The ‘Holy Grail’ in Phylogenetic Reconstruction: *Seeing the Forest for the Trees?*

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Abstract

Systematic/macroevolutionary biology has dedicated much of the past 50 years of its energy and resources in an effort to resolve definitively the one true ‘tree of life’ and to explain materially its cause. But, no matter the quantity/quality of data, experimentation, and analysis, the effort is hampered by persistent and ever-accumulating contradictory observations. This may be an indication that the source of the problem lies in the observer rather than the observed. Observations do not conflict with themselves; they conflict with theoretical expectations. Thus, systematic and evolutionary biology requires epistemological overhaul. Rather than continued misaligning of evidence with theory, theory must be realigned with the evidence. Evidence suggests that the Darwinian reductionist perspective is the epistemological driver of considerable conflict/contradiction in systematic/evolutionary research, and that robust non-Darwinian theories not only better reconcile observations, but also provide a superior investigative perspective.

Key Words: phylogenetics, phylogenetic comparative analysis, data conflict, Darwinism, autopoiesis, chaos, hierarchy, evolutionary idiosyncraticity.

Background: conflict in phylogenetic evolutionary analysis

Olmstead and Medoya (2019) remarked on phylogenetic evidence from whole genome sequencing, which they characterized as the ‘holy grail’ of molecular phylogenetics. They commiserated over persisting evidential conflict in phylogenetic reconstruction, which they noted is “as old as phylogenetic systematics.” In fact, the specter of conflict is *much* older than that. Aristotle’s *Scala Natural* highlighted ambivalent resolution of the natural relationships of flying organisms. This theory is not founded in ‘descent with modification,’ but rather teleological organism-driven orthogenetic evolution of more perfect ‘higher’ forms. Among notable 18th –19th century systematists that addressed evidential conflict were several Creationists. These pre-phylogenetics debates hinted that character distribution mosaicism is intrinsic to biodiversity, independent of how it is parsed, and that parsing it one way or another per se does not eliminate or explain it.

Yet, for the past century, evolutionary systematists have probed ever deeper into organisms, expecting to find a magic bullet that retraces phylogeny perfectly. In this trajectory, the ‘holy grail’ has *not* been per se the genome, but a fully resolved and well-corroborated ‘tree of life’ (e.g., Soltis and Soltis, 2018) and its causal explanation. The earlier 20th century heralded the first subcellular bandwagons, especially cytotaxonomy. The 1960s–1970s added chemotaxonomy, ultrastructure, and protein electrophoresis; the 1980s, desktop phylogenetic computation and, concomitantly, diverse (and themselves conflicting) epistemological models and methodologies. Like greasy rags, these successive approaches, separately and together, often blurred more than they clarified the picture.

Then appeared DNA sequence data, which were heralded as the ultimate arbiter in systematics. Rather abruptly, the PCR-to-PAUP paradigm practically purged the entire discipline. Molecular systematics laboratories became warships. ‘More data! More sampling! More megahertz! More memory! More MCMCs! And damn the variability, *barcode* those species!’ For a while, it *seemed* that this ‘shock and awe’ attack was on course to annihilate the last resistance to cladistic conquest. But the tide seemed to turn. Sometimes adding more data reduced resolution. Bombarding one unresolved node sometimes yielded, like Medusa, several in its place.

As Olmstead and Medoya (2019) noted, whole genome sequencing represents reductionism's last stand. Genome-scale sequencing is yielding novel information on macroevolution, but not as much cladistic resolution as expected. But should it? Should 500,000 base pairs of arbitrarily isolated DNA sequence resolve clades better than 5000 base pairs *preselected* for their theoretical/empirical high-quality resolvability? As Olmstead and Medoya (2019) also noted, explanations for this flood of new conflict appeal by default to mechanically plausible but not always demonstrable hybridization and lineage-sorting. Thus, phylogenomics has us retreating from explanation back towards speculation. Moreover, hybridization and lineage sorting hardly are earth-shaking discoveries. That was the battlefront 50 years ago. And what about transposons?

Darwinian 'tree-thinking' as an epistemological cause of data conflict

Hershkovitz (2018a, b, 2019) addressed the question of phylogenetic data conflict, but approached it differently. This work concluded that the source of evidential conflict in evolutionary biology is not per se in the evidence, but in its epistemological interpretation. An inadequate epistemology, in turn, engenders an *expectation* of observations whose *exceptions* are described ad hoc as 'data conflict.' But phenomena ideally cannot generate observations in conflict with themselves. Recall that good explanations make better predictions than poor ones. If, as in the case of phylogenomics, a two-order of magnitude increase in observations does not increase or even *decreases* predictability, maybe it is time to trade up to a better crystal ball.

