Prediction in Selectionist Evolutionary Theory

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Selectionist evolutionary theory has often been faulted for not making novel predictions that are surprising, risky, and correct. I argue that it in fact exhibits the theoretical virtue of predictive capacity in addition to two other virtues: explanatory unification and model fitting. Two case studies show the predictive capacity of selectionist evolutionary theory: parallel evolutionary change in *E. coli* and the origin of eukaryotic cells through endosymbiosis.

1. Introduction: The Critique. Selectionist evolutionary theory has often been faulted for not being able to make novel predictions (e.g., Smart 1963; Popper 1974; Laudan 1977). More precisely, insofar as they even care about predictions, practitioners of selectionist evolutionary theory are taken to task for making neither (1) surprising nor (2) risky novel predictions. That is, they are critiqued for

1. inferring new phenomena that could *also* be inferred using alternative theories, such as structural, developmental, and historical contingency theories. The predicted phenomena are not surprising;
2. not being sufficiently rigorous about risky, novel predictions.
   A. When risky predictions are *not* borne out, this failure is either (i) downplayed and not reported or (ii) responded to by making ad hoc modifications to relevant parts of selectionist evolutionary theory in order to save it.
   B. Scant attention is paid to whether successful novel predictions

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> are even risky or not. Note that a prediction that is not risky is not a real test of selectionist evolutionary theory since the theory would not be falsified even if the prediction were not satisfied.

Such strategies indeed would be epistemically objectionable.

The standard response is to note that selectionist evolutionary theory does not make novel predictions but instead unifies and provides empirically adequate models. I accept the two theoretical virtues defended by the standard response, but go further. I argue that while the complexity and historicity of the systems investigated by selectionist evolutionary theory make predicting methodologically difficult, the theory indeed values and can formulate—under certain conditions—novel predictions that are surprising, risky, and correct.

This article is a preliminary report on prediction in selectionist evolutionary theory. In what follows, I briefly discuss unification, model fitting, and predictive capacity as theoretical virtues that provide credentials to the theory as a science. After this philosophical discussion, I use two case studies to show that selectionist evolutionary theory can indeed make novel predictions in an epistemically appropriate manner.

2. Three Theoretical Virtues. There are two standard responses to a Popper-style critique of the scientific credentials of selectionist evolutionary theory: appeal to the theoretical virtues of (1) explanatory unification or (2) model fitting (or both). While selectionist evolutionary theory may not make surprising and risky predictions, the argument goes, it still exhibits one or both of these theoretical virtues. In contrast, I hold that the theory expresses explanatory unification and model fitting as well as predictive capacity. Moreover, each virtue is deeply connected to empirical adequacy.

2.1. Explanatory Unification. The defense of explanatory unification as a virtue of selectionist evolutionary theory has roots in Darwin's use of Whewell's notion of consilience. Darwin (1903) wrote: "I have always looked at the doctrine of natural selection as an hypothesis, which if it explained several large classes of facts, would deserve to be ranked as a theory deserving acceptance" (1:139–140). This virtue of selectionist evolutionary theory continues to de defended (see, e.g., Ruse 1979; Kitcher 1981; for opposing arguments, see Lloyd 1983; Hodge 1989). The theory productively and reliably brings together disparate types of evidence—hybridization, developmental, morphological, biogeographical, and paleontological phenomena are placed under a single theoretical frame. Selectionist evolutionary theory conjoins multiple kinds of old evidence.

Consilience is a nontrivial achievement. Successful unification provides confirmation "boosts" for each piece of the theoretical structure (e.g.,

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Friedman 1974, 1981; Kitcher 1981, 1989). This is because confirmation is acquired indirectly: the empirical adequacy of one part of the theory strengthens a distinct, but *connected*, part.[1] Moreover, our confidence in the empirical adequacy of the whole theory also increases as a result of unification.[2] Lynn Margulis (1975) and E. O. Wilson (1998) speak to the importance of unification in evolutionary theory.

