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SYMPOSIUM

Why More Biologists Must Embrace Quantitative Modeling

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Synopsis Biology as a field has transformed since the time of its foundation from an organized enterprise cataloging the diversity of the natural world to a quantitatively rigorous science seeking to answer complex questions about the functions of organisms and their interactions with each other and their environments. As the mathematical rigor of biological analyses has improved, quantitative models have been developed to describe multi-mechanistic systems and to test complex hypotheses. However, applications of quantitative models have been uneven across fields, and many biologists lack the foundational training necessary to apply them in their research or to interpret their results to inform biological problem-solving efforts. This gap in scientific training has created a false dichotomy of “biologists” and “modelers” that only exacerbates the barriers to working biologists seeking additional training in quantitative modeling. Here, we make the argument that all biologists are modelers and are capable of using sophisticated quantitative modeling in their work. We highlight four benefits of conducting biological research within the framework of quantitative models, identify the potential producers and consumers of information produced by such models, and make recommendations for strategies to overcome barriers to their widespread implementation. Improved understanding of quantitative modeling could guide the producers of biological information to better apply biological measurements through analyses that evaluate mechanisms, and allow consumers of biological information to better judge the quality and applications of the information they receive. As our explanations of biological phenomena increase in complexity, so too must we embrace modeling as a foundational skill.

> Statistical thinking will one day be as necessary for efficient citizenship as the ability to read and write.
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> — Wilks (1951) paraphrasing H.G. Wells (1903)

> One of the most valuable, significant, and also useful attributes of human thought generally, is its ability to reveal and explain the fabric of reality. … Prediction–even perfect, universal prediction–is simply no substitute for explanation.
>
> — Deutsch (1998)

Biologists, indeed scientists generally, are increasingly called upon to provide explanations of natural phenomena based upon a thorough understanding of the mechanisms that drive them (Dauer et al. 2021; Mayes et al. 2022). Ecosystem biologists are asked for explanations of how landscapes will respond to changing climatic conditions (Edwards 2011; Rehfeldt et al. 2012; Palubicki et al. 2022); population biologists are asked to explain the likely impact of ecosystem changes and management decisions (Faust et al. 2004; García-Díaz et al. 2019; Baker and Bode 2020); physiologists are asked to explain the impact of extreme conditions on individuals (Sergio 2018); and molecular biologists are asked to explain how the interactions among the molecular components of cells drive responses to drugs, environmental stimuli, or other cells (Iyengar 2009; Le Novere 2015; Zewde 2020). Inevitably, greater and greater accuracy is expected in the explanations scientists provide, which has led to increased use of quantitative modeling in biology (Mogilner et al. 2006). At the same time, however, the demand for accuracy, and attendant mathematical or computational complexity, have amplified barriers to learning and applying quantitative modeling within biology. Such barriers lead to

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the perception that modeling is only for a subset of practitioners, "the modelers," who are distinct from the rest of "us biologists." Not only is this view an inaccurate depiction of biology, it is also detrimental to the field's advancement and indeed to its ability to provide exactly those explanations we desperately need to address myriad challenges (Gunawardena 2014; Joshi 2022).

In our view, every biologist is a modeler, an explainer of reality. Whether or not working on complex mathematical or computational models, we all create models of the world in our teaching, our research, and in the representations we use to interpret the work of others and communicate among ourselves. Despite the universal applications of models, there is, of course, a continuum of the degree to which each biologist includes quantitatively rigorous models within their repertoire. It is our view that many biologists can benefit from increasing the quantitative rigor in their own work, their own understanding of the world, and the way they consume information produced by their colleagues. Unfortunately, the perceived dichotomy between "modelers" and "us" serves as a barrier against individuals moving along that continuum by expanding an understanding of the relevance of models and modeling for their own work (Joshi 2022).