Hershkovitz (2018b, 2019) inferred the cause of conflict in contemporary phylogenetics and tree-based evolutionary analysis generally: biological reductionism, in particular *neo-Darwinian* reductionism. Prevalent macroevolutionary theory and methods trace their origin to the neo-Darwinian Modern Synthesis (cf. Fábregas-Tejeda and Vergara-Silva, 2018, Olson, 2019). This, in turn, emerged in the form of the statistical population genetic incarnation of Darwin’s (1859) reductionist theory of evolution by means of Natural Selection (NS), restated succinctly as ‘survival of the fittest’ (Darwin, 1868).

The relation of NS to phylogenetic conflict is that the theory was supposed to explain diversification not *within populations*, but *among taxa*. Although NS is conceived as initiating in populations, validation of Darwin’s theory requires its consummation with *phyletic* divergence. Although overlooked/ignored by 20th century Aristotelian ‘evolutionary’ systematists, Darwin conceived that taxa and their traits evolve integrally/synchronously and diversify *cladogenetically*. He diagrammed macroevolution as a tree (but see Podani, 2019), or cladogram. This diagram idealized anagenesis unidimensionally (lines) and diversification events nondimensionally (bifurcation points). Terminal taxa, whether species or ‘genera’ (Podani, 2019), also were idealized nondimensionally. It is critical to appreciate that this clado-anagenetic model is essential to NS theory. It purports to explain not merely anagenesis, but also the historical consequence of species differentiation via NS. Other evolutionary mechanisms would yield other phylogenetic patterns.

During the Modern Synthesis’ first decades, the systematics discipline retained an Aristotelian mindset, in which both taxa and diversification were conceived and diagrammed multidimensionally. Indeed, texts and diagrams in ‘evolutionary’ taxonomy literature implied diversification histories/mechanisms incompatible with cladistics. Armen Takhtajan, in particular, in his 1959–2009 texts, emphasized that angiosperm families possess mixtures of characters that he regarded as *intrinsically* primitive or specialized. He described this as ‘heterobathmy.’ Takhtajan vehemently rejected cladistic theory, so he did not parse conflicting characters as parallelisms or reversals. Rather, his phylogenetic narrative resolves as a network, such that a heterobathmic family evolved from/alongside an *assortment* of not otherwise most closely related 'primitive' and 'specialized' families that collectively possessed the various individual characteristics. Thus, the heterobathmic family derived its traits effectively polyphyletically. [But see Rieppel (2016) for a discussion of Hennig's cladistic interpretation of Takhtajan's 'heterobathmy.']

Meanwhile, evolutionary population genetics placeheld for the neo-Darwinian macroevolutionary paradigm, pending the eventual conceptualization and development of cladistic and later tree-based macroevolutionary theory/methods. Tree-building, or, more accurately, 'tree-thinking' (e.g., Baum and Smith, 2012) is what consummated (and evidently consumed) the Modern Synthesis. By the time molecular systematics came along, conflicting cladistic data was well known and much debated.

Molecular data conflict ought to have been anticipated on the basis of transmission and molecular genetic evidence, as well as theoretical phylogenetics. Possibly molecular systematists proactively avoided it. In contrast to molecular phylogenetic data, phenotypic data were informative biologically whether or not they resolved phylogeny. But few systematists (e.g., Hershkovitz and Zimmer, 1996) concerned themselves with comparative *biology* of DNA loci. In systematics, a DNA sequence alignment was not more or less than a sterile phylogenetic data matrix. The overriding concern was whether the sequences resolved phylogeny and thus merited publication and thus advanced an academic career. Quite likely, filtering out of poorly resolvable data (and researchers who obtained them) itself enhanced the perceived reliability of molecular data in phylogenetics. The early emphasis on single, hence non-conflicting, loci tipped the balance further. But with increased locus and taxon sampling, data conflict became the rule rather than the exception. Still, there evidently persisted a superstitious belief that whole genome sequences would thresh out these conflicts.

A funny thing happened on the way to the genome. For example, and hardly an exception, a phylogenomic analysis among Portulacineae (especially cacti; Wang et al., 2018: *Fig. 2*) revealed that numerous statistically maximally-supported nodes in the taxon tree were supported evidentially by a *minority* of harvested loci, the majority at least weakly discordant. Another analysis, coincidentally involving cacti (Copetti et al., 2019: *Fig. 2B*), superimposed over a presumed taxon tree a diffuse cloud of gene trees and their divergence time estimates. This revealed that a large proportion of alleles had not co-diverged with speciation, but merely had assorted among lineages since the origin of the family. Other alleles manifested horizontal transfer. These results, along with phylogenomic 'splits' networks of *Claytonia* spp. (Stoughton et al., 2017: *Fig. 1B*), suggest that the phylogenetic 'holy grail' might be, after all, more like Bessey's Cactus than a cladogram. Is it possible that the rudder of tree-thinking had rusted and steered neo-Darwinian reductionism adrift?

