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SPECIAL FEATURE:
EMPIRICAL PERSPECTIVES FROM MATHEMATICAL ECOLOGY

Writing mathematical ecology: A guide for authors and readers

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Citation: Shoemaker, L. G., J. A. Walter, L. A. Gherardi, M. H. DeSiervo, and N. I. Wisnoski. 2021. Writing mathematical ecology: A guide for authors and readers. Ecosphere 12(8):e03701. 10.1002/ecs2.3701

Abstract. Mathematical techniques have a long and rich history in ecology, often serving as a virtual laboratory to test hypotheses, generate novel predictions, and investigate underlying ecological mechanisms. Recently, novel simulation techniques, advances in computing power, and numerical methods for implementing statistical models have significantly advanced our ability to integrate empirical and theoretical ecology. However, a divide still remains between mathematical and empirical studies, their readership, and integration into the broader literature. Because insights from mathematical ecology are far more general than the techniques employed, limitations in communicating mathematical advances to a broad spectrum of ecologists have arguably hindered ecology's progress, particularly in confronting theoretical predictions with empirical experiments and data. Here, we present a guide for both authors and readers of mathematical ecology, with the aim of increasing the accessibility of mathematical ecology for a broad group of ecologists. We provide a list of best practices when both writing and reading mathematical ecology, incorporating examples from this Special Feature of *Ecosphere*. This guide complements current guides for writing science, focusing specifically on effective communication of mathematics.

Key words: equations; notation; scientific writing; Special Feature: Empirical Perspectives from Mathematical Ecology.

Received 7 January 2021; accepted 5 March 2021. Corresponding Editor: Lei Zhao.

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Introduction

Ecology and its various subfields have a long history of close synergy between mathematics and empiricism across theory, statistics, and more recently with the integration of computer science and machine learning. Foundational mathematical theories dating back to the early 1900s played critical roles in shaping both the historical path and current focus of ecological research, such as in examining invasion and range expansions (Skellam 1951, Hastings et al. 2005), population dynamics and species interactions (Lotka 1925, Volterra 1926, Ricker 1954, May 2001), and disease spread (Ross 1911, Kermack and McKendrick 1927, Keeling and Rohani 2008). Furthermore, ecological applications are central to the development of modern applied statistics (Efron 1998, Hald 1998). More recently, spurred on by novel computational techniques, increased computing power, and the rise of "big data," new areas of mathematical ecology have emerged (Table 1). These include complex systems science (Dunne et al. 2002, Grimm et al.

Table 1. Recent subfields in mathematical ecology.

Method	Description and origin	Common applications within ecology	Selected references
Machine learning	A discipline within computer science where computational algorithms built on sample, training datasets make predictions or classifications of novel datasets. Inspired by the structure of the human brain, applications of machine learning algorithms in day to day life range from email intelligence to image or vocal classification, and medical diagnoses.	Image recognition, Acoustic recognition, Image processing in GIS, Species distribution modeling	Martin et al. (2018), Christin et al. (2019), Tabak et al. (2019), Lucas (2020), Harte and Newman (2014)
Complex systems science	The study of large-scale systems where the collective behavior of components cannot be understood as the sum behavior of the individual components. Insights from chaos theory were crucial in the development of complex systems theory.	Network theory, especially as applied to food webs and microbial ecology Individual-based modeling, Chaotic dynamics, Multi-scale systems	West et al. (1999), Dunne et al. (2002), Grimm et al. (2005), McCreery et al. (2016), Ponisio et al. (2019), Liu et al. (2020), Zamkovaya et al. (2021)
Bayesian modeling	A method of statistical inference where Bayes' theorem is applied to update the probability of a random event as more evidence becomes available. While Bayes' theorem has a long history, its applications are relatively recent and rely on novel computational techniques and increased computing power.	Population dynamics and extinction risks, Multispecies communities Foraging dynamics	Ellison (2004), Hobbs and Hooten (2015), Carpenter et al. (2017), Goodrich et al. (2018), Conn et al. (2018)
Structural equation modeling (SEM)	A multivariate statistical analysis technique used to analyze relationships between measured and latent variables that cannot be measured. SEM techniques were initiated by geneticists in the early 20th century and were popularized by social scientists.	Aquatic ecosystem ecology, Soil ecology, Plant Community Ecology	Grace et al. (2010), Pugesek et al. (2003), Jonsson and Wardle (2010), Firn et al. (2019)