2.2. Model Fitting. The defense of model fitting as a theoretical virtue of evolutionary theory stems mainly from twentieth-century population genetics. Common statistical procedures for model fitting include (1) regression analysis and (2) Neyman-Pearson techniques for hypothesis testing (e.g., Godfrey-Smith 1994; Sokal and Rohlf 1994; Mayo and Spanos 2006). Model fitting is generally fleshed out in terms of accommodating, rather than predicting, the evidence.[3] In evolutionary theory, model fitting has been articulated in terms of the general notion of empirical adequacy (e.g., Beatty 1980; Lloyd 1983, [1988] 1994].

Models are often overfitted. That is, variables, parameters, and functions are altered or added in order to accommodate all of the available data. Lipton (2005) calls this "fudging." Hitchcock and Sober show that accommodation is easy. Moreover, they argue that "accommodational plasticity entails predictive impotence" (2004, 7, 22): "When a background theory is sufficiently plastic that it can accommodate any data that may come along, it is in no position to make predictions about what data will come along" (2004, 7). Overfitting occurs when accommodational plasticity is too high. This is a serious epistemic problem.

But *some* accommodation in the face of correcting evidence is necessary. Hitchcock and Sober (2004) suggest an accommodation strategy that employs the Akaike Information Criterion (AIC). The AIC estimates predictive accuracy in terms of both the fit-to-data and the simplicity of a model (Hitchcock and Sober 2004, 12). Accommodation and prediction are intertwined in this account. However, in evolutionary theory per se

1. For example, Friedman 1981, 9. Kitcher (1981) provides a response to "spurious unification."

2. At least in the 1980s, both Friedman and Kitcher emphasized the relation between unification and realism. The very presence of a unified theory seems to provide evidence for an inference to the (existence of the) best ontology. This real ontology grounds the unification. Van Fraassen (1980) and Laudan (1981, 1990) critique realist inferences based on unified theory. But van Fraassen also writes, "presumption of unity is pervasive in scientific practice" (1980, 83).

3. See Achinstein 1994, Brush 1994, and Hitchcock and Sober 2004 for clear *contrasts* between accommodation and prediction. Only the third paper argues that the two are intimately related. Williams (1982) conflates accommodation and prediction of evolutionary hypotheses.

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the emphasis continues to be on (1) models that are confirmed and are accommodated to the evidence through regression analysis, curve fitting, and hypothesis testing, rather than on (2) the predictive capacity of models in new evidentiary contexts.

2.3. Predictive Capacity. There is a strong tradition in the philosophy of science arguing that the weight or relevance of a particular observation or piece of data for theory testing, confirmation, and choice is significantly greater if it is a novel prediction. A novel prediction meets the following conditions: (1) it was not known before the theory was constructed, or it was not used in the construction of the theory, and (2) the observation or data follows—deductively or even with high probability—from the theory (e.g., Popper 1963; Lakatos 1970; Zahar 1973; Gardner 1982; Giere 1983; Howson 1988; Worrall 1989, 2006; and Laudan 1990). The view emphasizing the importance of novel predictions is sometimes referred to as "historicist" or "heuristic," as opposed to the "logical" view (e.g., Musgrave 1974; Mayo 1996; and Hitchcock and Sober 2004).

In contrast, the logical view holds that neither temporal order nor construction independence are epistemic issues directly relevant to theory justification (i.e., theory testing, confirmation, and choice). *Formalist* adherents of the logical view consider novel prediction to be completely irrelevant to theory justification (e.g., Hempel 1945, 1965; Carnap 1950; see Musgrave 1974). Other partisans are more forgiving. For *screening-off* advocates of the logical view, novel prediction is relevant to theory justification but only *indirectly*, as it gets philosophically screened off by more fundamental epistemic matters. Recent screening-off defenders have highlighted the following epistemic concerns: (1) severe testing through Neyman-Pearson, error-probing hypothesis testing (Mayo 1991, 1994, 1996, 2008; Mayo and Spanos 2006) or (2) contrastive testing through either (*a*) maximum likelihood measures or (*b*) model selection criteria, such as the AIC (Forster and Sober 1994; Sober 1994, 1999, 2008; Hitchcock and Sober 2004). Although Mayo and Sober disagree on basic aspects of theory justification (e.g., Need it be contrastive? How important is it to evaluate and control for erroneous inferences of theory rejections and theory likelihoods?), they agree that novel predictions are not necessary.