Resolving data conflict epistemologically rather than empirically

Hershkovitz (2018a, b, 2019) attempted to formulate an evolutionary synthesis of Montiaceae around data, not dogma. This synthesis aspired to span all divergence levels between outgroup and individual, and all phenomenological dimensions, ecological, morphological, and molecular. The effort was a mental exercise, focusing on conflicts and contradictions, and seeking to explain the collectively unexplained data. Nominally conflicting data were revisualized in the light of alternative theories.

What emerged, and not at all expectedly, was a consilient non-Darwinian evolutionary synthesis. Yet, none of the theoretical components are per se novel. All have been corroborated in scientific disciplines marginal to if not remote from ‘mainstream’ reductionist systematic and evolutionary biology. These include complexity theory, systems biology, neurobiology, cybernetics, as well as related areas of biological philosophy. In these disciplines, Darwinian reductionist theory – and its applications – are considered obsolete, if not utterly false. Additional theoretical sources and arguments are documented in Hershkovitz (2018a, b; 2019). For brevity, only a few corroborative references are cited here. Essentially all but the oldest among these I located/read *after* developing the first-posted draft of this essay, and their consanguinity is reassuring. It should be recalled, also, that Popper (1976 [2002]) characterized Darwinism as “invaluable,” nonetheless as not a theory, but a “metaphysical research program.” Effectively, he criticized evolutionary research that did not test Darwinian theory per se, but merely sought Darwinian explanations under the assumption that the theory was true. Nonconforming observations generally have been variously explained ad hoc, unexplained, ignored, or, in any case, not proactively sought.

Towards the objective of reducing perceived data discordance in phylogenetics and tree-based evolutionary analysis, first and foremost is the understanding that living organisms are, by definition, *autopoietic*, i.e., self-organizing/maintaining/determining/regenerating (Varela et al., 1974; Maturana and Varela, 1980; Maturana, 1999, 2019; Meincke, 2019a, b; Villalobos and Razeto-Barry, 2019). From this principle alone, one can deduce that, in evolution, organisms are the *drivers* and not, as NS dogmatists maintain, the *driven* (e.g., Nürk et al., 2019; cf. Olson, 2019). Does autopoiesis falsify NS? As a matter of fact, it does. NS does not occur, not even sometimes, not ever (Maturana and Mpodozis, 2000). All ‘proofs’ of NS are statistical epiphenomena.

As corroboration, Hershkovitz (2018b, 2019) cited a recent description of NS (Pigliucci,

2010) that, remarkably, is patently *non*-Darwinian. In fact, it is a description of Natural Drift (Maturana and Mpodozis, 2000)! More bizarre, Pigliucci (2010) penned this non-Darwinian NS definition in a *defense* of NS against its non-Darwinian critics. No student of systematic/evolutionary biology should overlook this watershed paradigmatic development. In fact, autopoiesis *alone* invalidates pretty much all of a century of NS-based adaptationist evolutionary ecological and phylogenetic comparative research. Autopoiesis better explains myriad conflicts in the data and interpretation.

But, wait, there´s more.

As noted, phylogenetic character patterns are in ‘conflict’ only to the degree that they are not *predicted* by the underlying epistemological model and optimization criterion. But the self-determining quality of autopoietons (organisms) has the logical consequence that their enactivity (ontogenetic/evolutionary trajectory; Varela et al., 1992; see also Virgo, 2019) is not (statistically or otherwise) predictable. This proves to be a quality of formal mathematical chaotic functions – determinate, yet, if the function and initial conditions are not known, unrecoverable and unpredictable (Ferrière and Fox, 1995; Boeing, 2016; cf. Longo and Montévil, 2014). This suggests that organismal evolution is to at least a degree a substantially chaos-like rather than strictly a stochastic process.

Indeed, all biological replicative functions from the level of DNA to species manifest chaotic function qualities. The neo-Darwinian reductionist paradigm idealizes replicative events as regularly occurring, and replicative mutations as having *ideally* equivalent magnitude and effect. The paradigm is well aware that the ideal is not the real, whether in the case of genes or species (e.g., punctuated equilibria). But the lesson is not appreciated, and reductionist idealizations themselves seem to persist in analytical methods, e.g., Brownian motion evolutionary null models. Equally importantly, this irregularity of timing and magnitude of change characterizes replicative events at *all* organizational levels. A further characteristic is that, with the trivial and transitory exception of DNA bases and amino acids, evolutionary changes consequent to replicative events do not merely oscillate within fixed state spaces, as constrained in reductionist methods. Historically, they have expanded and transformed state space. This is characteristic of chaotic functions.