In this paper, we seek to focus attention on the ubiquity of modeling among biologists by examining what models and modeling are, how they are currently used and understood in our field, and how and why we might expand their applications. Additionally, we focus attention on the importance of quantitative modeling and why it plays a unique role among other types of modeling within biology. We recognize that every biologist does not play the same role within the social or bureaucratic institutions that guide scientific discovery, and therefore does not interact with models, quantitative or otherwise, in the same way or for the same reasons. Consequently, strategies for overcoming barriers and engaging with quantitative models will vary greatly among different communities of practice. Nevertheless, there are clear themes for improving facility with quantitative models. Consequently, we suggest specific guidelines that we hope will expand both appreciation of quantitative modeling's crucial role in biology, and the abilities of practitioners who serve in diverse roles to engage more effectively with quantitative modeling.

Scientists use models in everything they do

Many answers exist to the question, "What is a model?" The common thread within biology is that a model is a simplified description of a subset of phenomena that occur in nature (Oreskes 2003; Mogilner et al. 2006). This clearly encompasses all quantitative models, which are based upon a collection of mathematical quantities and their interactions. However, this definition also encompasses laboratory and field experiments, which examine a subset of the spatial and temporal diversity of life. Perhaps less intuitively, this definition also encompasses our various verbal, mental, and visual explanations of natural phenomena (Cowan 2010; Gruszka and Nęcka 2017).

If all of the aforementioned examples are models, then the act of modeling is simply the process of creating them. More precisely, modeling is the process of mapping portions of nature onto the simpler conceptual spaces that we use to depict it (Rosen 1991; Joshi 2022), with the goal of improving understanding of how the corresponding natural phenomena would respond under analogous, though more complex, circumstances.

Biologists do this type of mapping all the time, often without even realizing it because humans in general have evolved to do this masterfully. There is no such thing as a group of biologists who "model" and another who does not. Likewise, there should be no expectation that "modeling" is a domain of activity unto itself and separate from biology.

Quantitative models have distinct benefits over informal modeling frameworks

While all biologists are modelers, it is also clear that not all biologists use quantitative models as part of their data analysis repertoire. This is unfortunate, because quantitative models offer important and potentially unique benefits. Here we identify four benefits of particular value.

(1) Formal deductions increase confidence in predictions about complex natural phenomena

Human minds are inept at the task of determining the necessary consequences of a set of predicates. That is to say, we are not good at predicting the outcome of phenomena based on observed conditions, especially if those conditions are numerous or if they interact. This reflects well-known cognitive biases and inaccuracies of judgment, present even in trained professionals, when heuristics are used in problem solving (Tversky and Kahneman 1974; Korteling and Toet 2020). Quantitative models of all sorts, indeed all of mathematics, have emerged as the most efficient way to develop rules to rigorously measure the mechanisms for how phenomena operate. Quantitative models can be constructed to contain many more objects than humans can possibly consider, yet we remain confident in their accuracy because they are built on a foundation of formal deduction, which can be scaled and adjusted to handle complexity. They improve upon fallible mental logic with a formal process of deduction, thereby detecting patterns and increasing confidence in predictions.

(2) Quantitative models reveal counterintuitive outcomes that may otherwise go undetected

