

An Empiricist's Guide to Using Ecological Theory

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ABSTRACT: A scientific understanding of the biological world arises when ideas about how nature works are formalized, tested, refined, and then tested again. Although the benefits of feedback between theoretical and empirical research are widely acknowledged by ecologists, this link is still not as strong as it could be in ecological research. This is in part because theory, particularly when expressed mathematically, can feel inaccessible to empiricists who may have little formal training in advanced math. To address this persistent barrier, we provide a general and accessible guide that covers the basic, step-by-step process of how to approach, understand, and use ecological theory in empirical work. We first give an overview of how and why mathematical theory is created, then outline four specific ways to use both mathematical and verbal theory to motivate empirical work, and finally present a practical tool kit for reading and understanding the mathematical aspects of ecological theory. We hope that empowering empiricists to embrace theory in their work will help move the field closer to a full integration of theoretical and empirical research.

Keywords: hypothesis testing, experiments, experimental design, methodology, theory, mathematical models.

The great book of nature is written in the language of mathematics. (Galileo Galilei ca. 1600)

Introduction

Scientific inquiry should operate as a feedback loop in which theory that describes the natural world is developed, tested empirically through carefully articulated hypotheses, modified to better represent reality, and then tested again. When this feedback loop works, theory provides a framework to guide inquiry, experimental design, and the interpretation of observed patterns, supplies mathematical tools to harness information from collected data, and connects individual experiments to general ideas about how nature operates. In turn, empirical research can be used to support, refute, or revise theoretical predictions, indicate which theoretical assumptions are consistent with the natural world, and point theoreticians to overlooked processes that can be integrated into models.

Feedback between theory and experimentation has always been essential for the progress of ecology (Gause 1935; Huffaker 1958; Simberloff and Wilson 1969; Tilman 1977), and as collaborations across disciplines become more common, theoretical and empirical research have the potential

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to be more tightly linked than ever before (Rossberg et al. 2019; Laubmeier et al. 2020; Servedio 2020). Moreover, in confronting global challenges such as climate change, biodiversity loss, and emerging diseases, humanity can benefit enormously from the ecological understanding that arises from a fully functional scientific process (Marquet et al. 2014; Ferrier et al. 2016).

Unfortunately, the links between theoretical and empirical research in ecology are not as strong as they could be (Caswell 1988; Kareiva 1989; Fawcett and Higginson 2012; Scheiner 2013; Haller 2014; Rossberg et al. 2019). Up to 45% of articles on empirical ecology make no mention of any theory whatsoever (Scheiner 2013), and fewer than 10% of ecologists and evolutionary biologists agree with the statement that “theoretical findings drive empirical work” in their fields (Haller 2014). This disconnect has been attributed to several underlying challenges, including a lack of emphasis on theoretical training in ecology (Rossberg et al. 2019), a lack of motivation on the part of some theoreticians to engage with the language of empiricists (Grimm 1994) or with the elements of nature that empiricists focus on (Krebs 1988), a general lack of mutual appreciation between empiricists and theoreticians (Haller 2014), and persistent communication barriers between these two groups (Servedio 2020). A major cause of the communication barriers between theoretical and empirical ecologists is that in ecology, as in other scientific fields, theory is often expressed in the language of math. Ecologists come to the field through a variety of educational and experiential pathways, are often drawn to ecological research by an interest in natural history or hands-on field and lab research, and may not be formally trained in advanced math. Likewise, theoretical research may not be written for a general audience and can contain unexplained assumptions, terminology, or notation that hinders comprehension (Dee-Lucas and Larkin 1991; Grimm 1994). As a result, the mathematical aspects of theory can feel inaccessible to empiricists (Fawcett and Higginson 2012; Haller 2014). Indeed, the more equations an ecology and evolutionary biology article contains, the fewer citations it receives (Fawcett and Higginson 2012). Of the empirical articles that do cite mathematical theory, only about half do so both correctly and specifically (Servedio 2020). This barrier presents a major challenge to the full integration of theoretical and empirical work in ecology.