In the meantime, reductionist tree-based evolutionary analyses use contemporary empirical data to reconstruct probabilistically ancestral conditions and the evolutionary dynamics. Based on this model estimation, the evolutionary history is then the one that, effectively, conflicts least with the empirical data. To the degree that the true evolutionary dynamic is indeed stochastic and correctly modeled, analysis of more data (e.g., whole genome sequences) is expected to converge on the true history. The key is 'correctly modeled' (cf. Olmstead and Mendoya, 2019). If the model is incorrect, adding data yields inconsistency and converges on a *wrong* solution.

Yang and Zhu (2018: *1854*) remarked that molecular phylogenetic models are approximations and "are never true in real data analysis." In context, it appears that Yang and Zhu (2018) consider conventionally estimated models to be *epistemologically* correct, but *misspecified*. But, to the degree that evolution is at least partially chaos-like (consequent to autopoiesis), conventional models also are *epistemologically* misspecified. Increasing data should reduce concordance, and conflict-minimization is bound to converge on error. No conventional phylogenetic method can correct this. To paraphrase an aphorism from chaos theory (Boeing, 2016), the exact ancestral conditions predict the exact evolutionary history, but the approximate ancestral conditions do not predict the approximate evolutionary history.

In addition to autopoiesis and chaos theory, an important aggravating source of perceived conflict can be understood in terms of hierarchy theory (Salthe and Matsuno, 1995; Fábregas-Tejeda and Vergara-Silva, 2018). ‘Conflict’ generally refers to discordance of trees estimated from different but presumably co-evolving characters, be they infragenic, intergenic, different morphological traits, or molecules versus morphology. Mechanisms that cause such discordance are well known. This sort of nominal conflict was embodied in the old aphorism ‘gene trees are not species trees’ (e.g., Doyle, 1992). In truth, the persistent perception of such discordance as ‘conflict’ owes to overzealous Darwinian tree-thinking. Discordance between histories at different hierarchical levels is not per se conflict.

To appreciate the preceding, it must be understood that all thermodynamic systems, including autopoietons, are organized hierarchically. A given hierarchical organizational level functions within its lower bound (its requisite starting conditions) and its upper bound (its tolerance range). For example, an engine piston will not work without air, fuel, and ignition. But even with these, it will fail under conditions that compromise its functional integrity, e.g., any sort of cylinder imperfection.

Biological organisms can be organized hierarchically in multiple levels, e.g., chromosomes, organelles, cells, meristems, organs, and, at the supraorganismic level, colonies, microbial metagenomes, sexual demes, and symbionts, among others. Reductionist biologists are familiar with these. But because they are unfamiliar with autopoiesis, they do not appreciate that *each* biological level of organization *also* manifests autopoietic character, even though such levels themselves may not be living entities (cf. Virgo, 2019). This should not be surprising, since some levels themselves derive from once free-living autopoietons (organisms, remember?). Retained autopoietic quality permits considerable evolutionary independence at different levels, as long as adequate starting /operating conditions are maintained at lower/upper bounds, respectively. The consequence is that evolution at different organizational levels is not *predicted* to be lockstep. Their different histories might be described as incongruencies, not conflicts.

Thus, the meaning of the aphorism ‘gene trees are not species trees’ must be clarified. It does not refer to a conflict inferred from discordance among different gene trees and/or morphology. It refers to the ontological distinction between genes and species, such that gene trees *cannot be* species trees, even when gene trees and species trees are *fully* congruent. Axiomatically, the ‘true’ species (or taxon) tree is *not* a consensus of a plurality of concordant gene trees, as misconceived explicitly in many molecular phylogenetic and, more so, phylogenomic analyses. This should be clear from hybrid species formation. From the perspective of the species level, the genes having different histories are not ‘discordant’ or ‘conflicting.’ They are integral to the species. The species would be *different* ontologically (and functionally, if viable at all) if the so-maligned ‘foreign’ loci were rounded up and deported. Put another way, *all* incident loci pertain to the ‘true’ species tree.