The results of quantitative models compared to prior expectations often reveal that prior expectations and expert judgment are (at least partially) incorrect (Allesina and Tang 2012; Holden and Ellner 2016); that is, counterintuitive outcomes are not uncommon. Allocation of millions of dollars, years of work, and international policy may be affected by inadequate understanding overturned by counterintuitive quantitative models. Marine turtles were long thought to be in decline mainly as a result of predation occurring on nesting beaches; however, careful analysis of their entire life cycle revealed mortality at sea to be more important in causing decreases in population abundance (Crouse et al. 1987; Crowder et al. 1994; Heppel et al. 1996). Consequently, turtle exclusion devices to prevent accidental death of turtles associated with fishing were developed, and international treaties now require their use by shrimpers and other fishers serving the US fish market (U.S. Public Law 101–162, section 609). Such results are a direct indication of failure of human mental deduction of consequences from predicates, but this failure is only evident after quantitative modeling reveals previously undetected relationships (Allesina and Tang 2012). Further, incorrect prior expectations may be held strongly, even by experts, and over long periods of time. For example, it is widely expected that Fisherian sexual selection (Fisher 1930; Henshaw and Jones 2020) is a strong driver of, and hence a potent explanation for, elaborate mating displays and other traits involved in pre-mating isolation. In reality, however, this driver is much weaker than expected (Greenfield et al. 2014) and may actually progressively disappear from populations (de Servedio and Bürger 2014). Interactions among different life-history stages can lead to unexpected outcomes such as dominance by a species that is both a worse competitor and less able to avoid predation (de Roos 2020). While the effect of measurement error on inference has been studied for over a century (Kummell 1879; Fuller 1987; Stefanski 2000; Altman and Krzywinski 2024), its complex effects remain unappreciated by practitioners (Brackenhoff 2018; Shaw et al. 2018; Innes et al. 2021). Contrary to expectation, when predictor error is present, our ability to identify correct models of nature may decrease, not increase, with increasing effect size and sample size (Manthey et al. 2023). Furthermore, increasing sample size may be less effective for improving inference than reducing heterogeneity (Rosenbaum 2005). These and similar examples illustrate that reliance on informal verbal, mental, or visual models may come at the cost of incorrectness and even result in massively misdirected resources.

(3) Quantitative models permit rigorous assessment of uncertainty

One prominent reason that informal (i.e., not explicitly quantitative) models yield incorrect results is that human minds are inept at incorporating uncertainty, as is widely evident from the work of Daniel Kahneman on the irrationality of many human decisions, especially in the face of uncertainty (Tversky and Kahneman 1974; Garner 1982; Schustek and Moreno-Bote 2018). All non-trivial models (i.e., complex enough to not have obvious outcomes) involve uncertainty (Heisenberg 1927; Kampourakis and McCain 2020; Korbel and Wolpert 2024). They are subsets of nature, so factors left out may (and generally do) have an impact on the outcome. Additionally, the representation of the subset that is included may be inaccurate and lead to even more uncertainty. Thus, biology practitioners need ways to quantify the level of uncertainty within any given analysis. More importantly, we need ways to track and propagate uncertainty through every stage of analyses to determine its impact on the ultimate outcome. This can only be done effectively through the use of quantitative models of stochasticity. The importance of quantifying uncertainty is especially evident in cases that require concrete decisions to be made. The US Fish and Wildlife Service has a mandate to maintain stable populations of wildlife while also allowing ongoing harvest, either purposefully or incidentally, even when critical parameters such as survivorship and fecundity rates are highly uncertain. For example, assessment of allowable harvest of golden eagles (*Aquila chrysaetos*) in the western United States depends crucially on quantifying uncertainty in the allowable harvest limit (Millsap et al. 2021). Without explicit quantification of how uncertainty in many demographic parameters affects the uncertainty in the harvest limit, it would be impossible to arrive at clear permitting guidelines that allow, for example, wind energy development. It would also be difficult to recognize that even though the population of golden eagles appears stable and has been for decades, it is unlikely to be resilient in the face of increased harvesting

(Millsap et al. 2021). Our ability to reason informally about such complex situations is woefully inadequate to the task, so quantitative models of uncertainty are essential.