2005), the application of Bayesian modeling (Hobbs and Hooten 2015, Weiss-Lehman et al. 2017), and machine learning approaches (Peters et al. 2014, Martin et al. 2018)—elements of which are also components of the emerging field of computational ecology (Poisot et al. 2019). As implied in this list, we take a broad view of what constitutes mathematical ecology, considering it to include theoretical and system-specific models as well as statistical and computational tools, particularly those that are not yet standard tools of ecology. Mathematical ecology, thus broadly defined, continues to push our field forward by connecting theoretical and methodological developments to ecological applications (Elith et al. 2011) and represents a virtual laboratory where we can test hypotheses, generate novel predictions, and investigate mechanisms underpinning observed patterns (Petrovskii 2018).

In practice, however, a divide often occurs, where mathematically complex papers are most frequently read by like-minded scientists and reach empiricists less frequently (Fawcett and Higginson 2012*a*, Kane 2012). For many papers, especially those introducing new or new-to-ecology mathematical and computational techniques, mathematical content is central to the heart of the manuscript, and therefore must be communicated effectively to maximize impact on the field. Because the insights from mathematical ecology are often far more general than the context of an individual study, limitations in communicating mathematical advances in ways that are approachable to a broad spectrum of ecologists have arguably hindered progress in ecology, particularly in confronting theoretical predictions with data (Fig. 1). In this Special Feature, the included manuscripts highlight the current state of mathematical ecology across a diversity of subfields, its generality to empirical systems, and the integration of mathematical modeling with empirical perspectives. Here, we, a group of authors who use different combinations of empiricism, theory, and statistical/computational approaches in our own work, consider how to improve communication of mathematical ecology in scientific papers. Although this effort is germane to a broader contemporary conversation on quantitative training in ecology (Hobbs and Ogle 2011, Thompson et al. 2013), we focus on strategies for effective communication in the context of scientific papers and intend our recommendations to be pertinent to ecologists at many career stages.

Guides on scientific writing are abound for both students (Bolker 1998, Turbek et al. 2016) and established scientists (Sand-Jensen 2007, Silvia 2007, Schimel 2012, Heard 2016). However, much less has been written, especially in the peer-reviewed literature, about the effective scientific communication of mathematical constructs (but see Scheinerman 2011). Mathematical notation can be considered its own "language" with conventions that aid those that are already fluent in its notation, but can inadvertently serve as a gatekeeper for more broad communication. Many ecologists are primarily self-taught in mathematics and its communication (especially as applied to ecology), exemplifying the need for a guide.

While many techniques of effective science writing also apply to mathematical ecology, unique requirements and challenges also arise (Box 1). These challenges exist both for effective communication by the author and for comprehension of readers—especially those new to reading papers with advanced mathematical content. Here, we bridge this gap between scientific writing guides more generally and applications for mathematical manuscripts, providing a guide specifically for mathematical ecology papers. We recommend techniques for both