The historicist view and the screening-off logical view agree that surprising, risky, and successful novel predictions, *when they can be had*, are impressive.[4] Under this cogent perspective, such predictions are sufficient for theory justification, though they are still not necessary according to screening-off philosophers. Predictive capacity (i.e., the ability to make

4. Even Carnap seems, at times, to agree—e.g., Carnap 1945, 93.

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surprising, risky, and correct novel predictions) is the theoretical virtue, and aim that I focus on in the case studies.

3. Selectionist Hypotheses: Alternatives and Levels of Specificity. Popper and his students critique evolutionary theory *tout court* for lacking predictive capacity. I focus on a lower level of specificity: the predictive capacity of different types of theories within evolutionary theory. Alternatives to selectionist evolutionary theory include the following evolutionary theories: (1) structural (Gould and Lewontin 1979), (2) developmental (Amundson 2005), and (3) historical contingency (Beatty 2006). Selectionist evolutionary theory adopts *empirical* and *methodological* adaptationism (Godfrey-Smith 2001):

> *Empirical adaptationism*: "Natural selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance" (2001, 336).
>
> *Methodological adaptationism*: "The best way for scientists to approach biological systems is to look for features of adaptation and good design. Adaptation is a good 'organizing concept' for evolutionary research" (2001, 337).

Indeed, selectionist evolutionary theory is committed to (1) a single overall genealogy and (2) natural selection as (*a*) the main mechanism of evolutionary change and (*b*) the only mechanism that can be appealed to for predicting and explaining adaptations (Darwin [1859] 2001).

But the story is complicated. First, selectionist evolutionary theory and its models often exhibit each of the three theoretical virtues analyzed in Section 2. Second, many causes are operative in evolution. Thus, selectionist theory is not exhaustive (e.g., Beatty 1997; Winther 2008). It successfully predicts only *some* sorts of evidence (ditto for its alternatives!). Ultimately, a full evolutionary theory must integrate different kinds of predictive theories, as well as distinct types of evidence.

4. Two Case Studies. The case studies show how, through its predictive capacity, selectionist evolutionary theory can be successfully tested against its alternatives.

4.1. Parallel Evolution in the Bacterium E. coli. *Causal intervention* in the sense of controlled and randomized experiments can be used to ground the predictive capacity of selectionist evolutionary theory. For 2 decades,

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Richard Lenski and coworkers have performed a remarkable set of experiments on the bacterium *E. coli*. In 1988, Lenski founded 12 populations of *E. coli* from a single ancestral population. Each day, the bacteria are transferred into new liquid media and are allowed to reproduce. They exhaust the glucose in the media after approximately seven generations (i.e., 8 hours). The bacteria then enter into a lag phase and "must wait until their 'springtime' appears again the next day" (Lenski 2004, 226). The experiment has already surpassed 30,000 generations of bacteria.[5] The external conditions are controlled. The selection regimes are thus effectively isomorphic across the 12 lines. Evolutionary change can be measured in the laboratory.

Various kinds of parallel evolutionary changes have been observed. Each one of the 12 replicate populations has evolved larger-sized cells (Lenski 2004). Every population has lost the ability to catabolize most sugar sources other than glucose (e.g., each one is now unable to catabolize ribose; Cooper et al. 2001). These traits correlate strongly with fitness (Cooper and Lenski 2000; Lenski 2004). Moreover, the genetic architecture underlying the traits is modified in impressively similar ways across the 12 populations (Cooper, Rozen, and Lenski 2003).