Previous articles and books have discussed the causes and extent of the disconnect between theoretical and empirical research in ecology (Łomnicki 1988; Kareiva 1989; Fawcett and Higginson 2012; Scheiner 2013; Haller 2014; Rossberg et al. 2019). The value of theory in ecology and evolutionary biology has been emphasized, and many have advocated for a better integration of theory into empirical work (Caswell 1988; Pickett et al. 2010; Marquet et al. 2014; Servedio et al. 2014; Servedio 2020). Detailed step-by-step

instructions for building biological models and fitting them to data have been provided (Pielou 1969; Otto and Day 2007; Bolker 2008; Bodner et al. 2020). Recent work has helped to demystify the process of theory creation (Otto and Rosales 2020), has advocated for the training of more theoretical ecologists (Rossberg et al. 2019), and has provided an overview of some of the challenges associated with communicating theory to a broad audience (Shoemaker et al. 2021). However, this still leaves many empiricists who are interested in motivating their research with theory but who have little prior experience with math and models struggling to take the first step.

We seek to fill this gap by providing an accessible guide that covers the basic step-by-step process of how to approach, understand, and use ecological theory in empirical work. We achieve this by (1) briefly reviewing how and why mathematical theory is created, (2) outlining four specific ways that mathematical and verbal theory can be used to motivate empirical work, and (3) providing a tool kit for reading and understanding the mathematical aspects of ecological theory. We are ecologists and evolutionary biologists spanning the full spectrum from empiricists to theoreticians, and this guide is the outcome of the empiricists among us feeling intimidated by the mathematical aspects of theory and reaching across the divide to our theoretical colleagues to build the tool kit needed to understand and use theory. While we recognize that the onus should not fall entirely on empiricists to bridge the theory-empirical divide and that fostering collaborations between theoreticians and empiricists and encouraging theoreticians to present their theory in a clear and accessible way are also critical for achieving this goal, in this article we focus on the steps that empiricists can take. Our aim is not to teach empiricists how to create theory or to express it as math but rather to empower empirically minded ecologists to read and understand mathematical theory and to integrate theory into their work at every step in the research process.

A Primer on Theory

We begin by introducing the general concept of theory: what it is, what it aims to do, and how it is created. While we focus on ecological theory, many of the ideas discussed here will also apply to evolutionary theory and to other scientific fields. We focus primarily on theory that is expressed mathematically because these elements of theory often present the steepest accessibility barrier to empiricists, while recognizing that theory and math are not inexorably linked. Indeed, many excellent theories do not involve math (e.g., the theory of evolution by natural selection; Darwin 1859), and many uses of math in ecology are not theory (e.g., practical applications of statistics). Finally, we restrict our discussion to model development that does not use data but discuss

statistical model fitting as an empirical approach (see “Approach 3: Use the Mathematical Equations”).

What Is Theory?

We define *ecological theory* broadly as an explanation of an ecological phenomenon. These explanations take the form of narratives that explain how an ecological process works or why an ecological pattern is observed and that become scientifically useful when expressed in a logical structure (Pickett et al. 2010; Rossberg et al. 2019). The transformation of an idea in narrative form into a logical, testable theory often, though not always, involves the use of mathematical models (Otto and Rosales 2020). A *mathematical model* is an equation or a set of equations that describes how different aspects of a system relate to one another (Otto and Day 2007). The term *model* refers to the fact that mathematical models are idealized and simplified versions of reality, just as architectural models represent key features of complex structures and model organisms represent a group of organisms that share common attributes (Kokko 2007). The translation of ideas in a theoretician's mind into math on a page serves several purposes: math provides a clearer and more objective expression of relationships, it brings to light assumptions and logical errors that may be obscured in verbal hypotheses, and it places ideas and hypotheses into a concrete and concise form (Grimm 1994; Kokko 2007; Marquet et al. 2014; Otto and Rosales 2020).

How Is Mathematical Theory Created?

The process of expressing theory in mathematical terms can seem mysterious to those who have never attempted it, which can make theory seem unapproachable. Here we pull back the curtain on theory creation by describing the typical steps that a theoretician takes when creating a mathematical model (Otto and Day 2007; Bolker 2008) and, in doing so, highlight the many similarities between conducting theoretical and empirical research.

Step 1: The Motivation. The first step in theory creation often parallels that of empirical research: the theoretician thinks of a biological question that she is interested in or a biological process that she wants to understand. The question may be motivated by an unsolved problem, for example, how temperature affects consumer-resource dynamics (O'Connor et al. 2011; DeLong and Lyon 2020). Or it could be motivated by an empirical observation, for example, evidence of interspecific differences in plant species' susceptibility to pathogens and an interest in the implications for plant coexistence (Stump and Comita 2018; Ke and Wan 2020). Or it may be motivated by a practical problem, for example, the need to understand how population structure influences COVID-19 dynamics (Britton et al. 2020).