(4) Latent variables of greatest interest can be inferred in quantitative models

Interestingly, verbal, mental, and visual models are often full of quantities that cannot be observed directly but are generally of most direct interest. These are described as latent variables (Skrondal and Rabe-Hesketh 2007; Blei 2014; Bartolucci et al. 2022) and are naturally, almost unthinkingly, included in the qualitative models that humans use to describe our world. In contrast, they are often excluded from quantitative models. This practice diminishes the utility of quantitative models and can contribute to inaccurate predictions. Latent variables can, however, be included explicitly and effectively in quantitative modes. For example, cancers can be characterized by models that explicitly ascribe patterns of microarray data, genome sequences, and transcriptome counts to underlying, but unobserved, that is, latent, tumor types (Mo et al. 2018). The unobservable, but obviously important, state of health can be quantified (Hyland et al. 2014). Features characteristic of vocalizations can be identified as latent factors (Sainburg et al. 2020). In landscape genetics, latent factors can capture genetic variation explained by, for example, demographic history, patterns of ancestry, or environmental factors not otherwise measured (Frichot et al. 2013). In fisheries and wildlife biology, state-space and related models are used to quantify unmeasurable parameters of critical scientific or management importance (Thorson and Minto 2015; Westcott et al. 2018). The unobserved but explanatory latent variables included in these models are generally informed by multiple contributing measured variables, even if they are measured in different units, at different times, or using different sampling schemes. Importantly, all of these examples capture explicitly the types of quantities that often occur in the conceptual models we use as explanations but are nevertheless beyond the reach of measurement. Many quantitative models in common use, however, do not include latent variables and can be misled by measurement error (Brackenhoff 2018; Shaw et al. 2018; Innes et al. 2021). This is a case in which non-quantitative models are in some sense better than some quantitative ones, because at least they do include the unobservable, latent variables of interest. However, this is not an indication that quantitative models should not be used or that they cannot include latent variables. Indeed, they can, as the previous examples show and as is well known from the array of hierarchical and structural equation models that have been used with success (Grace 2006; Langrock et al. 2014). Instead, the lack of latent variables in commonly used models, for example, most regressions, is an indication that when biologists turn to quantitative models, they often use ones that can be misleading rather than try to capture the nuances already developed in the informal ones. This trend directly supports our thesis that biologists will benefit from increasing the rigor of their quantitative modeling skills so that they can recognize these problems and seek solutions that already exist, but are not currently widely used (Brackenhoff 2018; Shaw et al. 2018; Innes et al. 2021).

Clearly, quantitative modeling offers many benefits, including those that cannot be provided by alternative modeling approaches. To reap those benefits, biologists would profit from increasing the rigor with which they approach their modeling. All biologists are modelers, and all can benefit from improving their quantitative modeling skills so that their explanations of biological phenomena are better.

Models are experiments for testing hypotheses

Modeling, like laboratory and field activities, is best characterized as an experiment. In the lab or field, one identifies a set of factors to control and others to vary in hopes of revealing that the latter, not the former, are responsible for observed responses. Often, such an experiment is undertaken to determine which of several possible factors has the greatest impact on the observed response. Modeling should be regarded in the same way. That is, it should be regarded as an endeavor seeking to determine which of several potential factors leads to the greatest improvement in our understanding of the response(s). Fitting a single model to data is rarely the most appropriate path to this end; rather, competing multiple models is as important as entertaining multiple working hypotheses (Chamberlin 1890). Researchers should define two or more models (or model families) corresponding to distinct hypotheses regarding how the natural phenomenon might work, and then compare them in the face of the data obtained (Edwards 1972). The relevant questions are: which model is best supported by the available data and what is its range of applicability (Lawing et al. 2021; Proust et al. 2021)? Because the models differ systematically by design in underlying hypothesized mechanisms, their relative support can answer the questions. This process can, in turn, lead to better experimentation. The ensuing feedback between explicit modeling of alternative hypotheses and evaluation of given data can lead to a much improved understanding of the mechanisms involved in natural phenomena.

Every biologist needs a working knowledge of quantitative modeling, regardless of their field or the role they play