Parallel evolutionary change is readily predicted by selectionist evolutionary theory. In fact, parallel evolution in diverse lineages with a common ancestor is expected, and *demanded*, given similar selection pressures. This prediction is

1. *Risky*: The absence of any significant parallel evolution would be a falsification of selectionist evolutionary theory.
2. *Surprising*: Parallel evolution is not readily predicted under alternative theories/models such as historical contingency theory, which emphasizes random genetic drift (RGD) as an evolutionary force.[6]

The novel prediction of parallel evolution in these experimental populations is a contrastive test of selectionist versus historical contingency theory. As Cooper and colleagues observe, "Parallel evolution of a trait across multiple lineages is often used as an indicator that the change is adaptive and has been shaped by natural selection" (2001, 2834). Note also that the data were not used to construct the predictions of either theory. In short, defenders of the mechanism of selection should be relieved that selectionist evolutionary theory shows this sort of predictive capacity.[7]

5. This number of generations is roughly equivalent to 750,000 years of human evolution.

6. However, perhaps novel predictions of *other* types of data will corroborate alternative theories (Lenski and Travisano 1994; Beatty 2006).

7. Similar types of parallel evolution, under isomorphic experimental protocols, have recently been found in yeast (Segrè et al. 2006).

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4.2. On the Endosymbiotic Origin of Eukaryotes. I now turn to a second type of case in which *comparative* (i.e., *phylogenetic*) *inference* is used in the context of selectionist evolutionary theory to formulate novel predictions. Causal-experimental manipulations are not possible here.

A scientific controversy during the '70s and '80s concerned the evolution of eukaryotic cells and their genome-containing organelles (e.g., mitochondria and chloroplasts) (Sapp 1994). There were two explicit alternatives:

1. The *endosymbiotic theory*, which postulated the serial union, and uptake, of radically different sorts of prokaryotes over evolutionary time (e.g., Margulis 1970, 1975, 1976).
2. A family of *autogenous theories*, which explained the internal origin of genome-containing organelles through the "pinching off" of membranes and subsequent intracellular sequestering of different internal genomes and metabolic networks (e.g., Raff and Mahler 1972, 1975; Uzzell and Spolsky 1974; Cavalier-Smith 1975; Reijnders 1975; Taylor 1976).

Although both appealed to selection, they provided different explanations and novel predictions.

Let me be very specific regarding the predictions made. Margulis (1975) provides an impressive list of 15 predictions inferred from the endosymbiotic theory. Natural selection is an explicit part of her framework (e.g., 1975, 23). She claims that while "several" of the "experimentally verifiable predictions are not absolute requirements of the theory, the phenomena listed here would be much more likely consequences of the serial endosymbiotic theory than other suggested models of eukaryote organelle origin (e.g., Raff and Mahler 1975)" (Margulis 1975, 28). Now, by observing that they are "much more likely consequences," she certainly considers the novel predictions surprising. But by noting that they are not "absolute requirements," she downplays their risky aspect. Even then, it is clear that four predictions were indeed risky: had they not been satisfied, Margulis's theory would have been significantly weakened, even falsified. Here are the novel predictions:

1. *Eukaryote transformation* (Margulis 1975, 29). "The phenomenon of gene transfer from prokaryotes or eukaryotic donors to eukaryote nuclei will be demonstrated." Compare: "the integration of the endosymbiont-proto-mitochondrion required wholesale transfer of genes from the endosymbiont genome to an unrelated nuclear genome. A mechanism by which this end may have been achieved is extremely difficult [!] to conceive" (Raff and Mahler 1972, 575–576). Margulis's surprising and risky novel prediction of gene transfer has

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been borne out; Raff and Mahler's hypothesis has been falsified (e.g., Adams and Palmer 2003; O'Malley and Dupré 2007).