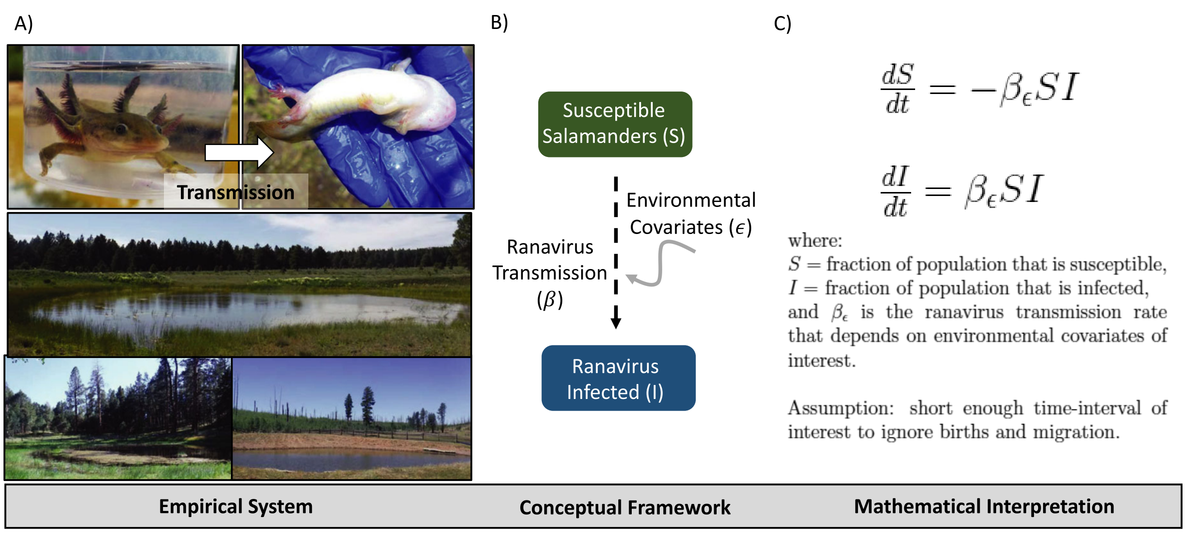

Fig. 1. Both empirical (A) and mathematical ecology (C) often use similar conceptual framings (B) to describe their overarching questions and research focus. We suggest that explicitly incorporating these conceptual framings—as is commonly done in oral scientific presentations but less so in manuscripts—can help bridge the gap between empirical and mathematical ecology. Photographs in (A) are kindly provided by Kathryn A. Cooney.

Box 1.

Common challenges when communicating mathematical ecology

Clear communication of mathematical ideas to a broad audience presents a set of challenges for authors and readers alike. In order to make mathematical ecology more accessible, it is important for theoretical researchers to be aware of the common challenges encountered by empirical researchers and vice versa. Through shared awareness of these challenges, communication may be improved in both directions.

1. *Lack of familiarity with previous theory and lack of continuity with literature*. Many empirical readers, and likely some fraction of theoreticians and computational ecologists, will be unfamiliar with prior theoretical work upon which a current study builds. Brief summaries of the key insights from essential literature are helpful for communicating the advances of the present study.
2. *Readers may be inexperienced with the mathematical methods used in the paper*. As a result, it is prudent to explain in words what the major steps of the analysis accomplish for readers that do not fully grasp the methods. Similarly, it is critical to define mathematical notation and terms—even if it will be review for researchers familiar with the previous literature.
3. *False sense of mathematical understanding by readers*. Readers likely understand some aspects of the material presented in mathematical ecology papers; without careful reading, this previous knowledge can actually lead to misconceptions, as assumptions about notation or equations are easily made. As a result, insufficient understanding could lead to confusion if theory is misunderstood or misapplied in an empirical context.
4. *Equation fatigue*. Readers may be less accustomed to following long sections of equations with little explanation. Each additional equation provides a new opportunity for a reader to start skimming the math or abandon the paper altogether. Providing clear examples of key parameters from each equation in terms of ecological responses may help to keep the reader's attention.
5. *Lack of clear connection between biology and math*. When a mathematical approach is not properly motivated by a biological question, it could be difficult to translate theoretical advances back into appropriate biological contexts. Consequently, the model may not inspire empirical tests or future theoretical analyses, or the statistical analysis may not be applied under potentially appropriate scenarios.
6. *Unclear or poorly justified assumptions*. Empiricists with extensive natural history backgrounds may struggle to accept or understand the implications of key simplifying assumptions that mathematical ecologists use. Likewise, modelers could make poorly justified assumptions that limit the relevance of the model. Lack of justification or transparency about assumptions could hinder communication, both of what the model demonstrates and its limitations.
7. *Journal silos*. Mathematical ecologists and empirical ecologists largely tend to publish in different journals, with a few exceptions. As a result, exposure of more discipline-specific advances may be limited to audiences closely aligned with the authors. For example, hypotheses developed in theoretical papers may not be encountered by empirical ecologists unless published in a handful of the top journals, while natural history notes that describe new behavior based on observations or experiments may not receive theoretical investigation. Broader acceptance of purely theoretical research in general ecological journals may help bridge the gaps between journal readership.
8. *Mathematical rigor cannot be avoided*. Theory can often require a level of technical detail and development that cannot be omitted or deferred to other references. As a result, authors of complex mathematically oriented research may be tasked with making their work especially clear and well organized in order to facilitate dissemination into broader ecological disciplines.

authors and readers by which ecologists can make the mathematical content of papers more accessible to a broad group of ecologists. To do so, we provide recommendations for authors writing mathematical ecology papers and for readers that are newer to theory and/or computational ecology. The manuscripts highlighted in this Special Feature provide concrete examples across sub-disciplines of applications of best practices.

