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Theory in Service of Narratives in Evolution and Ecology*

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ABSTRACT: Considering the role of theory in ecology and evolution, we argue that scientific theorizing involves an interplay between narratives and models in which narratives play a key creative and organizing role. Specifically, as scientists, we reason through the use of narratives that explain biological phenomena by envisaging, or mentally simulating, causal paths leading from a plausible initial state to an outcome of interest. Within these narratives, some parts may appear clear, while others may appear puzzling. It is at these tenuous junctions—junctions where reasoning is made challenging by conflicting possible outcomes—that we often build mathematical models to support and extend, or reject and revise, our narratives. Accordingly, models, both analytical and computational, are framed by and interpreted within a narrative. We illustrate these points using case studies from population genetics. This perspective on scientific theorizing helps to clarify the nature of theoretical debates, which often arise from the narratives in which math is embedded, not from the math itself. Finally, this perspective helps place appropriate creative weight on the importance of developing, revising, and challenging narratives in the scientific enterprise.

Keywords: modeling, mathematical biology, theory, narratives.

Introduction

A century ago, R. A. Fisher (1918) published his groundbreaking analysis showing how Mendelian genetics would account for variability in quantitative traits via the combined action of many genes. His article demonstrated the compatibility of Darwinism and Mendelism and set the stage for the emergence of the field of theoretical population genetics. With training in mathematics, statistics, and physics, Fisher saw deep connections between biological and nonbiological problems as well as the need for analytical tools to make sense of the increasing amount of biological data. For example, Fisher brought in the “calculus of correlations” to tackle the “statistical properties of any feature determined by a large number of Mendelian factors” (Fisher 1918), the “analytical treatment of the Theory of Gases” to describe the distribution of allele frequencies (Fisher 1922*a*), and maximum likelihood to use “the whole of the information supplied by the data” when analyzing crossover frequencies (Fisher 1922*b*). Theoretical modeling—roughly as we now recognize it—became an integral part of biology in three different areas at about this time: population genetics, ecology, and enzyme kinetics (Maynard Smith 1992). It is thus appropriate that the 2018 Vice Presidential Symposium of the American Society of Naturalists highlights the contributions of mathematical models to ecology and evolution over the past century.

Our goal in this article is to inquire about the nature of theorizing in evolution. We argue that theorizing involves an interplay between narratives and models (both mathematical and computational) and that the narratives play a key creative and organizing role. By narrative, we mean a form of mental reconstruction where we imagine a scenario and mentally simulate how processes interact to lead—in this case, evolve—from an assumed starting point to an outcome of interest. As scientists, narrative reasoning allows us to explore, at a high level, the possible trajectories that evolution may take.

The reader may be surprised at the emphasis we place on narratives, given that “stories” are usually singled out as examples of bad science. Gould and Lewontin, for example, decried stories of adaptation as ad hoc explanations in the absence of empirical support:

> Often, evolutionists use consistency with natural selection as the sole criterion and consider their work done when they concoct a plausible story. But plausible stories can always be told. (Gould and Lewontin 1979, p. 588)

This valid concern over just-so stories has, however, provoked a general dismissal of narratives and has prevented our field from discussing the critical role that narratives play in the theoretical exploration of scientific phenomena.

As eminent narrators of evolution themselves, Gould and Lewontin were not criticizing narratives per se but narratives with blinders—blinders that prevent theorizers

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from considering nonadaptive explanations for evolutionary phenomena (e.g., drift, pleiotropy, or constraint). It is not narrative thinking that they ask us to reject but overly constrained narrative thought.

Traditional views on theory and theorizing have focused primarily on the "laws" or "principles" that figure prominently in a field (e.g., Newton's laws, Darwin's principles) and on the mathematical models that underlie these and other theories (Suppe 1977; Lloyd 1994). Emphasis on mathematical models has also been pervasive within population genetics and population biology (Levins 1966; Maynard Smith 1974). For Levins (1966), a "satisfactory theory is usually a cluster of models." Narratives have largely been left out in discussions of theories and models (Morgan 2012; Rosales 2014; Morgan and Wise 2017).

We argue that in theorizing, narrative thinking allows a critical phase of exploration, motivates mathematical modeling, provides a contextual framework for interpreting empirical and theoretical results, and generates subsequent predictions for further testing via experiments, data analysis, modeling, and so on. At their strongest, narratives investigate alternative explanations, explore implications broadly, and consider what aspects in the narrative account are weak and require further elaboration and testing.