Epistemological solutions to phylogenetic data conflict: PEI and Wave Model

Not expectedly initially, the three theoretical phenomena discussed here, autopoiesis, chaos, and hierarchicity, threaded into a single consilient evolutionary dynamic, which I described as the **Principle of Evolutionary Idiosyncraticity** (**PEI**; Hershkovitz, 2018b, 2019). Not merely an aesthetic term, ‘evolutionary idiosyncraticity’ was described formally as an evolutionary product of simultaneous chaotic (determinate/unpredictable) and stochastic (indeterminate, statistically predictable) processes. It can be summarized as **EI** = ***f***(chaos)***f***(stochasticity). The determinate character is inherent in autopoiesis. The stochastic factor is a sum of the dynamics occurring at organizational levels hierarchically adjacent to a self-organizing process. I merely conjecture that the net evolutionary effects at hierarchically adjacent levels are stochastic. More precisely , PEI tentatively *defers* to these *adjacent* hierarchical levels the very stochasticity that the NS paradigm presumes to encompass the *entire* evolutionary process. Clearly the autopoieton itself does not behave stochastically, and the contrary assumption is the fundamental error of the NS paradigm.

As a demonstration of the preceding, replication presumably is affected by incident nucleoside concentrations, etc., at the lower bound (starting conditions), and cell environmental parameters (tolerances) at the upper bound. The response to these conditions is not fixed, nor stochastic, but dynamic (cf. Kritz, 2017). It varies at least somewhat unpredictably depending upon the enaction of base incorporation into the elongating DNA molecule. This enactivity itself modifies both the base availability pool and the functionality and thermodynamic tolerances of the molecule. I use this example, because it demonstrates that base substitution during evolution is not a stationary process, as neo-Darwinian reductionist molecular phylogenetic analyses idealize (Hershkovitz, 2018a). This nonstationarity itself contributes significantly to unexpected observations (‘conflict’). However, this nonstationarity characterizes evolution of biological systems at *all* hierarchical levels, yielding EI.

Also not initially appreciated, PEI proved to be consilient with a previously and independently developed (and as-yet unpublished) model of species called the ‘**Wave Model**’ (summarized in Hershkovitz, 2019). The Wave Model is not a species concept, but an attempt to describe and explain how entities perceived and named taxonomically as species (more heuristically as ‘specioids;’ Hershkovitz, 2019) form and degenerate in the *perceptual* dimension. Species ontology must be resolved in the perceptual dimension, because species have no established ontology in any material dimension. Yet all phylogenetic and tree-based macroevolutionary analyses specify species as operational taxonomic units. These necessarily are perceived and not materially real units. The Wave Model attempts to model what it is about relations among individuals that cause them to be perceived as species by any material criterion.

The Wave Model compared the perception of species to the perception of water waves. The relations ‘individual/species’ and ‘water/wave’ have several ontological and ontogenetic similarities. Water waves, as it turns out, can be described as fractals, which are chaotic functions. They also possess rudiments of autopoietic activity (cf. Dupré, 2017). This should not be surprising, since life itself evolved in an aqueous environment likely facilitated by wave action. Perhaps not coincidently, organisms *remain* composed mainly of water. In any case, the characteristics of the Wave Model suggest that it is a lemma of PEI.

The Wave Model demonstrates that it is the reductionist idealization of species as discrete entities that has yielded the plethora of 30-some species concepts, none of which ‘work’ (Hey, 2006). The taxonomic ‘goodness’ of species seems to be analogous to the perceived discreteness of waves. And, similar to water molecules in waves, individuals perceived as conspecific need not share the same historical trajectory. (This is unless shared history is obligated by the species concept itself, as in cladistic species concepts, which are untenable.) Finally, Hershkovitz (2019) discussed evidence that corroborates the prediction that, just as not all water can be classified into waves, not all individuals can be classified into species. These conclusions are significant, because reductionist ecological and evolutionary analyses treat species as effectively equivalent, independent, and identically distributed entities (Hershkovitz, 2019) to which all organisms pertain.

PEI addresses another dimension of phylogenetic conflict not discussed by Olmstead and

Medoya (2019). This conflict burdens reductionist tree-based macroevolutionary analysis, also known as 'phylogenetic comparative analysis.' In this realm, exemplified by Nürk et al. (2019), some 'A' is explained in terms of its phylogenetic correlation with some 'B,' where 'A' and 'B' might be variously a phenotypic or ecological trait or simply a difference in the number of extant descendent taxa. Here, phylogeny actually *matters*, viz., as the scaffolding for hypothesis-testing. Otherwise, phylogeny per se is innocuous. Yes, phylogenies provide an objective basis for taxonomy. But towards the objective of marketing phylogenetics in the modern reductionist institution, its utility in taxonomy is not a great selling point.

