Biology's Theoretical Kudzu: The Irrepressible Illusion of Teleology

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Is adaptation a tautology, or even real? Is teleology inevitable and necessary to life? Possibly.

The Argument from Design is a favorite weapon with which to whip evolutionary biologists and give aid and comfort to religious views on the nature of life. The idea that complex structures could not have gotten here just by chance comes in many flavors: *teleology* (that a structure evolved towards some end objective), *vitalism* (that living matter contains an immaterial inner guiding force), or *animism* (that all matter contains such a force). Is somebody in there? Out there?

Most biologists would never be caught (sober) endorsing such metaphysical views, and darwinism vigorously defends natural selection as a plausible and *sufficient* explanation for biological order. Yet ever since *Origin of Species* was published, prominent biologists, awed by wondrous and exquisite fits between organisms and their environment, have struggled to reconcile or rationalize the manifest appearance of purpose in biological structures with the dead hand of selection. In fact, many of the objections to natural selection raised in Darwin's time are still in circulation.[1] Like kudzu, the Japanese vine that in the southern US creeps relentlessly over everything in its path,[2] teleology pops up irrepressibly, even among biologists who rigorously argue that science should have no truck with mystic or immaterial causation.

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Evolutionary Anthropology 11:4–8 (2002)

Teleology arises in two basic ways. From a functional point of view, it does not seem too anthropocentric to say that organisms are "designed" to solve problems, from making eyes or lungs, to complex, homeostatic challenges such as transporting oxygen to cells, defending against microbial attack, or flying. In this sense, organisms seem just as functionally designed as airplanes.

From an evolutionary point of view, the fossil record can also give the appearance of systematic or directional change in form-following-function. It is not hard to see why we often just barely skirt teleological language. One may smile at Lamarckian notions of striving organisms, but we readily say bats evolved wings "to fly." A purist might object that this is just rhetoric, but bats fly today because their ancestors strove to fly, and those who did it successfully were passed by selection.

Why is the teleology urge so irrepressible? To see the issues, it may be useful to think of a scale of causal effects, like a number line, as shown in Figure 2, that reflects the degree of randomness or determinism that applies to evolutionary change. At one end is 0, or purely chance "causation" with entirely unpredictable outcomes, while at the other is 1, purely deterministic causation with entirely predictable outcome. In the standard way to denote numerical intervals, a square bracket ([or]) indicates an endpoint that is included, while a parenthesis bracket indicates an excluded end point. Where does the evolution of complex traits fall on this line?

PUTTING DESIGN TO REST? THE COMPLEXITY PROBLEM

Almost everyone in biology accepts darwinian adaptation as the best available explanation for the sometimes remarkable specialization of fit of organisms to their life-ways. But this is the sorest of sore points with religious fundamentalists, who always raise Archdeacon Paley's famous assertion that simply by seeing a watch you know there's a watchmaker. Organized life seems so obviously built to purpose that a creationist puts his money on the value 1, the rightmost extreme of the causation scale: things are purely teleological, entirely predetermined for a desired objective. They view with disdain the biologists' argument that a functionally organized trait could possibly, plausibly, with-a-straight-face be attributed instead to chance.

Of course, this grotesquely misrepresents what we mean by "by chance." What we mean is that mutations occur by chance relative to need or function. Selection works by screening the variation that by chance happens to be there at any time and place. No particular variation had to arise, and an ancestral mutation might have been possible that would have led to my having wings; by chance that didn't happen (but it did in the bat's lineage). By chance, those with viable traits did not perish prematurely from some other cause. Biologists reject teleology out of hand, because if selection can only screen existing variation