In the above sections, we outline an argument for the benefits of couching any biological question within a modeling framework and addressing the resulting hypotheses using explicitly quantitative models. Biologists who play myriad roles in biological research, resource management, implementation, and policy creation benefit from a strong understanding of mathematically rigorous modeling (Le Novére 2015; Holden and Ellner 2016; Murphy and Weiland 2016; Earl et al. 2017; Fuller et al. 2020). Here, we suggest benefits for biologists classified into two groups that broadly encompass the possible roles they might play, regardless of their field of interest: producers and consumers of information. Producers of information include researchers who develop novel methods as well as researchers who use established methods with a specific (often mandated) scope confined by their scientific focus, that is, molecular pathway, taxon, geographical region, application, etc. Consumers, in this context, are the practitioners and policymakers who implement "best science" to address specific applied problems (Murphy and Weiland 2016) and interested laypeople who do not work on a particular biological system professionally, but have a vested interest in the answers to biological questions. We believe that producers can benefit from organizing their experimental work into models that explicitly quantify the mechanisms that drive phenomena, their interactions, and the uncertainty within the measurements. In this way, they will be better able to describe the nuances of and uncertainty surrounding their conclusions (Holden and Ellner 2016). Practitioners who primarily play the complementary role of consumers may or may not need to create the quantitative models that inform their work, but do require a working understanding of their components, measurements of error and variance, and nuance in interpretation. Of course, no biologist is an expert in every aspect of biological research, and therefore, our individual roles shift depending on the topic of interest.

All researchers benefit from organizing their work within the framework of quantitative models

The producers who use quantitative models to the greatest extent are those who develop new methods or who seek to identify previously unmeasured mechanisms that drive trends in biology. Molecular biologists apply quantitative models to identify previously unknown cellular processes, from the scale of specific molecular actions to entire cellular-scale behaviors (Mogilner et al. 2006; Iyengar 2009; Le Novére 2015). Thermal physiologists increasingly recognize the value of quantitative models to track organismal responses to heat stress that go beyond critical thermal limits to incorporate physiological and environmental variables (Feng et al. 2019; Gamliel et al. 2020). Population biologists develop quantitative models to improve their understanding of the mechanisms that determine population sizes and genetic connectivity across time and space (Balkenhol et al. 2016; Milligan et al. 2018; Peterson et al. 2019; Rohde 2022). Biologists who seek to identify and quantify mechanisms that drive relationships at higher organizational levels, such as communities and ecosystems, embraced quantitative modeling, and in particular models that include latent variables, earlier than biologists from other fields (Canham et al. 2003; Grace 2006; Bondavalli et al. 2009; Warton et al. 2015; however, see Pritchard et al. 2000 for an early example from population genetics) and continue to develop models of greater complexity as computational power permits (Shoemaker et al. 2019; Pollock et al. 2020; Thompson et al. 2020; Pałubicki et al. 2022).

Researchers who work within the constraints of some predefined scope using established methods are the most prolific producers within biology. They create the most published data and their work likely has the greatest direct influence on policy and implementation decisions because it composes most of what is considered "best available science." Best available science is the standard by which many government and policymaking organizations make and defend implementation, conservation, or management decisions (Doremus 2004; Murphy and Weiland 2016; Lindsay 2020). The term is most commonly used in reference to environmental protection and restoration actions (Lindsay 2020), but is, in practice, equally applied in consumer-focused biology, such as food and medical science (Chiu et al. 2023). There is no single legal definition of best available science (Oil and Hazardous Substance Liability, 33 U.S. Code § 1321(a) (27); 50 C.F.R. § 600.315 National Standard 2- Scientific Information; The Endangered Species Act, 16 U.S.C. §§1531 et seq.; The Clean Air Act 42, U.S.C. 7401 et seq.; Sullivan et al. 2006; Ryder et al. 2010; Lindsay 2020). Standards vary based on field, jurisdiction, and practitioner interpretations (Doremus 2004; Sullivan et al. 2006; Esch et al. 2018; Lindsay 2020), which has often led to litigation (i.e., Southwest Center for Biological Diversity v. Babbitt, 215 F.3d 58 2000; American Wildlands v. Kempthorne, 530 F.3d 991 2008; San Luis and Delta-Mendota Water Authority v. Locke, 776 F.3d 971 2014). In practice, best available science is often defined by the majority consensus of a body of scientific literature that addresses a specific taxon or problem of concern (Lowell and Kelly 2016); furthermore, it often varies in completeness among applications (Doremus 2004). If this is the standard by which decisions are made, it is imperative that the studies that inform that body of literature do not perpetuate oversimplifications of systems of study, misunderstandings of mechanistic drivers, or misrepresentation of confidence around analyses that could misinform downstream actions. Following this logic, research biologists who publish the literature that informs policy and implementation decisions bear a heavy responsibility to apply the best available methods to their work. Alarmingly, this is also the category of researchers who are most likely to start a sentence with the phrase "I am not a modeler. . .," perpetuating the false expectation that working biology researchers belong in a separate domain from quantitative modelers (Joshi 2022). We do not argue that it is the responsibility of all researchers to develop novel applications of quantitative modeling, which would be counterproductive to progress toward solutions for specific biological problems; however, it is the responsibility of all researchers to understand and transparently discuss the limitations of the analyses that they perform, to quantify the uncertainty in their conclusions, and to learn about and adopt better methods when they are made available (Jackson et al. 2000; Mogilner et al. 2006; Shafer et al. 2015; Holden and Ellner 2016; García-Díaz et al. 2019; Joshi 2022). A shift toward a quantitative modeling framework for all biological research would allow for quantification of mechanisms that drive relationships, measurements of true variables of interest (even if they are latent), and quantification of uncertainty. Importantly, hierarchical quantitative models also provide a means to measure the mechanisms that link research performed at each of many organizational levels (Zewde 2020; Perennes et al. 2021; Lu et al. 2023) to better inform predictions of organismal and systemic responses to change.

