An Effective Mutualism? The Role of Theoretical Studies in Ecology and Evolution*

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Abstract: Theoretical models often have fundamentally different goals than do empirical studies of the same topic. Models can test the logic of existing hypotheses, explore the plausibility of new hypotheses, provide expectations that can be tested with data, and address aspects of topics that are currently inaccessible empirically. Theoretical models are common in ecology and evolution and are generally well cited, but I show that many citations appearing in non-theoretical studies are general to topic and that a substantial proportion are incorrect. One potential cause of this pattern is that some functions of models are rather abstract, leading to miscommunication between theoreticians and empiricists. Such misunderstandings are often triggered by simplifying logistical assumptions that modelers make. The 2018 Vice Presidential Symposium of the American Society of Naturalists included a variety of mathematical models in ecology and evolution from across several topics. Common threads that appear in the use of the models are identified, highlighting the power of a theoretical approach and the role of the assumptions that such models make.

Keywords: ecology, evolution, mathematical models, proof of concept, theory.

The 2018 Vice Presidential Symposium of the American Society of Naturalists, “Advances through Theory: An Exploration of Mathematical Models in Ecology and Evolution,” was atypical in its choice of focus on a research technique rather than a conceptual topic. Theoretical studies are tied together in important ways, however, ranging from the procedural (e.g., their need to employ simplifying assumptions) to their goals (to use mathematics and/or statistics to abstract biological processes)—and often to their reception by empiricists. Here I briefly discuss the prevalence of theoretical studies in ecology and evolution, the perception of theory by empiricists, and how theoretical studies are cited in empirical articles. I then elaborate on the roles that theoretical studies play in ecology and evolution, concentrating on abstract models, which must make many assumptions that can cause distrust among readers. I use the articles in the symposium collection to highlight points throughout the latter half of this introduction, stressing the ways in which they illustrate the properties of theoretical studies. I end with some suggestions of ways in which the mutualistic relationship between theoretical and empirical work can be strengthened.

Theory Is Common but Often Misunderstood

Theoretical studies have a very long history in ecology and evolution, starting their heyday from the times of G. Evelyn Hutchinson and Robert MacArthur on the ecological side and R. A. Fisher, J. B. S. Haldane, and the founders of the modern synthesis on the evolutionary side. Theoretical analyses are quite common in these fields and have only increased in prevalence with time. Scheiner (2013) tracked the percentage of articles that tested or developed models across three of the most prominent ecological and evolutionary journals, Ecology, Evolution, and The American Naturalist, as ranging from approximately 20% or lower in the 1920s (before the journal Evolution was founded) to approximately 50% (for Ecology) and 80%–85% (for Evolution and The American Naturalist) in the 2010s. Otto and Day (2007) conducted a similar survey for the year 2001, finding that 96%–100% of the articles in these three journals used models in the most general sense (including phylogenetic and statistical models). They also tallied the percentages of articles that used models specifically and presented equations as being in the 33%–38% range for Evolution and Ecology and a whopping 58% for The American Naturalist. While these tallies include articles that “used” or “tested” models rather than deriving them, they...
are a testimony to the importance of modeling in these fields. An estimate of purely theoretical studies—those that derived new models—can be found in the more topically specific examination of articles in the fields of “sexual selection” (including articles since the 1970s) and “sexual selection and speciation” (including articles in the past 20 years) by Fitzpatrick et al. (2018). This analysis puts the percentage of purely theoretical studies at 10%–12% of this literature, which is still quite appreciable.