In this article, we discuss both classical examples and recent examples from our group to highlight the important interplay between narratives and theoretical models, as celebrated in this collection. We end by discussing how a stronger consideration of the role of narratives can affect both scientific practice and training.

On Narrative Reasoning

Traditionally, psychologists hypothesized that humans reasoned via formal rules of logic and inference. According to Johnson-Laird (2010), this view of reasoning faced several challenges. In practice, we do not think solely by processing axiomatic statements and their conclusions. Moreover, the errors in logic that humans make indicate that we bring experience, knowledge, values, and context to bear as we solve problems.

As an example, Johnson-Laird (2010) recounted an experiment where subjects were asked to consider the following logic problem:

> All of the French in the restaurant are gourmets.
> Some of the gourmets in the restaurant are wine drinkers.
> What, if anything, follows?

Most subjects spontaneously inferred that some of the French in the restaurant are wine drinkers. Contrast this with the results when subjects were asked to consider a variant of the logic problem:

> All of the French in the restaurant are gourmets.
> Some of the gourmets in the restaurant are Italian.
> What, if anything, follows?

Now, very few subjects spontaneously concluded that some of the French in the restaurant are Italian. Logically, the problems are identical. But we reason in different ways, depending on the context of the problem.

Johnson-Laird argued for an alternative view of human reasoning (see also Nersessian 1992, 2008):

> Reasoning depends on envisaging the possibilities consistent with the starting point—a perception of the world, a set of assertions, a memory, or some mixture of them. . . . On this account, reasoning is a simulation of the world fleshed out with our knowledge, not a formal rearrangement of the logical skeletons of sentences. (Johnson-Laird 2010, p. 18243)

In the example given above, we are much more likely to mentally simulate a scenario where the French people in the restaurant drink wine, because of the long association between wine cultivation and drinking in France, than we are to mentally simulate French people who are also Italian, even though dual citizenship is possible. We simulate scenarios in a manner that depends on our knowledge.

In attempting to understand evolutionary phenomenon, we argue that we also envisage the possible paths leading from a plausible initial state to an outcome of interest. We carry out a mental simulation of evolutionary processes unfolding along such a path or paths. Johnson-Laird calls this process of reasoning a "mental model," while Nersessian (1992) refers to "thought experimenting" or "simulative model–based reasoning." We prefer the term "narrative" because modeling and experimenting tend to imply a more detailed, linear process of rigorously evaluating each step along the path. By contrast, when we reason narratively, we often dive deeply into some details while skating over others. We do not figure out all of the details along the way if we are confident with the overall direction. We may not even bother to specify all of the intervening steps. We can focus narrowly on one outcome of interest, but we can also zoom out to consider how new pieces fit into the larger story arc that scientists use to understand and investigate the world. Furthermore, reasoning is not always entirely linear. We can make creative leaps or change course midway in our thinking. This ability to skate along the surface and creatively explore in our thinking is familiar to us in our traditions of storytelling—in our narratives. For this reason, we use the term "narrative thinking" to refer to the mental exploration and mental simulations that we use when theorizing and that motivate us to construct theoretical models to better understand evolution.

On Narratives and Models

It is said that theoretical models inform us of what is possible in nature (Lewontin 1968; Caswell 1988), and in this sense they contribute to our explanatory understanding of phenomena. While we ascribe this capacity to explain to "models," it is actually the narratives within which theory is born that provide models with their explanatory power, not the equations themselves.

To illustrate this point, consider the differential equation

$$\frac{dx}{dt} = a\,x(1 - x). \tag{1}$$

This equation is used and interpreted in very different scientific contexts: to describe selection (x being the allele frequency and a the selection coefficient) or to describe logistic growth (x being the number of individuals relative to the carrying capacity and a the intrinsic growth rate). It is not equation (1) or its solution that tells us how rapidly a population evolves or grows in size, it is the narrative that poses this question and gives rise to the equations that provide insight. Equation (1), on its own, would be read and interpreted differently by an evolutionary biologist (response to selection), by an ecologist (density-dependent growth), or by a chemist (autocatalytic enzyme concentration). The same equations can be used to explore different phenomena and answer different questions, but without the framing provided by the narrative, equations carry no explanatory weight.