In other cases, the creation of new theory is motivated by the desire to extend an existing model rather than to develop a new model from scratch. Indeed, most models are variants of previous models, extended to include different biological features, to tailor the model to a new system, or to address a slightly different question. One underappreciated initial goal of some theory is to provide a *proof of concept* that verifies or refutes ideas that may have previously been expressed only verbally (Servedio 2020). This use of theory demonstrates that something can happen under certain conditions but not necessarily that it is likely to occur under all or even most conditions (Servedio et al. 2014; Otto and Rosales 2020; Servedio 2020). These models can serve as hypothesis tests themselves and may not be meant to be tested empirically (Caswell 1988; Servedio et al. 2014). More broadly, it is important to note that creating theory and translating it into math is a means of scientific discovery unto itself, and while in this article we focus on the ways in which empiricists can use theory, theory need not be tested empirically in order to be useful. Theory can have a major influence on a field without any empirical testing, for example, theory demonstrating that transient dynamics can be prevalent and long lasting (Hastings 2001). Recognizing that not all theory was necessarily meant to be tested empirically can help empiricists focus on the types of theory that are most relevant to their scientific goals.

Step 2: The Method. Next, the theoretician looks at the approaches that theory addressing similar questions has used and decides whether these approaches are relevant, justified, and suitable. The approach a theoretician takes is likely to be guided and constrained by her background; for example, a theoretician who is most familiar with *dynamical models* (those that track how a system changes over time) may be drawn to research questions that can be answered by that type of model, just as an empiricist who works with plankton mesocosms may focus on questions that are well suited to that approach.

A feature of this stage of theory development that may not be obvious to empiricists is the variation in the degree to which a new model builds on, tweaks, and combines existing models compared with conceiving of an entirely new mathematical approach. For example, parameterizing predator-prey population dynamic models with expressions for temperature-dependent biological rates from metabolic theory led to new insights about how temperature affects the abundance of interacting consumers and resources (O'Connor et al. 2011). Likewise, many COVID-19 models are variants of the classic epidemiological model documenting transitions among susceptible, infectious, and resistant hosts. In contrast, mathematical approaches drawn from physics were adopted by ecologists to understand the complex dynamics of animal grouping behavior (Okubo

1986), and math from information theory has yielded new perspectives on ecological problems such as energy flow in food webs (Rutledge et al. 1976) and biodiversity (Jost 2006). For empiricists interested in creating models, the recognition that theory is often created by combining existing models in new ways can help reduce the perceived barriers to participation.

Step 3: The Equations. In this step, the theoretician first decides which parameters and variables are necessary to describe the biological process of interest. A *parameter* is a quantity that has a value that does not vary within a given equation (e.g., resource supply rate), while a *variable* is a quantity whose value can vary within the equation, for example, through time (e.g., population size). In the simple model describing a linear relationship between x and y ($y = mx + b$), x and y are variables (there are multiple values of x and y), and m (the slope) and b (the y -intercept) are parameters (there is only one slope and one y -intercept for this equation). Note that while parameters do not vary within an equation, the biological processes that they represent do vary in nature (e.g., across space, time, organism identity), and changing the value of parameters and exploring how that affects outcomes of interest is a common exercise in theory development (see “numerical approaches” below). A helpful exercise when deciding how multiple related equations should be written out is to draw stock and flow diagrams that show the relationship between the different variables in each equation (Otto and Day 2007).

In determining the equations, the theoretician must make difficult choices between how broadly the model can be applied across systems (generality), how closely the model mimics real-world processes (realism), and whether the model produces specific quantitative predictions or general qualitative predictions (precision) (Levins 1966; Servedio et al. 2014; Bodner et al. 2020). For example, models can be written with more terms or relationships to capture more biological detail, but additional terms may render the model less general. Note that the aim of mathematical models is to increase our understanding of some phenomenon, not to describe nature perfectly, and so a model making unrealistic assumptions or simplifying a process is not necessarily a failing of the theory or a reason to discount its ability to guide empirical research (Levins 1966; Pielou 1969; Grimm 1994; Kokko 2007; Phillips 2015; Servedio 2020). Just as empirical studies vary widely in their realism, from field-based observational studies to highly manipulated lab experiments, so, too, do ecological models. And just as each type of empirical study has value, so, too, does each type of theory.