Yet despite this long history of theoretical models and the relatively prodigious use of these models in ecology and evolution, they are not without their detractors. Personally, I have encountered open questioning about the usefulness of more abstract types of theory in my experiences during seminars, grant panels, and hiring decisions. (Anecdotally, I will note that when I was younger, an older male colleague who was also a theoretician told me that he had never encountered verbal doubts about the usefulness of theoretical approaches. I am curious whether this opinion—the expression of open doubts about the utility of a research field—is more likely to be raised outside the context of anonymous reviews when the investigator targeted is junior, female, or both.) A testimony to the universality of such doubts about the application of mathematical approaches across fields comes from the ubiquity of defenses of theory. These are seen in many areas, including economics (Johnson and Lux 2011), physics (Polchinski 2007), psychology (Smaldino 2017), and molecular and cellular biology (Gunawardena 2014) as well as ecology (Levin 1981; Caswell 1988; Kokko 2007; Scheiner 2013; Marquet et al. 2014) and evolution (Haldane 1964; Servedio et al. 2014).

Perceptions of the interactions of theoretical and empirical work in the ecological and evolutionary communities also indicate that the course of theoretical research does not necessarily run smoothly. Haller (2014) conducted a survey-based study assessing such interactions. He found that while the overwhelming majority of ecologists and evolutionary biologists felt that theoretical and empirical work should inform one another in a continuing feedback loop (an opinion held by 91% of self-identified theoreticians and by 80% of empiricists), only 18% of these scientists felt that this was actually the case. Interestingly, there were some notable discrepancies in the opinions of theoreticians and empiricists. One concerned the statement that “theoretical findings drive empirical work”; 8% of empiricists but no theoreticians thought that this was currently true (instead, 26% of scientists thought that “empirical findings drive theoretical work”). This indicates that theoretical work is widely perceived to be less of a driving force for research than is empirical work. Discouragingly, close to 50% of empiricists agreed with the statement “I find theoretical methods intimidating and/or obscure,” which hints that perhaps the source of the problem is either the complexity of theoretical methods or the fact that they are undertaught during training or undercommunicated by theoretical authors.

Despite these doubts and questions about theoretical studies, they are not underrated. In fact, if anything they seem to be cited more often than empirical studies, but as it is very difficult to know what should be used as a “null model” for citation patterns, it is difficult to say whether they are “overcited.” The analysis by Fitzpatrick et al. (2018) mentioned above, of articles in the areas of “sexual selection” and “sexual selection and speciation,” was a citation network analysis. It found that theoretical studies within limited networks of articles in these areas were cited on average roughly two and a half to three times as often per article than empirical studies when tallying only the citations within each network. There are a large number of possible explanations for this discrepancy, reviewed in Fitzpatrick et al. (2018). One thing to note is that both theoretical and empirical articles cite their own type of article (theoretical or empirical) roughly 60% of the time, which was within the range of times that cichlid articles cited other cichlid articles (68%), *Drosophila* articles cited other *Drosophila* articles (42%), stickleback articles cited other stickleback articles (also 42%), or *Heliconius* articles cited other *Heliconius* articles (40%). This may be a reasonable percentage of citations to articles that serve as background or a close tie-in for any study. Because empirical articles made up roughly 70% of the articles in the networks in Fitzpatrick et al. (2018) while theoretical articles made up only approximately 10%, this ratio of citing within type (∼60%) versus across type (∼20%) leads theory to be overrepresented among citations in general.

Whether theoretical articles are cited in a meaningful way, accurately and specifically referencing their findings, is another question. Citations may also, of course, be incorrect. To obtain a rough assessment of how often theoretical articles are cited in these different ways, I conducted a survey in which I asked theoreticians to classify citations to one of their own articles; authors were asked to classify citations to their own article to minimize errors in categorization. Specifically, authors were asked to choose a theoretical study (described in the survey as “pure theory . . . not connected to data”) they authored that had the closest to 40 citations to assess. The purpose of this criterion, based on an admittedly arbitrary number of citations, was to not bias the sample toward an author’s best-cited article, although of course given that articles could be of any age some articles in the sample may have been highly cited. The authors were then asked to classify 10 citations appearing in empirical studies or reviews as either (a) general to topic, (b) specific and appropriate, or (c) incorrect (regardless of whether it was otherwise general or specific).
The specific wording of the survey can be found in the Dryad Digital Repository, along with the data set (https://doi.org/10.5061/dryad.k98sf7m2m; Servedio 2020). Twenty-four responses were collected, of which eight were primarily “ecological” and 16 were primarily “evolutionary” (categorized by myself or, if I was uncertain which category better applied, by the author). Logistic regression of both the proportion of incorrect citations and the proportion of correct citations that were general showed no clear statistical evidence of an effect of discipline or time (one could imagine different reasons that such a relationship might exist).