Denniston and Crow (1990) also emphasize the point that equations are not unique to a particular biological scenario. The same equations, and the same dynamics, can be generated by multiple evolutionary models using different fitness assumptions. For example, diploid selection with overdominance can be described by the same dynamical equations as haploid selection with frequency dependence. Such alternative fitness sets always exist and have "quite different biological meanings" (Denniston and Crow 1990). What is the source of this "biological meaning"? We argue that it is the narrative in the mind of the modeler that leads to the construction, analysis, and interpretation of the equations.

Understanding the narratives that generate models is thus key to knowing why certain equations are produced and analyzed out of the infinitely large world of possible mathematical models. Mathematical models are born in a narrative context of theorizing. To better understand and teach modeling as a scientific method, we must thus pay greater attention to this birthing process.

When confronted with a problem phenomenon, the theorist envisages plausible routes leading to the phenomenon by using narratives. The structure of these narratives involves an initial scenario and sequence of stages leading to the event to be explained. Several of these stages may borrow support from previous theory, while the outcome at other stages may remain unclear. It is where the narrative is murky—where different possible trajectories can be imagined or where conflicting forces make the outcome unpredictable—that theoreticians focus their mathematical efforts, the results of which can provide support for the narrative account or cause it to crumble.

This perspective shifts the role of mathematical modeling. Narratives define the problem space in which modeling is needed. In turn, modeling (including mathematical analysis and computer simulations) plays both a supportive role, confirming or refuting the narrative, and a creative role, identifying unexpected outcomes that motivate new narrative reconstructions.

By mathematically exploring the possibilities suggested by a narrative, models guide the narrative toward feasible outcomes and away from impossible outcomes. In this sense, models are crucial accessories to a narrative understanding of the world. Without models, we run the risk of believing too much in our narratives without focusing on problematic components.

Narratives also allow creative exploration before spending too much time working out the mathematical details. They allow us to sail above the ecological and evolutionary dynamics, considering multiple stages and interacting processes. If the reasoning in a narrative appears solid throughout, a theoretician may conclude that there is little point to mathematical modeling—the results will likely be "boring" (i.e., in line with expectations). Modeling is worth the effort when there is some chance of surprise or some need for precision. Theoreticians thus seek motivation before embarking on a model, from kinks in their narratives, from unexpected or unexplained observations, or from conflicts between narratives (held by themselves or others).

Historical Case Studies

In this section, we use case studies from evolutionary theory to gain insight into the narrative explorations that occur in the field, choosing examples that highlight the importance of narratives in describing evolutionary processes (Crow 1992), in explaining why similar models can generate dissimilar conclusions (Fisher 1928; Wright 1929), and in reconciling different perspectives (Felsenstein 1974).

A Model without a Narrative

In 1992, Jim Crow recounted an interesting exchange between the physicist Erwin Schrödinger and J. B. S. Haldane about the "hornless cattle problem." In his letters, Schrödinger defines p as the proportion with horns, with q (heterozygous) and r (homozygous) defining the two classes of hornless cattle. He then wrote the recursion equations:

$$x' = \frac{x(1+y)}{2y}, \tag{2a}$$

$$y' = \frac{x(1+y-x)}{y}, \tag{2b}$$

where $x = r + q/2$ and $y = r + q$. Schrödinger goes on to discuss an approximate solution. What struck Crow, and what likely bothers you now as the reader, is that the story was missing from the letters. There was no narrative setting the stage for these equations or posing a question to be answered with them. Without this narrative, the motivation to solve the equations is missing, as is any sense of what we might gain from the solution.

Crow invites the reader to infer what the biological scenario might have been but is kind enough to supply the answer:

> Here is one situation that Schrödinger's equations describe. Suppose a breeder wants to get rid of his dangerous horned cattle. He can't afford not to breed each cow, but he can easily afford to discard some bulls, so each generation he mates only hornless bulls. (Crow 1992, p. 239)

Equation (2) then describes the frequency dynamics of the hornless allele (x) and the dominant trait (hornlessness, y) when selection is applied in only one sex and only individuals with the desired trait (hornlessness) are kept. With the narrative revealed by Crow, these two particular equations gain meaning and can be placed within the right context to ask questions, such as how long must breeding proceed before most cattle are hornless? Or how much less efficient is selection on males alone than selection on both sexes?