Step 4: The Analysis. The theoretician then uses mathematical procedures to understand the behavior of her equations within the range of parameters that she is interested in ex-

ploring. This can include solving for equilibria, investigating the stability of the equilibria, or studying how a response of interest (e.g., equilibrium density) varies across a range of parameters. These are common ways of determining the outcome of the processes being modeled. Models can be analyzed analytically or numerically. *Analytical approaches* use mathematical techniques to solve the equation (i.e., find the equation that has the output of interest on the left-hand side) (table S1, available online). This approach requires mathematical labor but produces more general conclusions (Otto and Day 2007). *Numerical approaches* (e.g., simulations) involve setting model parameters to specific values and observing the outcome graphically or as numeric values (table S1). Here, conclusions are limited to the specific range of parameter values being explored, but because no analytical solutions are needed, theoreticians may turn to this approach when a model is too complex to be approached analytically. Numerical approaches are somewhat akin to empirical experiments in that the theoretician varies a specific process (e.g., resource supply rate) to determine how that affects an ecological outcome (e.g., consumer population density). While analyzing a model’s behavior cannot match the biological realism of an empirical experiment, it does allow researchers to hold potentially confounding factors constant and to explore a wide range of parameter space, whereas empirical experiments need to randomize factors that cannot be controlled (e.g., individuals, sites) and are often logistically constrained to smaller ranges or discrete categories (e.g., low vs. high). Likewise, the ability to depart from the realities and constraints of the natural world allows theoreticians to explore questions that would be difficult or impossible to address empirically, such as the consequences of very long timescales, complex interactions, or extreme trait values.

Step 5: The End. Finally, the theoretician refines her equation(s) and writes up and publishes the research questions, model, analyses, and conclusions. To refine the equations, the theoretician will often check whether the results make sense, both logically and in light of previous empirical or theoretical work, and will revise the model and analyses accordingly. In writing up her findings, the theoretician will ideally adopt practices that help empiricists understand and use her work, such as describing how the model follows or departs from previous theoretical research, interpreting the results verbally, including a table of all model parameters and their biological meanings, and describing experiments that could be used to test the predictions. A full integration of theoretical and empirical research in ecology will depend on sustained efforts by both empiricists and theoreticians to bridge the divide, and these efforts will be most fruitful when theoreticians are motivated to write up their findings with

empiricists in mind and to highlight assumptions and results that can be measured and tested in the lab or field.

How to Use Theory in Empirical Research

In this section we outline four ways that theory can be integrated into empirical research. These classifications are

not strict categories, and a single theory may fall into several categories. This organization simply represents one way to think about theory that can guide empiricists as they move through different stages of their research. All four of these approaches could be used in a single study, as they are applied at different stages of project design (fig. 1).