Quantitative models improve interpretations of "best available science" for policy and implementation decisions

Policymakers and practitioners are the primary consumers of the information and materials that biological researchers create, as they are the biologists tasked with using the "best available science" to improve or defend applications of that knowledge. Shortcomings in this knowledge may result in misapplied importance being placed on research that emphasizes particular methods or biological mechanisms while others are ignored (Heppell et al. 1996; Holderegger et al. 2019). A strong understanding of quantitative modeling provides a framework through which policymakers and practitioners can assess the extent to which an existing body of knowledge sufficiently predicts the mechanisms of a biological system, the level of uncertainty within that body of knowledge, and how it informs any particular decision (Holden and Ellner 2016; García-Díaz et al. 2019; Baker and Bode 2020; Mayes et al. 2022). Decision-makers can apply this knowledge in two ways: first, by using it to assess the strength of various pieces of evidence for one hypothetical mechanistic relationship or another, and second, by creating formal meta-analyses of the available primary research on any given topic (García-Díaz et al. 2019; Baker and Bode 2020). Formal quantitative models that measure the likelihood of counterintuitive relationships or identify gaps in knowledge could reduce the impact of fallible mental logic in decision-making, improve the outcome of implementation efforts, and save millions of dollars spent on errant attempts to implement ineffectual solutions to biological problems (Holden and Ellner 2016).

Every human being is, in some context, a layperson with a vested interest in biological research and implementation. Even the most highly educated biologists are not experts, or even well-informed amateurs, in more than a few related fields. As such, every human being has an interest in being able to critically analyze evidence (or lack thereof) for or against any decision based on biological research, at least at a rudimentary level (though such understanding benefits from the guidance of trained experts). We have no expectation that laypeople should be able to consume primary biological literature; they are not the intended audience for that work (Berenbaum 2001; Sedgwick et al. 2021) and often do not even have access to it (Day et al. 2020; Racimo et al. 2022). However, laypeople are still important consumers of biological knowledge through other media (Rohde 2022), and their interests in solutions to biological problems are equally valid (Day et al. 2020; Sedgwick et al. 2021). As such, laypeople need training and tools to assess the quality of seemingly scientific claims. This ability has become increasingly important, as technology has improved world-wide communication to be practically instantaneous and free-of-charge, permitting the distribution and sometimes accidental or purposeful manipulation of information (Berenbaum 2001; Dahlstrom 2021). We assert that, as consumers of biological research, laypeople would benefit from considering the biological information that they receive through the lens of quantitative modeling because it encourages systematic exploration of the mechanisms that drive relationships, the uncertainty surrounding analyses, and acknowledgement of the complexity of natural phenomena. Similarly to how a professional decisionmaker may use quantitative models to assess the quality of support for hypothesized mechanisms within a biological system, informed laypeople may use them to differentiate between well-substantiated scientific conclusions and claims with little or no support.

