assemblages within animals show signs both of coevolution among microbe species and adaptation to the host. Primate poxviruses have undergone episodic selection on a gene whose product escapes immune recognition by mimicking a host protein, whereas in primates, the key enzyme that acts on this protein has evolved to distinguish the animal's own protein from the viral mimic. The structure of a web of interactions among plants and ants in Mexico remained similar for a decade, even though new species of both invaded during this time. These and countless other citations make *Relentless Evolution* a review of much of evolutionary ecology.

More important, Thompson and his collaborators have extended the key ideas in interesting and sometimes surprising directions. I was intrigued, for example, by his suggestion that “cospeciation should be uncommon in truly coevolving species” (p. 336) and by models in which the fitness of a parasite is found to be inversely proportional to the fraction of the host's range that it occupies. Thompson convincingly argues that focusing on directional long-term evolution, especially directional coevolution, misses important ecological and evolutionary dynamics. He proposes that ecological dynamics are often affected by rapid evolution, a possibility that has been almost entirely neglected by ecologists until recently. Noting that most plants interact with mycorrhizal fungi, endophytic fungi, pollinators, and—often—seed-dispersing animals, he suggests that “the evolutionary rate of a plant population depends on the combined evolution of all these species and their interactions” (p. 97). (He might have included herbivores and their natural enemies, such as parasitoids that use plant cues to find their victims.)

Thompson's principal conclusions, concisely summarized in the final chapter, are generally convincing and are certainly worthy of further testing. I have little doubt that species interactions account for considerable ongoing evolution and for much of the diversity of species' traits. Fluctuating selection within populations, together with variation among populations linked by gene flow, surely accounts for much of the stasis described by paleontologists, which, on close examination, resolves into constant low-amplitude fluctuation in morphology (Charlesworth 1984). Species interactions (including not only competition but also predation and mutualism) probably play a large role in spurring adaptive radiation. Many of the links in food webs stem from fortuitous “preadaptation” to newly encountered species, rather than coevolution *ab origine* (Janzen 1980), but ecological webs are also built by the evolution of new interactions, usually among multiple species rather

than specialized pairwise associations. It would be good to know more of the details, and indeed the ubiquity, of these points, which in broad outline can hardly be doubted. But, although it is clear that natural selection is often strong and adaptive evolution often rapid, it is less clear how likely it is to avert extinction, especially the anthropogenic mass extinction that, I fear, is already under way.

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