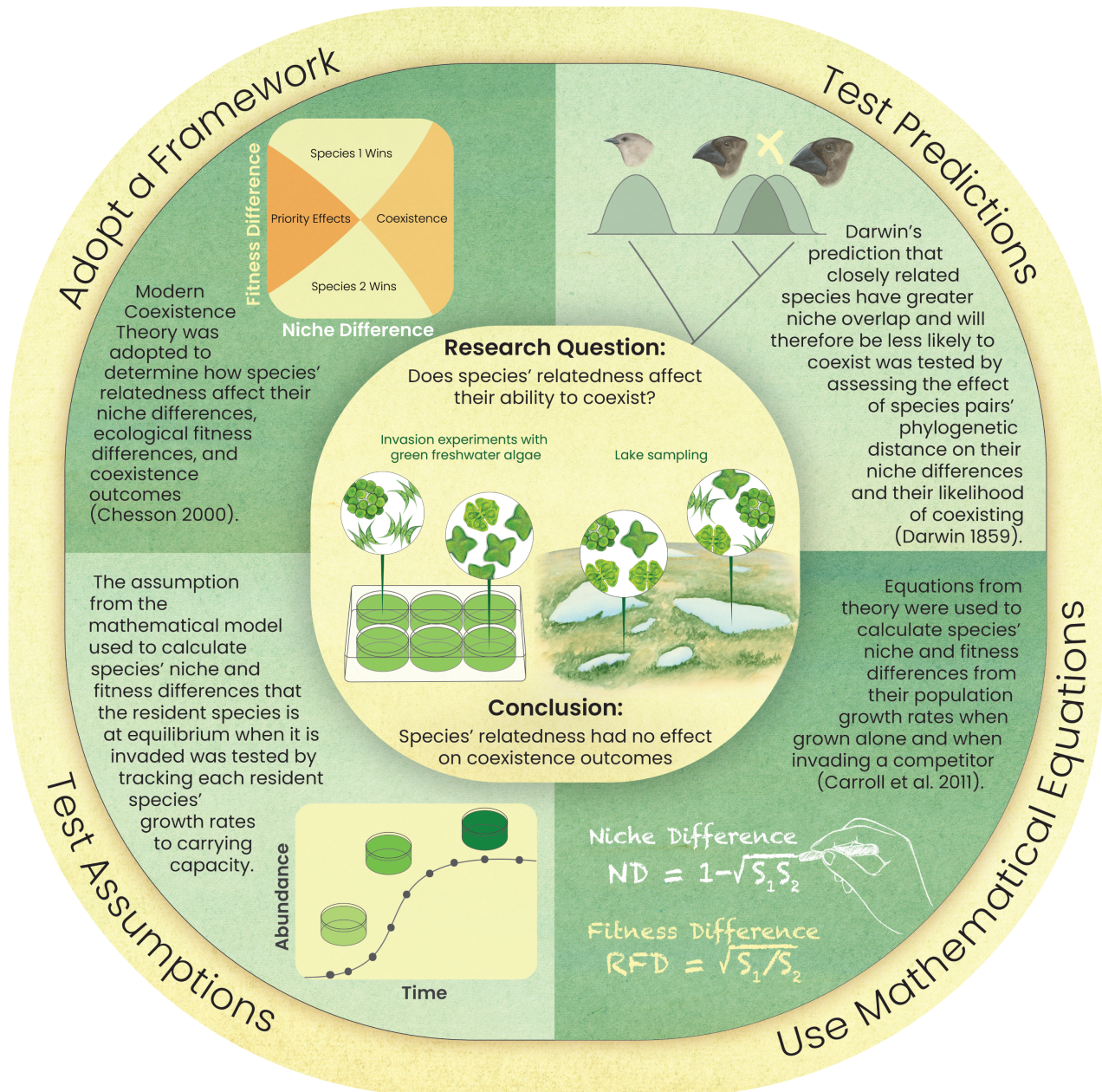


Figure 1: How to use theory in empirical research: a case study. The highlighted study (Narwani et al. 2013) uses theory in each of the four ways discussed in this article (see “How to Use Theory in Empirical Research”). Their research question, empirical methods, and conclusions are shown in the center, and the specifics of how they applied each of the four approaches are in the surrounding four sections. While Narwani et al. (2013) used all four approaches in their study, each of these four approaches can also be used effectively on its own.

An important philosophical question to consider when integrating theory into empirical work is what “testing a theory” actually means. To us, an empiricist tests theory by using empirical data to evaluate whether the outcomes predicted by the model or the assumptions it makes occur in a natural system, not whether the math is correct (Servedio et al. 2014). Two of the approaches covered below (test the predictions and test the assumptions) involve testing theory. The other two approaches (adopt the framework and use the math) do not actually test the theory but rather accept that it is applicable enough to be useful in guiding empirical research.

Approach 1: Adopt the Framework

Some ecological theories act as general frameworks for understanding ecological dynamics (in the broadest sense) or for understanding a major class of ecological processes (Pickett et al. 2010). While these theories may also provide specific mathematical equations or predictions, the larger contribution is often a new way of thinking about a problem or a unification of related ideas. Examples of this type of theory include the theory of evolution by natural selection (Darwin 1859), consumer-resource theory (Lotka 1926; Volterra 1927), Grime’s triangle of plant strategies (Grime 1977), life history theory (Pianka 1970), modern coexistence theory (Chesson 2000), the neutral theory of biodiversity (Hubbell 2001), the metabolic theory of ecology (Brown et al. 2004), and the maximum entropy theory of ecology (Harte and Newman 2014). Some of these theoretical frameworks are purely verbal, some are heavily mathematical, and some involve a mixture of both verbal and mathematical reasoning. Theoretical frameworks create a scaffold within which ecological patterns and the processes that generate them can be understood, and they can provide the context in which to integrate evidence from experiments, observational studies, and mathematical modeling (fig. 1). In some cases, a new theoretical framework sparks the interest of empiricists and prompts a rapid rise in empirical work focused on a certain topic.

How to do it. Theoretical frameworks can enhance empirical research in several ways: they can reorient how we understand and study a biological process (e.g., the theory of evolution by natural selection), they can unite disparate lines of evidence into a unified framework (e.g., the effect of temperature across organizational scales in metabolic theory), they can help focus empirical research on a specific process or relationship (e.g., dispersal in metapopulation theory), or they can provide a null model for how patterns emerge in nature (e.g., the neutral theory of biodiversity). Although theoretical frameworks can be extremely useful, it is also important to keep in mind that they all have shortcomings, that many will eventually outlive their utility, and

that the lack of diversity among the authors recognized for generating theoretical frameworks in ecology has undoubtedly limited the range of perspectives represented.