Crow's account of the Schrödinger-Haldane episode is interesting because it reveals to us how little scientific meaning is intrinsic to equations and how much more meaning is imbued when a model is presented in its narrative context.

Fisher and Wright on the Evolution of Dominance

The majority of newly arisen mutations are recessive and masked (partially or fully) by the more dominant wild-type allele. Fisher and Wright pondered the evolutionary circumstances that would lead to dominance of the wild type, considering the possibility of modification of dominance over evolutionary time versus the (evolved) nature of physiological systems. They took different mathematical approaches to reach similar quantitative conclusions about the modification of dominance at mutation-selection balance, both finding that selection on genetic modifiers of dominance would be very weak. But this mathematical result was interpreted quite differently from the narrative perspectives of Fisher and Wright (Rosales 2014). The resulting debate between the two ultimately led Fisher and Wright to cease correspondence (Provine 1995), in what we consider to be a clash of narrative perspectives.

In his 1928 article, Fisher investigated the evolutionary fate of a gene that modifies the fitness of heterozygotes at a selected locus. As was typical in the theory of the time, he ignored genetic associations between the modifier and selected loci (see Ewens 1965). Instead, he calculated the fraction of future generations that would descend from deleterious mutations in heterozygous form, reasoning that this fraction would determine the possible scope for dominance modification. From his result, Fisher drew the conclusion that "the fraction of ancestry is . . . exceedingly small," being proportional to the mutation rate. Despite this inauspicious result, Fisher concluded the following:

> Nevertheless, considering the ratio of the periods of time available it seems not impossible, but rather probable, that the reaction of the wild type to the heterozygous phase of a recurrent mutation has in some cases at least been modified to an appreciable extent. (Fisher 1928, p. 121)

Wright (1929) used a different modeling approach, estimating the rate of change of an allele that modifies dominance (but still ignoring genetic associations), also reaching the conclusion that selection in favor of a modifier of dominance is "decidedly small," on the order of the mutation rate. He concluded that such weak selection in favor of dominance modifiers is unlikely to be the "*major* factor controlling their fate" (italics in original).

As described in more detail in his book *The Genetical Theory of Natural Selection* (1930), Fisher's narrative view of evolution focused on the average effect of an allele (Rosales 2017). Accordingly, the effects of an allele could be usefully averaged across all of the contexts in which it appears; the resulting average fitness effect ultimately determines the long-term evolutionary outcome. Within this narrative context, alleles that have beneficial average effects would spread, if slowly. Accordingly, even a minute selective benefit of a modifier of dominance would, over time, have significant effects and make heterozygotes resemble the wild type:

> In the course of time the height of a mountain is lowered by 1,000 feet. . . . What an improbable event! . . . Equally improbable seems the extinction or "fixation" of modifying genes, a very rare, but occasionally necessary, consequence of the slight constant tendencies at work in modifying their frequencies. (Fisher 1929, p. 556)

By contrast, Wright's narrative focused on the interplay of evolutionary processes (Rosales 2017). We see this narrative at work both in his derivation of the steady-state distribution for allele frequencies, incorporating selection, mutation, migration, and drift ("Wright's distribution"; Wright 1931), and when he highlights drift as a creative component in the shifting balance theory of evolution (Wright 1932). Wright (1977, pp. 520–521) highlights the following passage from Fisher as best expressing Wright's viewpoint on the modification of dominance:

> [Wright] suggests that the gene ratio of the modifying factors will either be held in stable equilibrium by more powerful forces so that a minute selective intensity will merely shift to a minute extent this position of equilibrium and produce no progressive effect . . . much as wind blowing along a railroad will not exert any effect in accumulating rolling stock at the leeward terminal. (Fisher 1929, p. 155)

Within Wright's narrative, very weak selection on a modifier of dominance would be overwhelmed by other processes, including genetic drift, pleiotropic effects of the modifier, and even mutation at the modifier genes themselves. Selection could not be isolated by averaging over all contexts but must be considered as part of an interacting system.

The key point for our purposes is that Fisher and Wright agreed about the core mathematical result: selection on modifiers of dominance is weak at mutation-selection balance. Mathematics was not the source of their disagreement. Their disagreement stemmed from the different narrative contexts in which they placed and interpreted the results of their modeling. Their narratives clashed.

Felsenstein on the Evolution of Sex

Our next example illustrates the opposite point: that clashing narratives can be unified through the construction of a new narrative that bridges the clash, using Felsenstein's classic 1974 article on the evolution of sex as a case study.