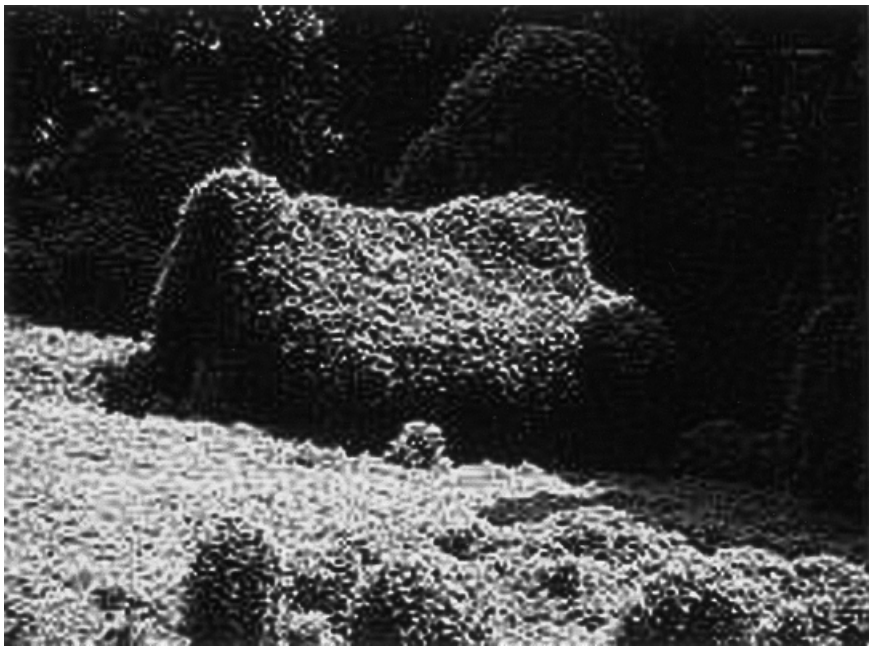

Figure 1. Kudzu, like teleology, the weed of weeds taking over everything (barn, tractor . . .) Courtesy J. Anthony.

it cannot have the foresight to build today what will be needed in the future. It can only move tomorrow's generation closer to today's environment, based on yesterday's mutations.

It is a semantic irony that while we insist that creationists are wrong to accuse us of believing that bats fly by chance, the key elements of evolution all involve chance. Indeed, at Year 0, the prospective probability that any specific life outcome like a warm, furry creature with web-winged nocturnal flight would be present in Year 4,500,000,000 (today), would be vanishingly small. The factors required to bring this about are so thoroughly unknown that even to speak of the "probability" of such an outcome is a stretch. Since there's no serious way we could predict such a creature, from an operational viewpoint, bats did effectively get here by chance.

Despite this, darwinians stress the essential role of causation directed by selection (see Figure 2), and view life as being on the deterministic side of the causation scale (indicated by the thickened line segment). As the figure shows, the fundamental difference with teleological views is that the end of the causal interval itself—purely predictable determinism, which essentially means pre-determinism—is not permissible to darwinians! We may not always realize how exquisitely this prohibition rests on a thin edge of randomness. The entire edifice of evolutionary theory could be deeply upset if anyone ever shows that mutations were, after all, directed in advance to satisfy need. Critics will then sneer at the arrogance by which we have claimed that the intricate complexity of life was undirected. But unless such discovery occurs, nonclairvoyant chance rules.

IS ADAPTATION BY NATURAL SELECTION A THEORY OR REALITY?

Natural selection is not a theory in the sense of some airy speculation, but an obvious, empirical, automatic, observable reality. But to make selection more than a vacuous tautology (survival of the survivors), there must be something systematic about who proliferates and who doesn't, and we can't leave that to chance!

But there's a problem. The effect of selection on specific genes is usually very difficult to observe directly. The chance aspects of reproduction are great relative to the strength of selection. The swiftest gazelle may break his leg in a gopher-hole and fall to a lion as a result. Our inability to observe long-term evolution directly constrains us to extrapolate that barely detectable signal as a steady, essentially deterministic force over long time periods (even millions of years). But the fact that the survivors survive means that whatever organisms do today have necessarily been successful. So what kind of explanation do our adaptive scenarios really provide? In this sense, adaptation is a somewhat trivial concept, if not indeed an illusion.

We bolster our confidence in the explanatory power of adaptive evolution by showing that most traits we can test on the farm or in the lab do respond to selection. We can achieve changes in a trait—like more milk yield or bristles on a fly—in only a modest number of generations of selection. Darwin himself rested much of his evolutionary argument on his observations of artificial selection on domesticated species like his famous pigeons. But artificial selection is imposed with a direction in mind, so what it really shows is that teleological selection works. That's somewhat irrelevant to whether natural selection explains evolution or where real evolution falls on the causation line.