Tree-based macroevolutionary analysis generates multiple layers of conflict/uncertainty. One form is inherited from the imported phylogenetic tree, as estimation procedures and statistical tests are sensitive to both tree topology and branch lengths and their certainties. Another arises, as in phylogenetic reconstruction itself, methodologically. All other things being equal, different data/methods disagree whether or not 'B' explains 'A.' This generates conflicts essentially identical to those in taxonomic phylogenetic reconstruction, because they trace to conflicting reconstructions of the evolution of 'A' and 'B.'

As an aside, in the neo-Darwinian reductionist framework, a peculiar relationship exists between phylogenetic reconstruction data and phylogenetic comparative data. Phylogenetic analysis optimizes by minimizing character conflict, and this, in turn, minimizes homoplasy. Strength of correlations in phylogenetic comparative analysis, in contrast, *increases* with homoplasy of analyzed traits. This, in turn, maximizes the number of times those traits can *co-evolve* independently. Thus, evolution seems to stymie its own analysis. Minimal character conflict maximizes phylogenetic resolution, but constrains statistical tree-based evolutionary analysis. Maximal character conflict maximally potentiates statistical tree-based evolutionary analysis at the expense of phylogenetic certainty. It is as though, reminiscent of the Uncertainty Principle in physics, evolutionary history cannot be simultaneously precisely ‘known’ and ‘understood.’

From a theoretical standpoint, however, the most serious conflicts emergent in tree-based macroevolutionary analysis are the exceptions to inferred phylogenetic correlations between ‘A’ and ‘B.’ This is analogous to conflict in the inferred phylogenetic relationship among taxa. Likewise, this conflict persists even in the case where all data/methods infer the same phylogenetic correlation, just as different data/methods may agree in ambiguity of support for particular phylogenetic relations.

Scrutiny of tree-based macroevolutionary analyses reveals that study organisms and traits commonly are cherry-picked for a priori high correlative potential, and the data then are ‘massaged’ to maximize it (Hershkovitz, 2018b). Yet, invariably, taxa within the study group (and more outside of it) either behave contrary to the expectation or manifest ‘A’ *or* ‘B’ but not both. It is as though the taxa, not having studied Darwin, evolved *wrong* (phylogenetic incorrectness?). In some cases, I have found independent analyses that conclude that the same ‘A’ evolved in response to some ‘C,’ with no mention of ‘B’ at all (Hershkovitz, 2019).

These exceptions are what demonstrate that ‘A’ and ‘B’ are neither necessary, nor sufficient, to ‘drive’ evolution in a predictable way (Hershkovitz, 2018b, 2019). To appreciate this, phylogenetic comparative analysis is no different from any other statistical application. Effectively, it reduces evolution to coin-flipping, where the coins are taxa. At least in Modern Synthesis population genetics, empirically observed ‘fitness’ is supposed to discriminate the fate of individuals in trait classes. But, in tree-based macroevolutionary analysis, what is the differential fate of taxa that buck the inferred evolutionary correlation? Are they less fit? The organisms themselves seem to go on living and reproducing just fine. Hershkovitz (2018b) suggested that, but for twists of fate, induced correlations might have been nullified or even reversed.

But the fatal flaw of the tree-based macroevolutionary paradigm is epistemological, not methodological. It is consequent to the Darwinian idealization of organisms as passive actors, evolution's flipped coins. This ignores or effectively or explicitly denies the autopoietic property of life. And, not coincidentally, the flaw is consequent to the Darwinian idealization of phylogeny as bifurcating lines (a tree) and diversification events and species as 'points.' Barcodes, anyone? As suggested by Hershkovitz (2018b), these erroneous Darwinian idealizations underwrite the reductionist tree-based macroevolutionary paradigm. They justify, in fact *obligate*, the successive and recursive statistical reduction of phylogenetic and taxonomic complexity. This, in turn, partitions observations into those that concord with the presumed phylogeny or evolutionary process and those that do not. And *this* is the source of the 'conflict' over which Olmstead and Medoya (2019) agonized. Evolution did not create it. Darwin did.

As Olmstead and Medoya (2019) noted, conflicting data typically are explained by appealing to one or a few simultaneous evolutionary processes bound to generate different data patterns. But there seems to be projected a sense that one process is 'good' and the other 'evil,' i.e., the one that is generating the conflict. There never is projected a sense that the mythical Darwinian clado-anagenetic process might be the culprit. And there is not at all a projected sense that a *singular* process might be generating *all* the data. In theory, evolution of incongruent data should subside only when phylogenesis and evolution *stop*, so that diversification no longer creates the specter of, e.g., hybridization or lineage sorting. *Ginkgo biloba* comes to mind. Paradoxically, this obviates phylogenetic and tree-based macroevolutionary analysis.