Why sex has evolved to be so commonplace is one of the oldest puzzles in evolutionary biology. One prominent theory stems from a point briefly touched on by Fisher in his book:

> For, unless advantageous mutations occur so seldom that each has had time to become predominant before the next appears, they can only come to be simultaneously in the same gamete by means of recombination. (Fisher 1930, p. 104)

A similar argument was voiced by Muller (1932). In the context of Fisher's evolutionary narrative, recombination allows alleles to experience their average effect over genetic backgrounds. Without recombination, many beneficial mutations would be lost because they happen to appear in an unfit context, separated from other beneficial alleles segregating within the population.

As theoreticians built models of the Fisher-Muller hypothesis, however, a controversy arose, with studies reaching seemingly opposite conclusions. To highlight the nature of this controversy, Felsenstein (1974) focused on two articles published in *The American Naturalist*: Crow and Kimura (1965) and Maynard Smith (1968).

Inspired by Fisher's argument, Crow and Kimura (1965) modeled how much time it would take for one beneficial mutation to become predominant, so that the next beneficial mutation would be nested within the same lineage as the first. In the absence of sex and recombination, beneficial mutations that were not nested within the first lineage would be doomed to extinction (assuming that the first lineage does indeed fix). With sex, however, these doomed mutations could be rescued by recombining onto the genetic background of the first mutation. From their mathematical results, Crow and Kimura concluded that sexually recombining populations could adapt faster, much faster in large populations with many weakly beneficial mutations.

Maynard Smith (1968) took a different approach, providing an interesting counterexample. He developed a two-locus haploid model of selection with multiplicative fitnesses between the loci. Starting from a population at linkage equilibrium, he showed that genetic associations would not develop between the loci and that sex and recombination would thus have no impact whatsoever on the rate of adaptation.

Reviewing these and a series of subsequent models, Felsenstein (1974) highlighted a key distinction between models that found an advantage to sex and those that did not: the former incorporated genetic drift. As argued by Felsenstein, mutations that occur within a finite population generate linkage disequilibrium by the very fact that they arise on a particular genetic background and are subject to stochastic variation as parents produce a finite number of offspring. Genetic associations do not arise in deterministic models of an infinite population with multiplicative selection, however, because mutations immediately appear on all genetic backgrounds, and there is no stochasticity when there is an infinite number of each genotype.

To bridge the controversy, Felsenstein (1974) connected the conflicting results on the benefits of recombination to an article by Hill and Robertson (1966). To determine the limits of adaptation in a finite population, Hill and Robertson had simulated adaptation at two loci. Even starting with no linkage disequilibrium, they demonstrated that genetic drift tends to hinder adaptation. They explained this phenomenon in two ways. The first views selection at one locus as reducing the effective population size (and, hence, increasing drift) experienced by another locus. The second emphasizes that selection in the presence of drift tends to generate negative disequilibrium, on average, an association that reduces the rate of adaptation and generates a benefit to recombination. This disequilibrium arises because evolution slows and genetic associations persist when, by chance, beneficial alleles occur on separate backgrounds, whereas evolution speeds up when beneficial alleles are found together by chance, which rapidly depletes the genetic associations. It is interesting to note that Hill and Robertson provided two narrative explanations for the interference observed in their simulations, allowing their result to be viewed from (and useful to) different narrative perspectives.

Tying together the narratives of Fisher, Muller (including his later work on Muller's ratchet), Crow, Kimura, Maynard Smith, and later theoreticians, Felsenstein argued that the advantage to recombination comes from reducing selective interference between loci, coining this advantage the Hill-Robertson effect:

> Even when there are initially many copies of each favorable mutant, a finite population should build up linkage disequilibrium by random genetic drift, and the average effect of such disequilibrium should be that different loci interfere with one another's fixation. So the chance that favorable mutants fix must be less in a population without recombination than in one having recombination. (Felsenstein 1974, pp. 745–746)

In this case study, we see how different evolutionary narratives can each be plausible as framed and yet conflict. While appearing to create an impasse, scientists can take elements of each narrative and reframe them under a broader narrative umbrella. In Felsenstein's case, the broader narrative focused on the effects of drift on selection, effects that were negligible in deterministic models but critical in stochastic models of finite populations.