2. *The red algal thallus was a multicellular heterotroph that acquired cyanelles* (Margulis 1975, 28). The proto-red algae were heterotrophs. That is, they ingested other prokaryotes and did not synthesize their own energy sources (e.g., sugars). They then entered into selectively beneficial mutualisms with blue-green algae. Hence, the "metabolic pathways and primary amino acid sequences" of their "photosynthetic plastids" should resemble those of "blue-green algae" and *not* those of red algae themselves, as the autogenous theory predicted. This novel prediction has been amply corroborated (e.g., Oliveira and Bhattacharya 2000). It confirmed endosymbiosis and helped falsify the family of autogenous theories.
3. *Hybridization between organelles and free-living micro-organism DNAs* (Margulis 1975, 30). "Direct nucleic acid hybridization studies will show homologies between organisms and organelles as sketched in Fig. 1 [the reticulated phylogeny on p. 27]." This was the clincher novel prediction. Consider three different genomes: (1) eukaryotic nuclear DNA, (2) mitochondrial DNA, and (3) the DNA from a contemporary free-living prokaryote hypothesized to be related to the proto-mitochondria (i.e., a photosynthetic alphaproteobacteria). Endosymbiosis predicts that (2) and (3) will be sister taxa, with (1) as the outgroup. In contrast, autogeny predicts that (1) and (2) will be the sister taxa, with (3) as the outgroup. Impressive gene sequence analysis, which controlled for differential rates of evolution and other confounding factors, has amply corroborated the novel predictions of endosymbiotic theory (e.g., Yang et al. 1985; Gray, Burger, and Lang 1999).
4. *Anastomosing phylogenies* (Margulis 1975, 30–31). "A consistent phylogeny at higher taxonomic levels (such as is available for tracheophytes and chordates) acceptable to botanists, zoologists and microbiologists . . . will only be possible after acceptance of the symbiotic theory. . . . Because of anastomosing [reticulating] relationships . . . the finalization of such a phylogeny may be difficult." Her surprising and risky novel prediction has been strongly confirmed. Endosymbiosis, and lateral gene transfer more generally, makes a neatly divisional, hierarchical tree of life difficult to draw.[8]

In summary, Margulis's 1975 paper presents a number of key surprising, risky, and correct novel predictions. She relies on comparative data and comparative inference to express the predictive capacity of her theory. At

8. See also Woese 2000; Doolittle and Bapteste 2007; and O'Malley and Dupré 2007.

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least one of the 15 predictions remains undecided: eukaryotic flagella stem from a spirochaete symbiosis (Margulis 1975, 30). However, most have been strongly supported. The predictive capacity of the endosymbiotic theory, which relies on natural selection and on a novel way to think about descent with modification—that is, reticulation—is strong.

5. Conclusion: Promises and Limits of Prediction. I have shown through two case studies that predictive capacity is an important theoretical virtue in selectionist evolutionary theory, contra the standard critiques it has received.

Some caveats are in order. By no means do I believe that predictive capacity is easily forthcoming in evolutionary theory, selectionist or otherwise.[9] It is hard work to make surprising, risky, and correct novel predictions for *complex systems* with *strong historicity* (see Pigliucci 2002).[10] However, through a well-designed causal-experimental protocol, Lenski managed to control and randomize experimental conditions in order to test selectionist evolutionary theory. And despite complexity and historicity, endosymbiosis is widespread and produces robust historical signals: gene transfers, gene homologies between eukaryotic organelles and related free-living prokaryotes, and reticulating phylogenetic patterns. Given these signals, comparative inference can be used to formulate novel predictions that test endosymbiotic selectionist theory.

There are other examples of the predictive capacity of selectionist evolutionary theory that should be developed: (1) Neil Shubin's prediction of an eventually found transitional fossil (Shubin 2008), (2) Richard Alexander's prediction of naked mole rats, (3) predictions made by sex-ratio theory (e.g., Schuster and Wade 2003), and (4) predictions regarding the structure and origin of the genetic code (e.g., Knight, Freeland, and Landweber 1999). Comparative inference is used for the first two predictions. Given the importance of mathematical modeling and simulation for the second two predictions, these require further philosophical exploration. This is a preliminary report.

In short, in addition to explanatory unification and model fitting, predictive capacity (i.e., the ability to make surprising, risky, and correct

9. Nor even in theoretical physics (Putnam 1981).

10. Popper also accepts the difficulty of making predictions in systems that are not "well-isolated, stationary, and recurrent" (1963, 339). He adds that "contrary to popular belief the analysis of such repetitive systems is not typical of natural science" (340). However, he also claims that "all theoretical sciences are predicting sciences" (339; see also "risky predictions," 36; "new kinds of test[s]," 118). He thus holds two views that do not fit together comfortably: prediction is rare in science, yet it is also its hallmark. I will not engage in exegesis here but merely note that it is the latter view that is most characteristic of Popper and his students.

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novel predictions) is a central theoretical virtue of selectionist evolutionary theory.

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