Despite appearances, this commentary in no way disparages one of history's most perceptive and rational naturalists and, by the way, also a *taxonomist*. Darwin's contribution was singular towards bringing then 'Natural Theology' belatedly into the Age of Enlightenment. Also, the legacy of NS overshadows and oversimplifies the breadth and depth of Darwin's natural history theorizing. But, while rational in its evident appeal to Newton's notions of motions, NS overshot the mark. Indeed, environmental forces influence the course of evolution, but they are not behind the wheel. But just as post-Newtonian metamorphoses of mathematics, physics, and astronomy do not diminish Newton, neither should new evolutionary theory diminish Darwin (cf. Longo and Montévil, 2014: *Chapter 1*).

Unfortunately, mainstream tree-based macroevolutionary theory does not seem to be advancing beyond Newtonian mechanics. Nürk et al.'s (2019) new 'Evolutionary Arena' (EA) platform, for example, provides not a new way of thinking about evolution, but a new way of thinking the old way. If anything, EA seems to be retrogressive, apt to overshoot Newton's orbit on a collision course with astrology. In particular, based on discussion in Hershkovitz (2018b, 2019), it seems inevitable that conclusions will vary wildly depending upon, e.g., which few among infinite 'arena' parameters are analyzed, which are applied among several artificially linearized phylogenies, age estimate extremes, different ways of describing/measuring phenotypic, genotypic, and environmental variables, and, of course, 'method.' And this will be true even in the case that evolution is strictly stochastic. Between this and ignoring autopoiesis and chaos and hierarchy theory, in terms of predictive power, EA might just as well incorporate the celestial charts on the day the taxa were 'born.'

I do not mean to single out Nürk et al.'s (2019). I cite it because it is recent and representative of the current mainstream comparative macroevolutionary paradigm that has prevailed during the past two decades. But, coincidentally, the 18 authors include E.J. Edwards, whose evolutionary analyses of Portulacineae are taken to task in great detail in Hershkovitz, (2018a ,b, 2019). However, from the present essay, it should be clear that the myriad point criticisms distill to just one: epistemology.

PEI provides an alternative framework for conceptualizing and analyzing evolution. Under PEI, the notion of conflict can be replaced with the notion of complexity. In particular, the 'true' phylogeny of an equivocally resolved node such as that highlighted by Olmstead and Mendoya (2019) is *not* one or another of its linearized resolutions, but the composite of all such resolutions, or its complexity. However, under PEI, macroevolutionary analysis needs to take a different trajectory altogether. Arguments that the evolution of some 'B' explains the evolution of some 'A' are specious postdictions.

PEI might be criticized for its current lack of an analytical heuristic. This criticism is spurious. It took more than a century for evolutionary biology to develop the heuristics for analyzing Darwinian macroevolution, viz., phylogenetics, molecular genetics/genomics, and the phylogenetic comparative method. And 160 years on, the best heuristics remain, at best, dicey. For example, towards the objective of conflict resolution, modern phylogenetic and tree-based macroevolutionary heuristics emphasize Bayesian methods. It should be emphasized that the procedures do not *alter* discordant empirical data patterns. They provide algorithms that simultaneously iteratively optimize solutions and weight the optimization, such that conflicting data effectively are sublimed. A critique is beyond the scope of the present commentary (see Hershkovitz, 2018a, 2019), except to say that the methods demonstrably are less reliable than a Boeing 737 MAX.

Hershkovitz (2018b) tendered suggestions for rudimentary development of EI analytical heuristics. These involved nonlinear mathematics, evaluation of performance of linear methods in reconstruction of idiosyncratic (chao-stochastic) phylogenetic functions (i.e., fractals), and epistemological hypothesis manipulation. For example, the NS paradigm considers random evolution as the null hypothesis (H_0). But, epistemologically, NS appears to be H_0, because it is the expectation, i.e., the default Darwinist explanation for departures from randomness (cf. Popper, 1976 [2002]). Under EI, evolution has a determinate trajectory that might generate patterns suggestive of NS (cf. Maturana and Mpodozis, 2000). Because truly random evolution is *unexpected*, it is not H_0, but H_1, equivalent to NS. Additional study by qualified theoretical/philosophical biologists should help advance an EI heuristic. However, Darwinian reductionists should not expect that these heuristics will be designed to resolve linear cladograms or test Darwinian evolutionary hypotheses, because these models are unrealistic.