With this bridge in place, Felsenstein then extended the narrative in a very insightful way. While all of the arguments described above are framed as a group selection benefit to sex—sex helps populations adapt faster—Felsenstein's narrative focus on linkage disequilibrium allowed him to consider the advantage of sex in a single population, using computer simulations to model the fate of a modifier of recombination in the context of the disequilibria generated by the joint effects of drift and selection (Felsenstein and Yokoyama 1976). This study inspired my (S.P.O.) later work with Nick Barton, attempting to solidify the analytical foundation for Felsenstein's narrative (Otto and Barton 1997; Barton and Otto 2005).

In short, it was Felsenstein's narrative bridge that allowed the field to make sense of conflicting results and to see why recombination could evolve to lessen selective interference among loci within finite populations.

Introspective Case Studies

In this section, we reflect on some of our own studies to discuss how narratives can inspire modeling and can be revised in light of the mathematical results.

As mentioned above, models can be profitably built wherever one finds conflicting narratives. For example, the model explored by Otto and Goldstein was born from such a narrative conflict:

> By having two copies of every gene, diploids are virtually assured of producing at least one normal copy of any protein. As a result, selection should favor diploids over haploids when both groups have the same deleterious allele frequency. . . . Diploids carry twice as many alleles as haploids, however, and therefore experience a higher mutation pressure. As a result, the mutational load at equilibrium in a diploid population is twice that in a haploid population. (Otto and Goldstein 1992, p. 745)

So which is it? Does evolution favor genes that increase the diploid phase and benefit from masking deleterious mutations or that increase the haploid phase and benefit from a lower mutation load? At this juncture, the narrative was murky and needed modeling to clarify how evolution would proceed.

Clues were provided in a simulation study by Perrot et al. (1991). They modeled a gene that determined the ploidy level at the time of selection, which was unlinked to a gene experiencing selection. As long as the masking advantage to diploids was high enough (the dominance coefficient, h, was less than ~0.5), diploid life cycles were favored. But this threshold was not exactly at 0.5, and Perrot et al. noted that linkage disequilibrium built up between the two genes. These results hinted that recombination between the modifier and the selected locus might play a critical role.

With these clues as inspiration, we developed a mathematical model to determine how recombination influenced the evolution of life cycles (Otto and Goldstein 1992; Otto and Marks 1996). Based on the results, we updated the narrative of the evolution of haploidy and diploidy to account for the role of recombination. Although masking by diploids allows deleterious mutations to persist and reach a higher frequency, this increased load is dissipated by genetic mixing with other individuals when rates of sex and recombination are high. Consequently, in highly recombining populations, genes promoting diploid life cycles spread because they benefit their carriers from masking deleterious mutations without imposing a much different mutation load. When sex and recombination rates are rare, however, haploids purge deleterious mutations more efficiently and are protected from the higher load carried by diploids by rarely recombining with them. Thus, in less recombining populations, genes promoting haploid life cycles spread because of their lower mutation load.

Modeling led us to revise our narrative thinking. Rather than focusing on the evolutionary advantages of diploidy, models helped us predict the circumstances under which selection and mutations would favor the evolution of more diploid versus more haploid life cycles. These predictions could then be tested empirically to determine whether an association exists between diploidy and high rates of sex and recombination. Although we lack sufficient data on rates of genetic mixing in clades with ploidy variation (Otto and Marks 1996), rough comparative analyses failed to find an association between inbreeding and life cycles in brown algae (Bell 1997) or between the degree of sexuality and life cycles in green algae (Mable and Otto 1998). Furthermore, this genetical theory does not explain the persistence of many taxa that alternate between multicellular haploid and diploid generations (Mable and Otto 1998). The lack of empirical support in turn led to the narrative exploration (and subsequent modeling) of other differences between haploids and diploids, including differences related to dispersal (Bell 1997; Bessho and Otto, manuscript in preparation), competition for resources (Hughes and Otto 1999), protection from somatic mutation (Orr 1995), and rates of adaptation (Orr and Otto 1994).

Furthermore, we developed an experimental system using the budding yeast, *Saccharomyces cerevisiae*, which can be propagated at different ploidy levels, to probe assumptions of these narratives, test predictions from models, and improve our ability to connect theoretical and empirical approaches more broadly. Often these experiments have thrown up unexpected results that led us to rethink our assumptions (e.g., finding that asexual diploids generate genetically variable offspring through mitotic recombination at biologically significant rates [Gerstein et al. 2014], that ploidy levels are labile over the course of an experiment [Gerstein et al. 2006], and that mutations do not have the same selective coefficient in haploids and diploids [Gerstein 2012]).