Theoretical authors were found to perceive citations to their work as general a mean of 36% (SD, 0.15) of the time, as specific and appropriate a mean of 45% (SD, 0.18) of the time, and as incorrect a mean of 19% (SD, 0.13) of the time (fig. 1). This is, in my opinion, a fairly large (roughly one in five) but not egregious proportion of studies where the substance of the theoretical article seems to have been missed by an author working on that topic. Given that a citation was correct, the percentages given above correspond to 45% of citations being perceived by their theoretician authors as general to topic versus 55% being perceived as specific and appropriate. This may not be surprising, but it suggests that even in a large percentage of articles that cite theory correctly, specific results from these theoretical articles do not motivate empirical analyses, or that empirical findings are not related back to specific theoretical results.

This analysis was very limited. The variance in the perception of citations was quite large; there may be several factors that account for this, including that there were many observers (theoretical authors) and that the articles were on many topics. A broader and more thorough analysis with a bigger sample size may be warranted, if the participants could be recruited. Additionally, an entirely open question is how these citations of theoretical articles compare to citations of empirical studies.

Goals and Assumptions of Theory:

The Contributed Articles

Both the correctness and the accuracy, as well as the frequency, of citations of theoretical work may vary greatly with the type of theoretical study in question. Theoretical

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**Figure 1:** Percentage of citations by nontheoretical articles to a theoretical article that the author of the theoretical article perceived to be incorrect, general to topic (and correct), and specific and appropriate. The size of each circle represents the total number of nontheoretical citations that the theoretical author identified in his or her sample. In one case an author reported a citation as both general and incorrect; this was categorized as incorrect. The survey that obtained these results was posted on the blog Dynamic Ecology and advertised on social media.
studies can have several different functions and goals. Some theoretical work, for example, develops statistics or other methods to use on data sets; since this work is directly applicable to empirical studies that utilize these methods, citations should be accurate and correct, presuming there have not been errors in applying the methods. The development of such methods can take place in steps, especially when the goal of the study is further removed from what has previously been done. In this collection of articles, for example, Goldberg and Foo (2020) depart from the memoryless assumption of the Markov processes used in almost all analyses of the macroevolution of discrete-valued traits to date. Instead, they explore how memory might be incorporated into macroevolutionary models. The idea is that the chance of a particular evolutionary transition occurring might be affected by the evolutionary history of the organism in question; for example, the longer a previously ocean-dwelling fish has lived in freshwater, the more difficult it might be for it to evolve back to living in an ocean habitat. Goldberg and Foo develop a series of models that incorporate the history of how long a character state has been present (“memory”) into the probability that a change in that state will occur. At this stage of the development of these techniques they use simulated data to test whether phylogenetic comparative data can be used to determine whether a trait has a signal of memory. The hope is that future development of these techniques will take this work to the point where memory can be estimated in empirical data sets.

The links between the type of theoretical work done by Goldberg and Foo (2020) and empirical work is very clear. There is a continuum, however, of how closely mathematical models intermesh with empirical data. Specific empirical systems, for example, can be described mathematically, often with the purpose of better understanding whether the empirical descriptions are complete. Least clear, at least for some, is the link between more abstract theoretical models and empirical studies of the same topic. At this far end of abstraction are what Servedio et al. (2014) call proof-of-concept models—models that serve as mathematical “tests” of the logic of verbal hypotheses. Proof-of-concept models are a vital part of the development of evolutionary and ecological theory because the hypotheses in these fields are often very complex, and long verbal chains of logic are prone to error.