It's easy to see how natural selection could lead to an appearance of directedness. Once a creature began taking to the air, increasingly aerodynamic body forms are easy to understand; an atmospheric environment that did not change over millions of years could consistently favor changes along this slippery path. Biological traits have often tracked a rather steady environment in this way, which can reasonably be thought of as being "guided." That's fertile soil for the teleology weed, but could things have been otherwise?

Suppose environments changed randomly and drastically each generation. How could an organism evolve to be adapted to it? Natural selection could still occur, but the favored genotypes would change each generation. In fact, it is by imposing unnaturally unpredictable environments that we prevent the adaptation of parasites to their host—for example, by crop rotation, or continually changing antibiotic or pesticide regimes. Don't

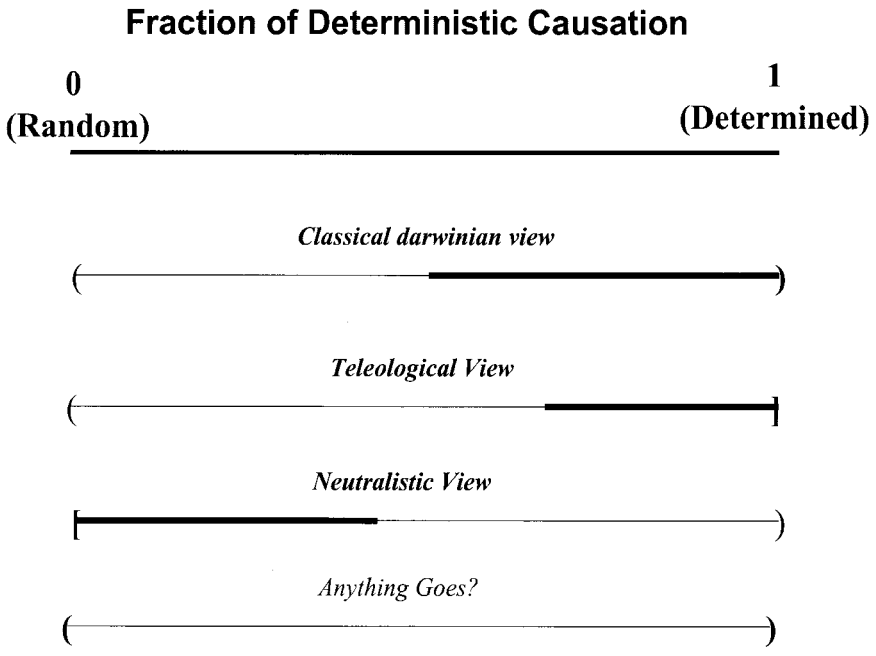

Figure 2. The causation explanatory line: where does evolution fall? Explanations for biological order can range from 0, purely random and unpredictable, to 1, purely predetermined and predictable causation. Round brackets-excluded endpoints; square brackets-permissible endpoints.

let the parasite get used to a predictable environment!

MOLECULAR INTERACTIONS: WAS EVERYTHING PREDICTABLE AFTER ALL?

Actually, there are respectable molecular reasons why we might view evolution as creeping very close to predictability. The autonomous self-organizing properties of biomolecules (e.g., their stickiness relative to specific other molecules) constrains variability and introduces something like inevitability to the kind of biochemistry we have today (e.g., Kirschner et al., 2000; Laughlin et al., 2000; Morowitz et al., 2000; Schuster 2001). A recent experiment that synthesized 6×10^{12} random short polypeptides (strings of 80 amino acids) produced ATP-binding proteins (a common biological function), showing that it was likely, not unlikely, for basic biological functions to arise randomly and rapidly (Keefe and Szostak, 2001) in a primal soup for all life.