Recommendations for Authors

Here, we provide a number of recommendations for authors of mathematical ecology papers, drawing on examples from articles in this Special Feature and the broader literature. Our intent is to highlight what we consider to be the best opportunities for authors to improve the accessibility of mathematical ecology papers, acknowledging that this is neither an exhaustive list nor do all suggestions apply equally well to all manuscripts.

Directly address ecological contexts and relevance

One common criticism of mathematical studies is that the math is sufficiently abstracted from the real world as to have limited usefulness for understanding real systems—or in other words, that the study is more of a mathematical exercise than an ecological one. While this may occasionally be true, the history of mathematical models informing our fundamental understanding of ecology points to a robust role of mathematical modeling in advancing the field. As such, the more common case is a failure by the authors to communicate effectively to a broad audience.

How can authors of mathematical studies address this criticism? We suggest that the authors' role in overcoming this problem lies in emphasizing the ecological context and motivation for theoretical studies. For example, to provide motivation for their study on tail associations in distributions of ecological variables, Ghosh et al. (2020) provide a graphical depiction of right and left tail associations and use a previously undescribed example of spring rainfall to depict plausible ecological scenarios that could produce different mathematical outcomes. By pairing relevant mathematical concepts with simple examples in the introduction, Ghosh et al. (2020) lay the groundwork for the reader to follow the central thesis of the manuscript—why tail associations are important to consider for extinction risks of populations.

Clearly state ecological and mathematical assumptions

It is particularly important to explicitly discuss methodological choices and model assumptions within the manuscript. Doing so allows the reader to easily determine why a specific model choice was made, the appropriate empirical contexts for applying the model, and where its key insights may hold. Place justifications for assumptions and their consequences in ecological terms, for example, by envisioning ecological scenarios in which a given assumption does or does not give a reasonable approximation of reality. For example, in building their dynamic plant-pollinator model, Ramos-Jiliberto et al. (2020) clearly state assumptions about the biology of the system after each equation. In some cases, they back up their assumptions based on empirical observations or previous literature, while in other cases, they state that a given assumption was made for model simplicity, rather than biological realism—an often necessary balance when building mathematical models of ecological processes (Ramos-Jiliberto et al. 2020). Statistical methods also carry their own assumptions, for example, about the nature of relationships among variables and how data are distributed, which likewise should be stated clearly.

Use clear signposting

All papers benefit from clear signposting that enables the reader to quickly grasp how a paper is organized, the take-away of each section, and whether a given section pertains to their own purposes for reading the manuscript. Given the volume of literature available, most readers will not read a manuscript in depth; if they proceed past the abstract, they will focus on the sections that are most pertinent to them. They may gloss over equations and other methodological details, unless motivated to achieve a deeper understanding. As such, it is pragmatic to write papers in such a way that readers can easily skim and understand the key components of a mathematical model or method, while they can dive into the equations for further detail.

Opening sentences of paragraphs are important features of a signposting strategy as they have a powerful position for establishing the content and tone of what follows. Likewise, closing mathematically dense paragraphs with sentences that recapitulate key points in an ecological context can help ensure understanding and transition the reader into the next passage. Other strategies we have found helpful include the use of descriptive sub-headings and opening the Methods section with a paragraph giving a high-level summary of the methodology. Such a paragraph typically addresses the general approach taken by the study and may also describe how the evidence presented will be evaluated to form conclusions. The order in which topics are presented in this paragraph will often parallel the order of their detailed presentation further in the methods. As an example, Ramos-Jiliberto et al. (2020) begin the methods section with a verbal and graphical overview of their dynamic plant-pollinator model before they dig into the details of the equations governing transitions between life stages. Similarly, Leach et al. (2020) provide an overview of their modeling approach, followed by sub-headings within the methods section that lay out the derivation of their models, ultimately leading to how they used this suite of models to investigate stochastic extinction risk.

Use illustrations and diagrams

Pedagogical illustrations, flowcharts, and diagrams can be extremely useful for communicating complex concepts, the structure of models (e.g., Fig. 1B), and analytical workflows in ways that are broadly intuitive to readers of diverse research backgrounds. Similarly, the Overview, Design Concepts, and Details (ODD) protocol (Grimm et al. 2010), a standard for the description of individual-based models, also advocates for diagrams of model structure. Similar diagrams are also useful for empirical studies with complicated workflows involving multiple steps or analyses, which may build on each other toward the paper's conclusion, or offer parallel lines of evidence toward inference. Leach et al. (2020) incorporate an excellent example of the use of visuals to describe model structure. In their graphical overview of their approach, Leach et al. (2020) communicate the flow between the three core components of their suite of models (group formation, mating systems, and reproduction), using circles and symbols to indicate group size and mating systems, and colors to illustrate the stochastic processes considered for each component.