Opportunities to develop a biological workforce and citizenry with a working knowledge of quantitative modeling

Biologists who work in any field within biology must be trained in mathematical and modeling concepts that form the foundation of quantitative modeling. Until now, formal biological training has implicitly fostered the "us biologists" versus "them modelers" worldview (Joshi 2022). Due to this misguided perspective, many practicing biologists never received this foundational training (Ioannidis et al. 2014). This perceived dichotomy is exacerbated by the often rigorous and time-consuming challenge of building models that accurately represent complex natural phenomena. Biologists without this necessary training might try to form collaborations with scientists who "are modelers" as a way to apply these rigorous analyses to their systems of interest without learning how they are created or how to interpret their uncertainties. Such partnerships of biological system experts and modeling experts may be productive in some cases but may also lead to mistakes in the parameterization of models if the creator does not understand the biological system well. Conversely, errors of model interpretation on the part of the biological systems experts could lead to miscommunication when they present their results to consumers. Collaborations have the potential to increase the application of quantitative modeling frameworks to complex biological problems, but they are most effective when all researchers involved have enough foundational knowledge to understand the components and outputs of the models.

Biologists with modeling expertise should work with their colleagues to build workshops and other training opportunities to help fill this training gap within our biological workforce. Here we must acknowledge that the development and implementation of such training opportunities represent a huge task for biologists whose mandates may often require other forms of productivity, such as literature publications (Kun 2018; van Dalen 2021) or management of implementation actions. We call on universities and agencies to recognize the importance of this work and to accept the training tools produced by it as equally valuable contributions to their mandates and their fields. As biologists with modeling expertise develop training tools to help their colleagues improve understanding and increase use of quantitative models within their fields, practitioners who play diverse roles within biology must agree to engage with those training opportunities. Without enthusiastic participation from all biologists, quantitative modeling is likely to remain underutilized.

Along with training the current biological workforce, secondary schools and universities must incorporate the foundational concepts of quantitative modeling into their biology curricula (Dauer et al. 2021; Mayes et al. 2022). Any student body that is sophisticated enough to discuss hypothesis testing within the framework of the scientific method could also learn the foundational concepts that support quantitative modeling. Such lessons should focus on the importance of latent variables, identifying mechanisms that drive biological relationships, and quantifying uncertainty. Once this foundation is established, more advanced classes could introduce specific modeling frameworks that best address the questions of interest in diverse fields. The addition of this training to the curricula of secondary biology courses and foundational general education courses at universities, while important, may represent a particular challenge because curricula in these cases are controlled to varying extents by state-run legislative authorities with competing interests (Park et al. 2020). Upper-division biology curricula at universities, however, are directly controlled by faculty. This educational freedom presents a relatively unencumbered path to improve collegiate biological education in quantitative modeling by incorporating this training throughout the biological curriculum, including in required biological statistical courses for undergraduate students and in required discipline-specific quantitative modeling courses for graduate students, whether in classroom settings or through direct mentorship. The addition of quantitative modeling to early biological education would circumvent, to some extent, the need for future generations of biologists to seek additional training in these concepts outside of their formal education (Mayes et al. 2022).

Finally, researchers who develop novel models or new applications of existing models must engage with other practitioners beyond publications of scientific literature to improve the uptake of these methods. This engagement includes producing freely available, user-friendly software and tutorials. Once again, we recognize that the development of these tools represents a huge effort that may be undervalued relative to other forms of productivity. We call on agencies and universities to recognize the development of user-friendly software that facilitates the uptake of quantitative modeling methods as a valuable contribution to biology. Previous examples of modeling frameworks that continue to be used include maximum entropy modeling to estimate species distributions and spatial densities (Phillips et al. 2006; Elith et al. 2010; Phillips et al. 2017), genetic structure analysis to map genetic diversity across landscapes (Pritchard et al. 2000; Guillot et al. 2005; Earl and von Holdt 2012; Besnier and Glover 2013), multivariate analyses of ecological data (McCune and Grace 2002), multivariate non-parametric regressions (McCune 2006), and general model structures (de Valpine et al. 2017; Ponisio et al. 2020). In all of these cases, free or low-cost user-friendly software (MaxEnt, STRUCTURE, GENELAND, PC-ORD, HyperNiche, and NIMBLE) and extensive documentation and training materials increased the uptake of the methods.