This molecular view was given an eloquently darwinian spin by Jacques Monod, who won a Nobel Prize for work on the regulation of gene expression that helped give the genetic theory of evolution its molecular underpinnings. As he put it, organisms are objects endowed with a "purpose." "Rather than reject the idea (as certain biologists have tried to do), it is indispensable to recognize that it is essential to the very definition of living beings." He calls this purpose *teleonomy*—to try to distinguish it from the mysticism of teleology, and to explain how purpose is brought about at the molecular level by the kind of chance and selection described earlier. Specific manifestations like bat flight are unpredictable (chance), but the principle of life as we know it is based on the Platonic invariants of molecular chemistry and hence inevitable (necessity).

This kind of view contains a molecular version of preformationism, by implying that the genome has the organism within it. Such notions play brinkmanship with teleology, if not, indeed with an inanimate form of vitalism (Monod was French, after all). Because, in fact, wouldn't the properties of molecular affinities and self-assembly imply that with perfect molecular knowledge at Year 0 everything was predictable after all? That would essentially close the causation interval on the teleological right, just as creationists would have us do, though without needing to invoke an external or conscious guide.

RANDOM SUITABILITY: COULD COMPLEX TRAITS BE HERE REALLY "BY CHANCE?"

So far, we've neglected the chance end of the causation interval. But how much determinism is actually needed to explain life? We're generally untroubled by the notion that a substantial fraction of mutations are selectively neutral, and their frequencies change over time by chance alone. The evolution of such neutral sequences is at the closed left (0) end of the causation line. Figure 3 shows a simulated allele that rose by chance to a high frequency today. Looking back at its trace (as if there were a fossil record of allele frequencies), it might appear that the allele was always being pushed by selection toward high frequency. We might view the alleles that didn't make it (Figure 3 shows a few) as the doomed unfit. The way we assess whether our survivor is just lucky or was selectively favored, would be to know the history of all alleles, so we could estimate the probability that what we observe could occur by unaided chance.

Given our comfort level with neutral evolution in genes, why do we feel so compelled to provide selective explanations for phenotypes? Do we ironically share with Creationists the reflex response that complex organization is too improbable to have come about by chance? If we remember that to be here today you must be adapted to something, perhaps such origin is not so implausible.

There is always phenotypic variation in a population. Quantitative traits change their characteristics (e.g., mean, variance) even in the short span of laboratory experiments in which there is no selection on the trait. A typical observation about natural traits is that there is selection on the extremes of their distribution, with the fitness of the rest being more or less the same. Failure at the extremes does not imply that the survivors are consistently alike in any par-

ticular way, at any particular time, or over long time periods. Just as adaptive selection is thought generally to work slowly and step by contingent step, a trait can change step by slow, contingent step without being channeled in any particular direction, by drift alone.

Looking retrospectively at the fossil record, such traits, like individual alleles, can appear to have been tracking in the present direction whether they were aided by systematic selection or not. Think of Figure 3 as graphing the fossil history of some trait like flying ability. That's the teleological illusion, and one of our most common arguments against the argument from design is to cite elements of the fossil record that show that change did not occur in a smooth unidirectional way. Bats were not really aiming at wingdom from the beginning, but instead got here by meandering contingently through phenotypic space. But what does meandering mean, if not randomness?

This brings up another standard challenge thrown at darwinism, the need to explain the incipient stages through which a complex structure is presumed to have gone on the way to its present complex form. The standard explanation is that the incipient stages were adapted by selection to some earlier function(s). Thus, the origin of bat wings may have been interdigital webbing selected for something else. But why is selection needed? Again we must keep in mind that of the essentially infinite array of traits that could be here, whatever is here was simply good enough to pass the overall test of survival. Rudimentary precursors may be just the kinds of traits that could increase just by drift, laying the groundwork for some next step to do the same. Who knows what trivial trait today is such a precursor?

It would be important to develop phenotypic criteria, equivalent to the probabilistic models we use for neutral alleles, by which to evaluate whether a trait is here strictly due to what we might call "random suitability." The latter possibility would close the left end of the causation interval, to include the forbidden darwinian antipode of evolution purely by chance (neutralist line in Figure 2), and would greatly alter our typical view of evolution.