Clearly define mathematical notation

Arguably, nothing impedes the accessibility of mathematical ecology papers, even among the mathematically savvy, like poorly defined, ambiguous, or unclear notation. Unlike an undefined word or phrase in a paper, it is often impossible to refer elsewhere for a parameter definition used in an equation, making it imperative that authors define all notation they use. The convention for doing so is that all output variables (also called state variables) are described *before* they are first used in an equation, while all parameters that modify the equation's dynamics are defined immediately after the equation first appears. State variables tend to be defined using upper-case letters, while parameters tend to be defined with lower-case and/or Greek letters. Notation should be consistent within the manuscript and with the broader literature, if possible (Scheinerman 2011). Authors should ensure that similar-looking symbols do not code for dissimilar things.

Despite its importance, it is surprisingly common that authors do not define all variables in key equations. Sometimes, this omission reflects conventions; for example, $\overline{x}$ very often denotes taking the mean of some variable x. However, not all readers may be familiar with such conventions, and standards change from field to field. For example, in wavelet analysis the overbar has been used to indicate taking the complex conjugate, not the mean (Keitt and Fischer 2006, Cazelles et al. 2008, Sheppard et al. 2016). Well-defined notation benefits all readers, especially as ecologists often draw on models and analytical approaches developed in disparate fields having their own conventions. Tables that provide easy reference to verbal descriptions of mathematical variables can be especially beneficial to readers. For example, in their manuscript introducing a novel method to determine the timescales of synchronous versus compensatory dynamics, Zhao et al. (2020) define all variables when they first appear in the text, including their notation for denoting the mean and covariance, rather than assuming the reader is familiar with these mathematical notations. Zhao et al. (2020) additionally provide a summary table for readers to refer back to while reading.

One area where we see a good deal of room for improvement is in the consistent use of subscripts and superscripts. Often in ecology, these aspects of notation clarify whether a variable changes with respect to space, time, species, or life stage and hence are vital to the ecological concerns of a study. Yet, in many cases subscripts and superscripts can be used inconsistently throughout a manuscript, leading to ambiguity and confusion.

Leverage open access and online supplements

Online publishing and the open science movement have facilitated two particularly important changes to scholarly publishing that authors of mathematical ecology papers can, and commonly, do to enhance communication of their science: (1) online supplements and (2) reproducible, archived open-access code.

Historically, the length of scientific papers has been constrained by space limitations, but recent trends toward online-only publication and the use of online supplementary material have eased such restrictions. The clear opportunity this provides, as we advocate for and exhibit in this Special Feature, is thorough description of mathematical content and other technical detail. While this level of detail may not be necessary for an expert in a given subfield or mathematical technique, organizing a manuscript such that these sections can be skimmed by an expert greatly facilitates readability and synergy between empirical and mathematical ecology. An excellent example of the appropriate use of online supplementary material in this Special Feature is from Taubert et al. (2020). In their study on the effects of species traits on grassland productivity, Taubert et al. (2020) make use of an individual-based mechanistic model called GRASSMIND to simulate species pairs that vary in selected life-history traits. A reader can follow their general approach easily without diving into the technical details of the GRASSMIND model; however, the authors also provide a robust and well-notated supplementary material for readers who may be interested in examining the model in more depth.

We argue, however, against hiding key mathematical details in the Supplementary Material. In many studies, these represent a key research innovation, and burying them in an online supplement both gives short shrift to the authors' efforts and misses the chance to share these innovations with readers. The supplement provides an excellent opportunity to provide additional detail to facilitate readability, such as an instructional guide that reviews key theories or historical mathematical derivations that may help readers translate between the focal manuscript and previous work (Melbourne and Hastings 2008).

Just as publishing data are becoming a requirement at many journals due to the current, exciting focus on open science, authors should publish well-annotated code for all mathematically focused manuscripts in open access repositories. We recommend publishing well-commented code for recreating all analyses included in the manuscript; code should include a ReadMe file to document the project and should be published in a code repository with a persistent identifier (i.e., DOI), such as Zenodo.