At the heart of a study that develops a proof-of-concept model, if it is to have any biological meaning, is what Otto and Rosales (2020) call in this collection of articles the “narrative.” In their article “Theory in Service of Narratives in Evolution and Ecology” they describe a narrative as the interpretation that develops a scientific theory (somewhat akin to the “verbal chains of logic” of Servedio et al. [2014]). The role of mathematical theory in this framework is to analyze those points in a narrative that are unclear or confusing. The fundamental importance of narratives is illustrated by the fact that the same mathematical expression can take on different meaning if overlain by different narratives. Otto and Rosales illustrate the importance of narratives and their interactions with mathematical theory to the forward movement of scientific inquiry using examples that show how models can play an illuminating role when narratives conflict.

When a narrative is complex enough—or questionable enough—to demand a model, what in turn does a model necessitate? Proof-of-concept models necessitate that the biological assumptions on which they rest both emerge from the narrative (i.e., match the biological question under study) and, for some assumptions, are biologically realistic. As stressed in the prior sentence, not all assumptions have to be biologically realistic—a point that can cause much confusion and mistrust of theory, especially among empiricists. Servedio et al. (2014) break assumptions into three categories. Critical assumptions are those that lie at the heart of the narrative, in that they are the assumptions that are directly tied to the hypothesis being studied. These must be biologically realistic if the study is to have biological applicability. Exploratory assumptions can be thought of as “side issues.” They may be interesting to vary to test their effect, but they are not central to the hypothesis. The third category of assumptions, logistical assumptions, are the most problematic in terms of creating confusion about the utility of theoretical studies. Servedio and colleagues argue that this is because logistical assumptions, which are made for tractability (e.g., haploidy or infinite population sizes), are not always biologically realistic. However, this is not an impediment to the creation of a meaningful and insightful model provided that the theoretician knows what effect violating these assumptions will have. The responsibility of carefully communicating the purposes for logistical assumptions and what is known about the consequences of their violation lies with the theoretician writing the article.

The lines between these types of assumptions—critical, exploratory, and logistical—can be blurry. This is exemplified in the article in this collection by Akçay (2020). Akçay explores several ways in which the evolution of social behaviors can be altered by the evolution of the setting in which these social behaviors occur. In many game-theoretical models, some of the rules of the game can be thought of as logistical assumptions; that is, some rules (fixed payoffs, fixed group composition, fixed population density, etc.) are simply set as background, as it were, to the question at hand, which is the evolution of the social behavior. Akçay reviews ways in which these formerly logistical assumptions can turn into critical ones by allowing them to coevolve along with the social behavior itself (e.g., for
the list given above, having these rules no longer be fixed). He shows that allowing this coevolution between fundamental rules of the game and the behaviors under investigation can lead to unexpected outcomes that cannot be predicted from models in which the structure of the games is fixed. In this case, these assumptions, although made for simplification and useful for exploring initial models, really must be challenged by further study for this theoretical work to develop fully.

The remainder of the articles in this symposium collection all present or review proof-of-concept models of outstanding questions in ecology and evolution. Vasconcelos and Rueffler (2020), like Akçay (2020), focus on the results of changing what are fundamentally structural elements of models, in their case of models of resource specialization. Previous models have generally analyzed whether the evolution of specific consumer traits can lead to evolutionary branching, that is, resource specialization instead of a species functioning as a generalist. These models generally found that this required strong trade-offs (e.g., for a very similar model to this new one, see Rueffler et al. 2006). By analyzing the effect of the evolution of one trait at a time while treating other consumer traits as parameters, I would argue that they were in essence treating this choice as a simplifying logistical assumption. In their contribution, Vasconcelos and Rueffler show how the results of these single-trait models are altered when either pairs of consumer traits, or three consumer traits, are allowed to coevolve. They find that changing this formerly logistical assumption can have dramatic effects, particularly in that under the coevolutionary models weak trade-offs can now allow the evolution of either one or two resource specialists. This study, as with many before it, thus serves as a warning that logistical assumptions—in this case, the prior assumption that one trait evolves at a time—must be made carefully, and the results of models that use them should be qualified if the effects of violating these assumptions is unknown.