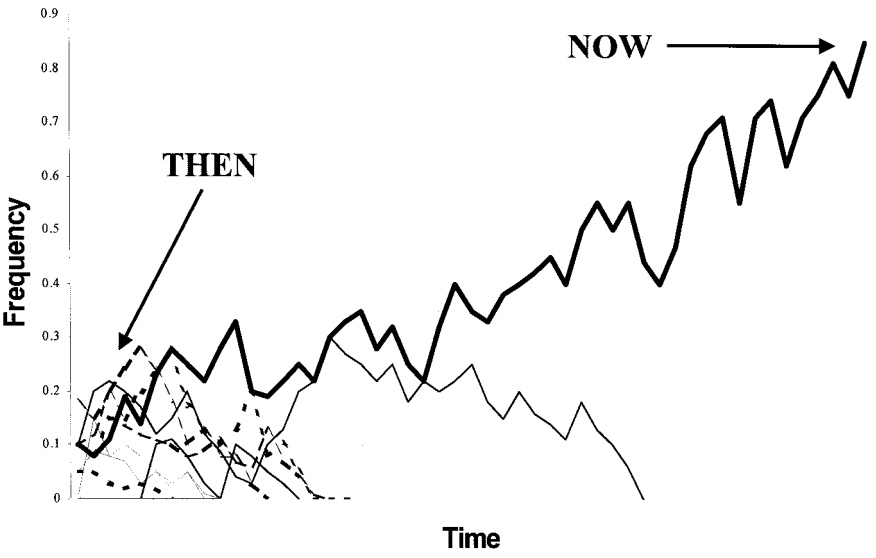

Figure 3. Change in allele frequency due to drift (schematic).

LIFE: GOD'S PLAN OR SATAN'S ILLUSION?

If we're careful about it, teleologically worded explanations of traits like bat wings seem to be reasonable rhetorical shorthand: they are there to fly, and they evolved to fly. But after my personal experience, rather than view bat flight as beautifully adapted, I'm inclined to view it as laughably clumsy, something only a drunk designer would make. The descendants of bat ancestors could just as easily have remained nonflying. Some did. We call them primates.

Now, consider the faces of these selfsame bats, as drawn by Ernst Haeckel in Figure 4. Haeckel's artwork could be fanciful, but at least some of these species have been identified. How are we to interpret their evolution? Most biologists would struggle valiantly to provide an adaptive explanation. One is that the faces reflect pleiotropic effects of variation in neural crest cell migration during craniofacial development. But that's just wing-flapping, unless we can specify the selective value of the unspecified pleiotropy. Though no expert, I know of nothing else about bat heads that requires such strange facial consequents. Another possibility is sexual selection. I know there's no disputing taste, but it's a challenge to conceive of bats swooning over such faces (even if they mated in the daylight). Maybe there simply is no adaptive explanation.

Ernst Mayr (1991) characterizes the modern synthesis—the implicit theoretical basis of evolutionary inference—as reaffirming "that all adaptive evolutionary change is due to the directing force of natural selection." I don't think the synthesis reaffirmed any such thing, and while it would be difficult to challenge the applicability-in-principle of standard darwinian explanations, adaptation and selection do lose luster when viewed through properly humbled lenses. One doesn't have to overdo selection to be darwinian. "If I have erred in giving natural selection great power . . . or in having exaggerated its power. . . . I have at least, as I hope, done good service in aiding to overthrow the dogma of separate creations." So wrote Darwin himself in *The Descent of Man* in 1871.

Life is a chiaroscuro of chance and direction. After a century and half of intense scrutiny, subtleties remain even in so central a concept as adaptation. The illusion of teleology is so strong that the mostrespectable of biologists are regularly tempted to dabble in notions that come awfully close to vitalism, from selfish genes and inclusive fitness, to extended phenotypes and Gaia. In fact, the whole interval of causal possibilities may be open to us after all (last line, Figure 2). When we play the evolutionary num-