In other cases, models are built to help us move past a point where our narrative reconstruction becomes stuck because the biological process is too complex to predict the outcome with any confidence. As an example, most narratives of sexual selection focus on males that do or do not bear a trait. What happens, however, in cases where there is overdominance in males? Overdominance arises often in models of sexual selection when the allele favored by sexual selection differs from the allele favored by natural selection as long as heterozygous males fare reasonably well on both fronts. Should mating preferences evolve to favor heterozygous males or one homozygote over the other? A narrative exploration of sexual selection can lead to this question but be unable to provide an answer with any certainty. The narrative thus framed and posed a question, motivating a mathematical model to more concretely explore what could evolve.

In models like this, where the outcome is so uncertain, surprises can happen. In this case, modeling showed that a new female preference allele is favored no matter how it alters female mate choice as long as the female preference and male trait loci are sufficiently linked (Otto 1991). Conversely, with loose linkage, no new preference allele would invade.

As bizarre as this result seems, modeling tools—in this case an evaluation of the development of linkage disequilibrium—can help provide insights that can be used to revise our narrative understanding. Here, disequilibrium builds such that a new preference allele that causes females to prefer one of the trait alleles (say T) becomes genetically associated with the other trait allele (say t). With tight linkage, the new preference spreads because this combination of disequilibrium with t and a preference for T produces more of the fittest type of offspring—heterozygotes. With loose linkage, however, recombination moves the new preference allele off of this genetic background (with t) and onto the other background (with T), making it more likely that homozygotes (here, TT) result from mating preferentially (with T), which prevents the spread of the new preference allele.

The results of this model, embedded into an expanded narrative of sexual selection, provide a novel explanation for the establishment of sexual preferences within a population via the spread of preference alleles linked to loci experiencing overdominant selection. This reasoning predicts that overdominance should lead to highly labile evolutionary changes in female preferences at nearby loci.

Models can also push narratives further. For example, in predominantly diploid organisms (like seed plants and animals), haploid selection may still occur among the gametes. This phase of selection is often ignored because it is so transient, but competition among gametes is often severe, allowing a short haploid phase to experience a disproportionate amount of selection. Accordingly, we have used models to extend our narrative understanding of how conflicting selection pressures between the haploid and diploid phase ("ploidally antagonistic selection") can impact the maintenance of variation (Immler et al. 2012), the strength of gametic competition (Otto et al. 2015), and even the evolution of sex chromosomes (Immler and Otto 2015; Scott et al. 2018). Extending the narrative through theory then suggests experiments, for example, to investigate the potential for haploid selection among sperm (Alavioon et al. 2017) or the nature of selection acting at sites linked to new sex chromosomes (Sandler et al. 2018).

In other cases, models are constructed not to clarify what is obscure in the narrative but to make quantitative predictions. For example, both empirical and theoretical work has shown that migration rates can evolve, so it is reasonable to imagine that fish could evolve lower migration rates around marine protected areas, reducing their mortality due to fishing. Nevertheless, there remains a quantitative question: Can evolutionary change happen fast enough to make a difference to the efficacy of marine reserves within our lifetimes? Modeling suggests that the answer is yes for some species that are currently overharvested and that have short generation times, such as skipjack tuna, but no for others, such as great white sharks (Mee et al. 2017). Here, the narrative was clear, but a model was still needed to provide a quantitative evaluation.

Finally, models can be born from the need for a new tool within the community. In these cases, the narrative may be clear, but interpreting data may necessitate a novel statistical framework that requires a model. As an early historical example, Fisher (1922*b*) developed a likelihood model to obtain a chromosome map from crossover data.