The contribution by Peischl and Gilbert (2020) is a model that tackles the issue of how the expansion of a species range is affected by two phenomena that are known to occur on the edges of a range: gene surfing and spatial sorting. Targeting these phenomena, they explore how expansion is affected by the coevolution of traits that affect relative fitness and those that affect dispersal abilities. Using a combination of numerical results and individual-based simulations, they show that there are regimes under which mean fitness will be reduced by expansion load and in which mean fitness will increase, as will average dispersal rate. They also find an intermediate region in which the evolution of higher dispersal can "rescue" a population after its mean fitness begins to decline as a result of a high expansion load. While they make several logistical assumptions, for some of these (haploid inheritance and no clonal interference) they explain why they think their results should be robust to changes in these assumptions. They also explain why other assumptions might not be robust if changed but may instead lead to different results (e.g., hard selection vs. their assumption of soft selection).

Sardell and Kirkpatrick (2020) in this collection of articles first use a meta-analysis to describe an interesting pattern in sex differences in recombination; they show that while in many eukaryotes recombination occurs at roughly similar rates across chromosomes in females, it is more frequent toward the telomeres in males. They review several potential explanations for this pattern, some of which have been tested and developed by proof-of-concept models, as well as assess the evidence for or against these explanations. They find that no single explanation seems to be a good fit for all cases. This review is an excellent example of an area where proof-of-concept models can be compared with empirical data to assess which narrative may be the best match for the biology of the question. It is a useful reminder of the complexity of evolutionary patterns that in this case no single narrative seems to fit.

Near the start of her contribution to this collection, Kokko (2020) raises the point that sometimes consideration of what does not occur can give insights that can explain what does occur. This is an approach that theoretical studies are particularly adept at; it is oftentimes, by definition, impossible to empirically study a phenomenon that is not occurring! Kokko raises this issue to introduce the problem of facultative sex as one example of a type of biological realism that she feels should be increasingly included in the theoretical foundation of the problem of the evolution of sex. She concentrates not so much on the conditions under which facultative sex (which is sometimes perceived to be rare) should occur as on how this is affected by whether facultative sex occurs synchronously or asynchronously by individuals in the population. Facultatively synchronous sex, for example, might occur if sex were triggered by an environmental stimulus. The results of her proof-of-concept model gave her clarity on how the very question she was addressing might be viewed the most productively—in her case, by inquiring why obligate sex can sometimes replace facultative sex. This refinement of hypotheses is a hugely constructive part of the scientific process in general, including when initial hypotheses are tested theoretically rather than empirically.

Increasing Understanding of Theoretical Work

While varied in topic, the articles in this collection all nicely illustrate some of the qualities of theoretical work and the assumptions that must be made in the construction of models. It is my hope that open discussion of these qualities, to which this introduction provides a modest contribution,
will become more and more common in ecology and evolution and that this will help to remove roadblocks to communication between empiricists and theoreticians. A better understanding both of the role of theory and of modeling articles will lead to a more effective mutualism between practitioners of theoretical and empirical techniques.

What might an effort to remove these roadblocks look like? The data from ecology and evolution journals presented above regarding the prevalence of theory shows that graduate students (or even undergraduates) in these fields will inevitably encounter models. Therefore, strongly encouraging or mandating a modeling course during training seems reasonable, if only to help these students navigate the theoretical literature in their subfield. As the above discussion of the results of Haller (2014) pointed out, many empiricists find the methods in theoretical articles to be "intimidating and/or obscure." While the complexity of many models cannot be changed without compromising the goals of the particular study, the authors of theoretical studies can consistently “pull back” and try to eye their manuscripts from the point of view of a reader unfamiliar with the methods. Points to highlight throughout the exposition of a model are why particular methods are being used and, in equations, what are the meanings of terms. Even more important, as is discussed in depth above, is to carefully present the assumptions that go into the modeling study and to be as transparent as possible about the effects of logistical assumptions in particular. While these steps may not provide a magic bullet, they will help.

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