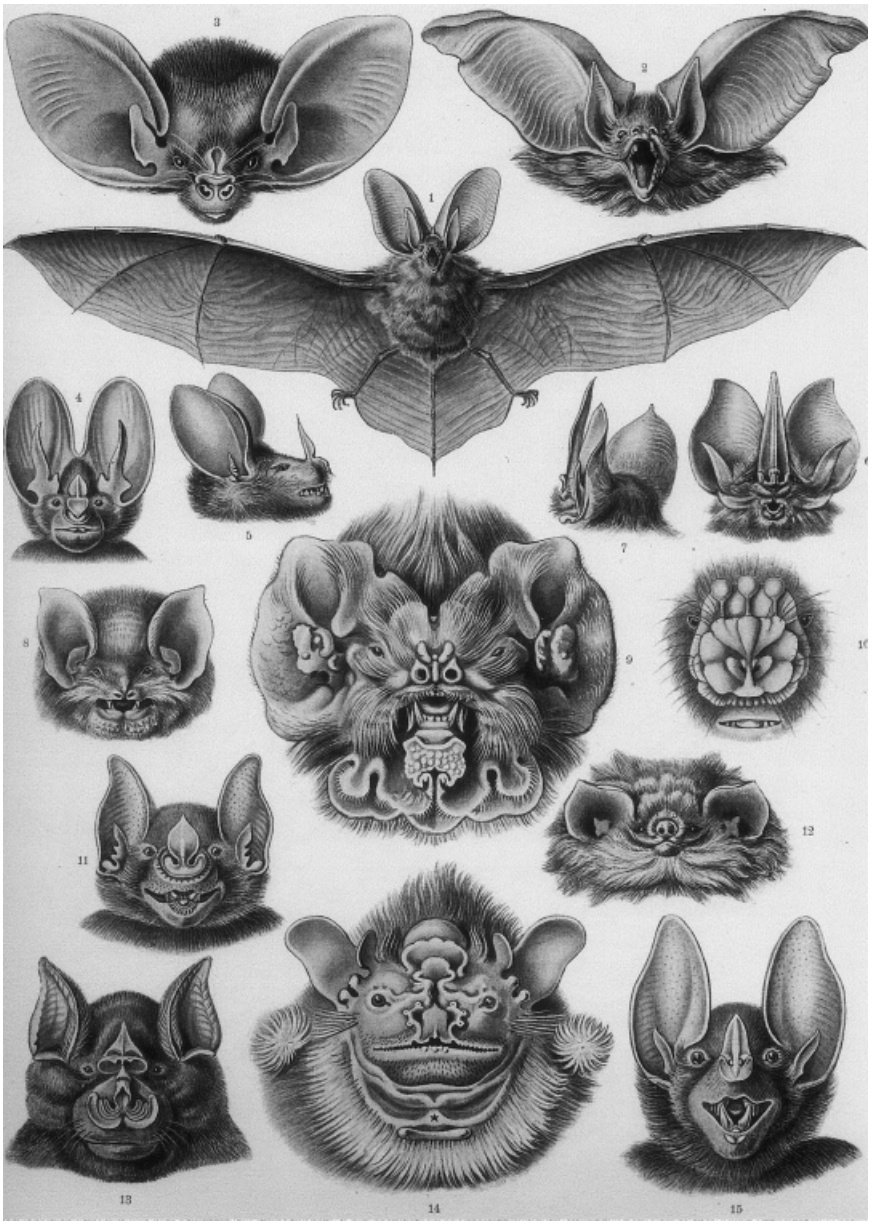

Figure 4. Bat faces (Haeckel, *Art Forms in Nature,* 1899, Dover reprint edition).

bers game, it is not clear where we should place our bets. Weed control is important, but we should be careful what we call a weed.

NOTES

I would welcome comments on this column: kmw4@psu.edu

Thanks to Anne Buchanan and John Fleagle for critically reading and purging this manuscript.

1. The arguments against blind adaptation were not just raised by fringe creationists. St. George Mivart raised the essential array of arguments in a widely read book in 1871; Darwin responded point by point in the 6th edition of the *Origin,* but the leading geneticist William Bateson was still raising many of these arguments in 1913.

2. On the evil weed, see: http://www.jjanthony.com/kudzu/

TO READ

Most things discussed here can be profitably explored by web searching.

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DOI 10.1002/evan.10018