As another example, we have used models to build a tool to measure how traits may affect the speciation or extinction rate of a species (Maddison et al. 2007). Traditionally, the correlation between a trait and diversification rate (the difference between the rate of speciation and extinction) has been assessed statistically by sister species comparisons (e.g., finding that plant-feeding among insects increases the diversity of clades with this trait compared with sister clades that do not feed on plants; Mitter et al. 1988). Yet more data exist within phylogenetic trees than just which groups are sister to each other. To fit data on trait evolution across an entire phylogeny, we needed to construct a probabilistic model that tracked both transitions between trait states and the branching pattern in a phylogeny. In Maddison et al. (2007), we developed such a probabilistic model, so that the likelihood of different parameters could be estimated from the data (the tree shape and the traits carried by species today). In this case, the narrative was fairly clear, but the approach was not. Why did it take so long to develop a tool given that the narrative and need were apparent? The mathematical solution that we used required a combination of perspectives among the authors (framing the process starting with the data and working backward in time, determining the right variables and modeling them dynamically, and seeing how the process could be encoded computationally), which led us to a place in our collective thought process that made it suddenly apparent to us (over coffee, of course!) what a mathematical route into the problem could be. That is, narrative theorizing allowed us to collectively explore and quickly consider different modeling approaches and their potential pitfalls (e.g., modeling forward in time would have to consider all of the extinct species that are not known) before hitting on an approach that might work. Once that narrative structure was in place, we could develop mathematical equations and compute the likelihood of the data to measure the impact of a trait on speciation and extinction.

Conclusions

In this article, we celebrate a century of modeling in evolution and ecology by exploring the nature of scientific theorizing. Evolutionary and ecological processes are complex. How these processes interact and affect the dynamics of populations can, in part, be narratively envisioned, building on prior knowledge and experience to predict what might happen using mental reconstructions. Probing that envisioned narrative and determining its weak points is essential to reject false reasoning. Exploring causal alternatives is necessary to identify the range of possible conditions that could account for an observed phenomenon. Iteratively challenging, expanding, and testing our narratives—empirically and theoretically—allows us to develop a more fulsome and robust understanding of the world.

Narrative exploration is also the birthing ground of mathematical models. Here we have highlighted the interplay between narratives and mathematical modeling. Beyond helping to account for which models are built and which are not, the perspective presented here helps to clarify the nature of theoretical debates. As we argue, these debates often arise from the narratives in which math is embedded, not the math itself. A recent example is the kin selection versus group selection debate, where both sides note that the mathematical results of the other side can be "right" but the sides differ dramatically in the narrative context in which the math is placed and obtains meaning (Kramer and Meunier 2016). A narrative context can also help to clarify the source of a scientific disagreement by considering it within the larger narrative framework that different people use to approach problems (e.g., the opposing views of Fisher and Wright on the evolution of dominance).

A narrative perspective also helps to see how a controversy over what is the "right" model of a given phenomenon can dissolve when the conflicting models are embedded within a more encompassing narrative framework (e.g., Felsenstein's [1974] perspective on the evolution of recombination).

Finally, a narrative perspective encourages those who want to develop theoretical models to focus on the uncertain—to examine each part of a narrative for a phenomenon in order to assess what has strong support and what does not. A narrative perspective also encourages reflection on our collective work, allowing us to see the scope and possible limitations of current models. This perspective places additional creative weight on the importance of developing, morphing, and challenging narratives. One of the biggest obstacles in science is becoming wedded to one's ideas and forcing evidence to fit into our narrative frameworks. Conversely, it is impossible to ever know if our narratives have explored a sufficient space of possibilities to account for a phenomenon. But we can actively and openly seek out conflicting ideas and data. This perspective encourages us to share our narrative understandings (e.g., through talks) and keep an eye out for where our narratives conflict with the narratives of others. Similarly, it encourages theoreticians to work closely with experimental and observational data, as these data can yield unexpected results that challenge our reasoning, as we have found repeatedly in our research with yeast. These cracks in our narratives are where we are most likely to find a treasure trove of unexpected results, which can in turn reshape our understanding of the world and lead to new empirical predictions and theoretical questions. Highlighting these weak spots can thus help us to recognize and loosen our blinders and to probe our narratives further, refining our reconstructions of evolutionary change.

Conversely, we should work as a field to avoid homogenizing how we see problems, which narrows our collective chances of forging new ground. We should encourage training that empowers students to develop their own narrative understanding of phenomena and to learn to identify and explore what is weak. This requires a stronger emphasis on listening and following their footsteps, probing their logic. We should also encourage diversity of backgrounds and experiences, as these shape how we think and approach a problem. We should also attempt to describe more fully our own narrative path, to explain how we corrected our understanding and our models, rather than describing only our final narrative, so that we can all become better and more rigorous interpreters of the world around us.

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