A useful first step when motivating empirical research with a theoretical framework is to become familiar with the framework and with existing empirical work that has adopted it. This can help clarify which aspects of the framework have been well explored and where gaps in our collective understanding remain. It can also help reveal common experimental designs that address the questions or capture the processes described in the framework (Grainger and Gilbert 2016; Broekman et al. 2019). This step can also help reveal situations in which new empirical methods are needed to apply an emerging framework, which can be an exciting opportunity for empiricists (e.g., methods to quantify selection on phenotypic traits on ecological timescales, introduced by Lande and Arnold [1983]; methods to account for phylogenetic relatedness in comparative studies, introduced by Felsenstein [1985]; methods to apply modern coexistence theory, introduced by Godoy and Levine [2014]).

Approach 2: Test the Predictions

Theoretical work often generates specific predictions, and testing these predictions is a common way that empiricists use theory (fig. 1). The central aim of testing predictions from theory is to determine whether a pattern that a theoretical model predicts matches a pattern that manifests in a natural or experimental system, ideally with the end goal of using the theory to deepen our understanding of the processes that create those patterns. Examples of recent empirical tests of classic theoretical predictions include the predicted increase in species richness with increasing island area and connectivity from the theory of island biogeography (proposed by MacArthur and Wilson [1967]; e.g., tested by Prugh et al. [2008]), the predicted negative density dependence of seed recruitment from the Janzen-Connell hypothesis (proposed by Janzen [1970] and Connell [1971]; e.g., tested by Harms et al. [2000]), and the predicted strategy of delayed germination in variable environments (proposed by Cohen [1966]; e.g., tested by Venable [2007]).

How to do it. The first steps in testing theoretical predictions are to consider what type of model the theory uses (box 1), to explore the model and understand (well enough) what the math means biologically (see “A Tool Kit for Understanding Equations”), and to determine what assumptions the theory makes (box 2). Next, the empiricist can consider how the theory can inform experimental design. The theoretical article will ideally lay out its predictions clearly, in words and in figures (see box 3), for example, the prediction that local diversity is maximized at intermediate levels of dispersal between habitat patches (Mouquet and Loreau 2003). The empiricist can then determine what needs

Box 1: Types of mathematical models

Determining the general attributes of a theoretical model by asking the following three questions can help empiricists understand a model and determine whether a model is a good fit for their research.

How does the model deal with the passage of time? Determining whether and how a model involves the passage of time will provide insight into the type of study system it describes. Models that describe how a system changes through time are called dynamical models and are very common in ecology. Some dynamical models include discrete time steps (e.g., from one life stage to the next or from one generation to the next), whereas others model time continuously. *Discrete-time models* will have something like $n(t + 1)$ or n_{t+1} on the left-hand side of the equation (which represents the value of a variable at the next time step), whereas *continuous-time models* will have something like dn/dt on the left-hand side of the equation (which represents a change in the value of a variable over time). This distinction can be important when determining whether a model matches a given study system. For example, because population sizes change when organisms reproduce or die, if the focal organism reproduces in discrete time steps with nonoverlapping generations (e.g., annual plants, birds), then a discrete-time model may be most applicable. However, if the organism reproduces continuously (e.g., zooplankton, aphids), a continuous-time model might make more sense. While understanding how time is passing in a model can be helpful to the empiricist, note that theoreticians may model time in a certain way for mathematical convenience and that it is possible to convert a model between discrete and continuous time under the appropriate assumptions (Otto and Day 2007). Finally, some models do not include the passage of time at all, including most metabolic theory (Brown et al. 2004) and optimal foraging theory (Charnov 1976).