The widespread use of languages like R by ecologists for data management, statistical analysis, and simulation modeling suggests that many ecologists may now have greater facility at reading code than at reading equations. Additionally, it is often challenging to translate code into verbal descriptions in a manuscript, so having reference code for readers will assist with overcoming any ambiguity that may accidentally arise. An advantage to reading and interacting with code is to see how a model or method becomes operational. Better yet, many authors have supplemented their manuscripts with extensive code embedded in a long-form narrative document (e.g., RMarkdown or Jupyter notebooks) that allows readers to interact with code, alter parameters, learn new computational techniques, and reproduce entire analyses. Likewise, graphical interfaces can make code more interactive (e.g., Shiny apps), which can extend the utility of code beyond reproducibility and transparency into a tool for learning quantitative approaches or exploring scenarios beyond the focus of the manuscript.

Recommendations for Readers

Communication of mathematical ecology is a two-way street, where both the author and the reader share responsibility (Fawcett and Higginson 2012*b*). As such, here we present recommendations for readers, drawing from our own experiences and training. These suggestions apply broadly and are the key steps we continue to apply, especially when reading papers outside of our own domains of expertise.

Expect to spend extra time engaging with math

Reading math is challenging and time-consuming, even for experts. While training and experience make it easier, especially when reading outside of one's immediate area of expertise, it will always take time to engage deeply with a mathematically complex study. This remains true even for those who self-identify as mathematical ecologists; many areas of mathematics are relevant to our field, but we may be most comfortable in only one or two, and we frequently encounter new approaches that take time and effort to familiarize ourselves with. This may involve breaking down equations, consulting textbooks or references on the technique, or reading through and running accompanying open-access code. This need to spend extra time to deeply engage with the details of a paper is, of course, not unique to mathematical papers; deep engagement with any science requires time and effort. For example, one can quickly read an experimental protocol for a general understanding, but to replicate a study, it takes far more time to understand each part of the protocol.

Reread papers

It is rare that a single read-through of a highly mathematical paper will reveal all the intricacies of the study. In fact, it may be unwise to try to understand all the math upon an initial read. Instead, it may be beneficial to first read for an overview of the aims, general approach, and assumptions of the model or statistical technique. Then, once the broad overview is established, there is a clearer mental scaffold upon which the detailed, technical sections of the paper can be built. Subsequent reads (in combination with the below recommendations) will gradually reveal the intricate and challenging aspects of the manuscript.

Learn with peers

Most scientists benefit from meeting in small groups (seminar courses, lab groups, journal clubs) to discuss peer-reviewed articles. Group paper discussion is often one of the best ways for scientists at all levels to improve learning comprehension and tackle complex ideas. Oftentimes, there is a tendency within ecology reading groups to avoid choosing papers with too many equations. We encourage reading groups to not steer away from papers with ample mathematical content and, to instead, spend time as a group breaking down equations and discussing the biological meaning of model parameters. When discussing methods that are newer to the group, it is often helpful to pair the paper discussion with a reading from a textbook or a review paper of the method to provide additional technical background. Good paper discussion groups provide a relaxed environment for peers with diverse perspectives and expertise to teach one another. Mathematical concepts that are challenging for some members of the group may come easily for others, which they can then explain in their own words. Early career scientists in particular will benefit from knowing that scientists at all levels struggle with new mathematical techniques.

Break equations down into their components

Mathematical equations are often presented holistically, making it appear that the authors sat down and immediately wrote a final, complete model or computational method. Rather, most equations are built component by component, starting from a conceptual formalization of question or topic (Fig. 1B), previous work in the literature, and gradually building to formal notation and the final form presented in a peer-reviewed publication.

To increase understanding as a reader, we suggest breaking apart equations into their individual components. To do so, the reader can print the pages with the equations and tables defining parameters and directly annotate equations. We suggest first writing out in words what is being modeled (i.e., what is to the left of the equal sign). Next, define each component at its most general. For example, population size is often modeled as some form of "births - deaths + immigration - emigration." Additional complexity arises from the countless ways to describe each of these components and their interdependencies. Finally, the assumptions behind each given process, and their corresponding parameters, can be interpreted for full understanding. Building upon the example above, does population size increase exponentially or logistically? Does population size explicitly depend on intra- and interspecific competition? Are stochasticity or other forms of variability explicitly incorporated into the model? Depending on your interest in the paper, you may want to dive into these underlying mathematical assumptions, or alternatively, just focus on the key components incorporated into an equation.