Motivations and barriers to a systemic shift toward quantitative modeling

The primary motivation for a universal shift toward the quantitative modeling framework within biology should be that it improves the capacity of scientific analyses to address important biological questions and reduces the instances of erroneous conclusions that could be unintentionally harmful to human societies and natural ecosystems. Regardless of the discipline within biology, there is an internationally accepted, if not always explicitly defined, ethos that demands integrity, professional competence, and professional discipline from working scientists (Weinbaum et al. 2019). This is the same ethos that requires rigorous self- and peer-review of any scientific findings and applications of "best available science" in policy and resource management decisions. As computational power increases and improved methods of data collection or analysis are developed, working scientists have an ethical responsibility to learn and incorporate those advances into their research where applicable. We assert that recent advances in computational power have made the application of quantitative modeling to complex biological questions feasible. As a result, all biologists should strive to improve their abilities to reap the benefits of quantitative modeling, which include harnessing the power of formal reasoning, identifying correct but counterintuitive outcomes, quantifying uncertainty, and focusing on latent variables, often the main targets of interest; all these benefits lead to improved explanations of the natural world.

We also recognize, however, that there are significant barriers to entry for shifting from a well-known framework of analysis to a novel one. Working biologists and, perhaps to a lesser extent, biology students have demanding schedules that may not permit intervals of reduced productivity to accommodate intensive training events like the ones that would be required to create a systemic change in analytical practices. This scheduling conflict is probably even more extreme for the quantitative scientists who would need to develop such training events and tools. Additionally, in many cases, there is not currently a financial incentive to incorporate quantitative modeling into research grant proposals, the primary source of funding for many biologists. In fact, there may be a disincentive because these proposals are reviewed by peer scientists who may also be unfamiliar with quantitative modeling, and research indicates that proposals with familiar methods are more likely to be funded than proposals with novel ones (Phillipps and Weißenborn 2019; Franzoni et al. 2022). Nevertheless, these challenges are not unique to quantitative modeling; they are common to any important shift in scientific practice (Kuhn 1962) and need to be embraced by everyone, producers and consumers of biological knowledge as well as funding agencies and journals, for science to progress. The relatively few biologists who currently apply quantitative modes in their work face all of these challenges and persevere. Rather than identifying these practitioners as something separate from "us biologists," they should be embraced as role models and incentivized to guide others to improve their understanding and applications of quantitative models.

Conclusions

In this paper, we have laid out an argument for shifting the dominant paradigm of biological research, application, and training from one that is often highly dependent on mental logic, which has been demonstrated to be often biased or flawed (Gruszka and Nęcka 2017), to one of explicitly quantified mechanistic relationships. We produced examples of the advantages of quantitative modeling to producers and consumers of biological information spanning many fields and levels of biological organization. Despite the many advantages of quantitative modeling for biological research and practice, biologists must overcome practical barriers to its application and possibly personal biases against its use before we can reasonably expect it to be widely adopted. Nevertheless, reliance on explanations for increasingly complex phenomena in biology requires improvement in the quantitative and modeling skills of biologists. We outlined several actionable steps that can be taken by researchers and institutions to increase the application of quantitative modeling: form collaborations between biological systems experts and biologists familiar with quantitative modeling, provide resources and support for the development of workshops and trainings for working biologists to learn foundational concepts, revise scientific curricula in secondary schools and universities to educate the future biological workforce, and provide resources and support for the creation of user-friendly software that facilitates the use of quantitative modeling.

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Conflict of interest

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