Is the model mechanistic or phenomenological? Although the distinction between mechanistic and phenomenological models is often fuzzy and will depend on the perspective of the investigator and the theoretical framework in which she is working, thinking about this distinction can help the empiricist decide whether a model fits her needs (Otto and Day 2007; White and Marshall 2019). *Mechanistic models* explicitly include underlying biological mechanisms or, put another way, explicitly model dynamics happening at a different level of organization. For example, in models that describe resource competition, a mechanistic model will model the amount of each resource produced and consumed through time. Classic examples include MacArthur's consumer-resource model (MacArthur 1970) and Tilman's resource competition model (Tilman 1977). In both of these, the resources being competed for are included in the model. In contrast, *phenomenological models* are focused on the patterns (i.e., the phenomena) that emerge from an underlying process rather than the process itself. For example, a phenomenological model of populations competing for a shared resource tracks population dynamics of consumers without explicitly including the underlying mechanisms that drive those responses (Otto and Day 2007; White and Marshall 2019). Instead of including the entity being consumed in the model, competition for limited resources is implied by including terms such as the carrying capacity or competition coefficients. A classic example is the Lotka-Volterra competition model (Lotka 1926; Volterra 1927).

If the empiricist has an interest in the underlying mechanisms (e.g., the nature of resource competition) and has the required information to apply a mechanistic model (e.g., the key resources underlying competition are known), then a mechanistic model can offer deeper insights about the system. If the empiricist does not, then a phenomenological model may be more appropriate and does not require as in-depth an understanding of underlying drivers.

Are the predictions qualitative or quantitative? *Qualitative predictions* state that x is related to y in some way and are very common in ecological theory. For example, the theory of island biogeography predicts that species richness is positively related to island size and proximity to the mainland (MacArthur and Wilson 1967). A qualitative prediction may describe a broad pattern, such as "Species reach carrying capacity" or " x affects y ," or may be more specific, such as "Carrying capacity scales linearly with intrinsic growth rate" or "There is a hump-shaped relationship between x and y ." By contrast, *quantitative predictions* include specific numerical values and are more common in ecosystem theory and metabolic theory. For example, metabolic theory predicts that an organism's metabolic rate scales with the $3/4$ power of its body mass (West et al. 1997). Considering the level of specificity of a model's predictions can help the empiricist start to think more precisely about the possible outcomes of an experiment that would support a given prediction.

Box 2: Meeting model assumptions

A critical step in designing empirical research that provides a robust test of theoretical predictions is to ensure that the study meets as many of the model's assumptions as possible. This is not always straightforward, as model assumptions may not be explicitly stated in words in a theory article. If assumptions are stated explicitly, they will often be found in the "model" section of the article, and some indication will hopefully be given of how critical the different assumptions are for the predictions generated by the model. For example, there may be a paragraph in the discussion that mentions the assumptions and limitations of the model and is somewhat analogous to a "caveats" section in an empirical article. If this is not in the article, the tips provided in "A Tool Kit for Understanding Equations" may help empiricists uncover assumptions that are described mathematically but not verbally and feel empowered to explore how sensitive the outcome is to the assumed relationship between variables and parameters using a plug-and-play approach (tip 4).

Some common assumptions in models used in ecological theory are as follows:

- The system is analyzed or observed at dynamic equilibrium.
- Species interactions are competitive (i.e., not facilitative).
- Resources are limited.
- Individuals interact with all other individuals with equal likelihood (i.e., no spatial structure).
- Individuals within a species are identical in terms of how they interact, reproduce, and survive (i.e., no intraspecific variation).
- There is a timescale separation between ecology (fast) and evolution (slow).
- There is a timescale separation between resource growth (fast) and consumption (slow).
- Dispersal rates are homogenous across species and are not spatially explicit (i.e., global dispersal).
- The outcomes of biological processes are deterministic (i.e., no stochasticity).
- Population growth is density dependent and follows a simple functional form (e.g., linearly declining per capita growth rate as the population size increases in the logistic equation).
- Predator consumption rates saturate as prey densities increase (i.e., type II functional response).

Note that some of these assumptions are made for mathematical convenience (e.g., no spatial structure, no stochasticity), whereas others reflect biological realities (e.g., resources are limited; population growth is density dependent). Likewise, some of these assumptions should be evident from the mathematical equations themselves (e.g., species interactions are competitive; predator consumption rates saturate as prey density increases), whereas others must be stated explicitly in words in order to be communicated (e.g., no spatial structure, no intraspecific variation).

While keeping these types of distinctions in mind can help the empiricist navigate the task of determining what a model's assumptions are and how closely they need to be matched experimentally, deciding how perfectly assumptions need to be met in order for a model to be useful is a subjective exercise. Our stance is that empirical work does not need to perfectly satisfy every model assumption and that the focus should be on understanding which assumptions are critical to the outcomes and which are more flexible. Ideally, this is outlined or at least alluded to in the theory article (Servedio 2020). Worthwhile questions to ask include "If these assumptions were broken, how would this change the predicted outcome?" and "Is it possible to meet the critical assumptions of this model in the biological system of interest, or is a different model or system needed?"