Connect to a general class of well-understood model

Science proceeds by building step-by-step on prior work, and mathematical ecology is no different. One strategy for greater understanding of the developments of a particular study is to draw connections between it and a general class of foundational models whose behaviors are well-understood and often are well described in basic resources (e.g., textbooks, Wikipedia, or review articles). By comparing and contrasting a particular model with its more general "family of models," the meanings of terms, expected behaviors, and new developments often become clearer. Notably, this strategy assumes some familiarity with foundational theory and statistical methods, which may still be a barrier for some readers.

Foundational papers may not be the best way to understand foundational models

Often, we read foundational papers to understand how an important idea was introduced to the field, but sometimes aspects of these papers make comprehension difficult. For example, standard terminologies and conventions on the structure and tone of scientific articles have evolved over time, and text often contains references to controversies ongoing at the time it was written, but that are opaque to modern readers. Papers about foundational theoretical and statistical models are similar and may be especially difficult for many ecologists to read if written for a math specialist audience.

Consulting a textbook can often be a more efficient way to understand models. Subsequent work addressing the full behavior of a model, and its strengths and weaknesses, will likely be addressed in language tailored for a broader audience, especially if the book is written for ecologists. In some cases, the method or approach itself may have sufficiently diverged from its initial conceptualization that the foundational paper is no longer an authoritative reference for how the model should be applied or analyzed. Wikipedia can also be a good resource. Many foundational ecological models, such as the Lotka-Volterra equations mentioned previously, have pages with relatively clear and deep explanations, with references to primary literature and standard texts that facilitate further learning. We note, though, that many Wikipedia pages for statistical methods lean toward the theoretical, as opposed to the applications that many ecologists are interested in, and also that the quality of Wikipedia entries can vary substantially as a function of author expertise and time invested. Further contributions by experts in ecology could enhance this resource.

Reconstruct models and explore parameter space

Many times, trying to fully understand a model in the context of the original publication may not be the optimal way to engage with mathematical content. Just as you truly and deeply only understand an empirical method by implementing it yourself, the same is true for mathematical models. If coding your own version of a published model, we recommend first using the parameter values from the published paper to replicate figures and verify that your code is correct. Once the model has been carefully implemented in the modeling platform, it is often instructive to explore parameter space. Investigate what happens to the model output as you dial up and down parameter values. Which parameters are the model most sensitive to? Which parameters have relatively little influence on the outcome? This exercise also helps connect your own biological intuition with the underlying model assumptions.

Conclusions

Mathematical ideas permeate ecology. Not only does math allow ecologists to explore new questions and generate hypotheses about how the natural world works through theory, mathematics also enable the development of statistical tools that ecologists use to test predictions and gain insight from complex patterns in empirical data. Conversely, empirical studies provide ground tests for previously developed theories and lay the foundation for new hypotheses. Thus, it is crucial that mathematical concepts be clearly communicated to both theoretical and empirical ecologists alike. In this piece, we acknowledge common challenges in the effective communication of mathematical concepts in research articles. To help overcome these challenges, we provide a suite of recommendations for both authors and readers that we believe would foster greater collaboration between mathematical and empirical ecologists, accelerate progress, and integrate a broader range of perspectives in the field. In particular, we note that it is essential for readers to understand the ecological context of theoretical papers and suggest that authors establish this context early on, using clear signposting, consistent notation, and visual aids to alert the reader to important biological insights established in the equations. For readers, persistence is key no matter how comfortable you are as a mathematical ecologist; it may take additional time and readings to fully digest the mathematical content, breaking down equations and making connections to existing, more familiar models. But this extra effort, either alone or with peers, will be important for becoming more familiar and comfortable with mathematical equations in papers. An important outcome of clear writing in mathematical ecology is increased synthesis between the theoretical and empirical literature that, together, will promote novel research aims and interdisciplinary collaborations.

Acknowledgments

LGS, MHD, and NIW were supported by the NSF EPSCoR Track 1 RII grant (NSF award #EPS-1655726). This project was additionally supported in part by the NSF EPSCoR Track 2 RII grant (NSF award #EPS-2019528). JAW was supported by a NatureNet Science Fellowship and NSF OAC-1839024. LGS and JAW contributed equally. LGS, JAW, and LAG organized the Special Feature; all authors contributed to manuscript writing and editing.

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Data Availability Statement

No data accompany this manuscript.