In the meantime, what is to be believed about the ‘tree of life?’ Is it wrong? Yes and no. As Podani (2019) emphasized, its idealization as a tree is overly simplistic, even if it has treelike Gestalt. Nodes such as that discussed by Olmstead and Medoya (2019) are wrong not in the sense that they are resolved incorrectly, but in the sense that they *cannot* be resolved linearly. No bifurcate resolution accurately describes the phylogenetic relations of those taxa. But what about apparently well-resolved nodes in the ‘tree of life?’ While still overly simplistic, in many cases, these can be accepted tentatively as historically informative *if* they are consilient. ‘Historically informative’ refers to the accuracy of the phylogenetic reconstruction of an analyzed organismal component, which is not the same as the phylogenetic history of the organism. Consilience means that the same nodes emerge from analysis of different data from different organizational levels and using epistemologically distinct approaches (e.g., maximum likelihood and maximum parsimony) across broad parameter ranges. These nodes thusly, in Popper’s sense, best survive refutation.

Unfortunately, the tree-based reductionist macroevolutionary paradigm does not fare so well under PEI, and it is not clear whether it can be salvaged. Mainly this owes to its Newtonian interpretation of organisms. But even ignoring this, there are many other reasons, one of which is its dependence on reductionist and inherently inaccurate phylogenetic trees. And even ignoring this, existing comparative analyses are wanting for both resistance to refutation (e.g., taxa bucking correlations and independent analyses yielding conflicting conclusions) and technical competency of character data analysis. Hershkovitz (2018a, 2019) highlighted examples involving Portulacineae, but these are typical of the paradigm more broadly (e.g., Wenzel and Carpenter, 1994; Franz and Engle, 2010). Even if evolution were purely stochastic and linear, vices and artifices of existing macroevolutionary analyses likely would invalidate the conclusions of most published studies. Moreover, not even the data from such studies can be rescued, because, per the reductionist assumptions, they emphasize biologically meaningless phenotypic 'means' of species, and often equally meaningless means of environmental variables, such as macroclimatic mean annual temperature and precipitation. There also is a tendency to reduce parameter states arbitrarily and biologically unrealistically for statistical expedience. Such reductions might be justifiable in the case of nucleotide bases and amino acids, but they are not in the case of complex phenotypes.

Conclusion: ***Time to bail on Darwin?***

Returning to Olmstead and Medora's (2019) lamentation on the persistence of phylogenetic conflict into the age of phylogenomics, the main counterpoint offered here is that 'conflict' in phylogenetic reconstruction *and* tree-based evolutionary analysis is not in the data, but in the epistemology. Given what we know about organisms, we should not expect all data to support a single linear and bifurcating cladogram, or, in many cases, even a single best-resolved one. Moreover, even a single best-resolved tree is not the 'true' one. Thus, what is perceived as conflict is merely a consequence of overzealous tree-thinking. Characters conflict because we *think* they do. This is Darwin's legacy. And it is part and parcel of his widely accepted rational Newtonian explanation of the Grand Design of life, viz., natural selection.

PEI emerges as a consilient evolutionary model that demonstrates that the error of tree-thinking is precisely its simplistic, reductionist, and linearized cladistic idealization of evolutionary history and its nondimensional idealization of cladogenesis and species. In fact, *both* are asymptotically complex and maximally dimensional. This is precisely the 'what' of biological evolution, the reason why we study it in the first place, and even the reason why *we are here* to study it in the first place.

PEI does not conflict with 'descent with modification,' but it recognizes that organisms are autopoietic, that their self-determinacy renders their evolution not utterly stochastic and at least partially chaotic, and that their hierarchical organization permits decoupling of the evolutionary history of organismal traits. With PEI, we can appreciate that characters conflict on linearized trees because *they damn well can*. These properties that yield EI also likely canalize the generation of 'statistically significant' phylogenetic patterns. But, like fractals, the patterns have no *proximal* cause, i.e., there is no NS.

Theoretical advances in biological epistemology may present a dilemma for systematic/macroevolutionary biologists. These advances suggest that the Darwinian model of evolution is false, or at the very least, far too simplistic to serve the discipline usefully. But all current heuristic methodology assumes Darwinian evolution. Should the mainstream empirical systematics/macroevolutionary discipline bail on Darwin and be left you-know-where without a paddle? Or should the band continue to play on a sinking ship and publish results and conclusions predicted to be invalid/erroneous? If, like NS, we establish that there is no Santa Claus, should we continue to explain how he delivers toys to a billion children across the globe in just one evening?

As Olmstead and Medoya (2019), among others, *ought* to make clear, Darwinian phylogenetic conceptualization is obsolete. At the very least, contemporary systematic and macroevolutionary biology would do well to reconsider its obsession with tree-thinking and resolving definitively a bifurcate ‘tree of life.’ Evolution, like a forest, evidently is more than the sum of its trees.

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