Thinking about assumptions can be a useful philosophical exercise for empiricists at both the microscale of an individual experiment and the macroscale of the entire field. At the microscale, there are assumptions in every empirical study, even those not based on theory, and grounding experiments strongly in theory can help bring assumptions to light and force researchers to explicitly state what they are and when they are bent or broken. This can encourage the empiricist to think more deeply about experimental design and can make it easier for future researchers to build on their work. At the macroscale, it is useful for the discipline as a whole to regularly examine the common assumptions that have become the default and to consider whether they indeed reflect reality and how outcomes might change if these assumptions were to be broken (see "Test the Model Assumptions").

to be manipulated and what needs to be measured: here, an experiment in which organisms' dispersal rates between local patches are manipulated and diversity is measured (e.g., Parain et al. 2019). Theory can also help inform the more detailed elements of experimental design, for example: Should all organisms have the same dispersal rates? How many dispersal levels are needed to detect the predicted relationship? Is repeated sampling over time necessary? For each question, the empiricist will have to consider trade-offs between matching the experimental design to the theoretical assumptions, matching the design to the attributes of a natural system, and designing an experiment that is feasible to implement (box 2; Grainger and Gilbert 2016; Laubmeier et al. 2018; Uszko et al. 2020).

At this stage, a careful consideration of what evidence is needed to strongly support or refute a theoretical prediction can be valuable. Powerful empirical tests of theoretical predictions document a pattern (or, ideally, multiple patterns) that are very unlikely to occur by chance or alternative mechanisms, that support a single hypothesis, and that (ideally) reject one or multiple alternative hypotheses (Platt 1964; Loehle 1987). They quantitatively measure responses to the manipulation of the independent variable, they have sufficient replication to detect the theoretically predicted responses, and they use experimental conditions that are consistent with the theory's assumptions. Doing so makes it possible to draw conclusions about the validity or generality of the theory, based on whether results are consistent with the theory's prediction.

However, a challenge with hypothesis testing in ecology is that the context and system-specific nature of ecological dynamics mean that results that fail to reject a null hypothesis are not necessarily a strong refutation of a theory (Hardin 1960; Loehle 1987). As such, it is worthwhile to carefully consider what conclusions can be drawn if experimental results do not support the theoretical prediction and how the experiment can be designed so that any outcome will provide interesting insight into the process of interest. One way to conduct more nuanced hypothesis testing is to ask "When does x affect y , as predicted by theory?" rather than "Does x affect y ?" The answer is more likely to be "sometimes" than "always" or "never." For example, research suggests that dispersal is a stronger driver of diversity in the absence of predators than when predators are present (Kneitel and Miller 2003; Chase et al. 2010). There is a good reason why many conclusions in ecology include the word "can": it takes a critical mass of empirical evidence from many systems in order for the field to accept that a theoretical prediction is broadly and generally supported. However, while contributing empirical support for a theoretical hypothesis is a worthwhile achievement, we also strongly encourage the dissemination of *negative results* (those that detect no effect), which make important but undervalued contributions to scientific

progress and can highlight areas where existing theory needs modification (e.g., fig. 1; Loehle 1987; Knight 2003).

Approach 3: Use the Mathematical Equations

Sometimes a valuable part of a theory to an empiricist is a specific equation that can be used to obtain a quantitative estimate of a biological process that is difficult or impossible to measure directly (fig. 1). For example, measuring the strength of competitive interactions or the rate of disease transmission is difficult, but established models can be used to estimate these from more easily measured quantities such as birth and death rates. Below, we discuss two specific ways that an empiricist can use equations from theory to gain new information: model fitting (in which parameters are estimated) and the direct use of an equation (in which the response variable is calculated). A third and very straightforward way that an empiricist can use mathematical equations, particularly those that are tailored to a given biological system, is to help determine which biological processes are most relevant to a particular outcome and should therefore be measured or manipulated in experiments. For example, models of flour beetle dynamics identify several types of cannibalism as important to population growth (Dennis et al. 1995), while annual plant models highlight germination rate and seed bank viability as key mediators of population growth rates (Levine and Rees 2004). This guidance can be particularly helpful for empiricists starting work in a new system.

How to do it. The first step in using equations is to figure out what information is desired and which candidate models can provide that information. At this stage, it is important to check that the assumptions of candidate models are satisfied by the biological system and experimental design being used (box 2), because once a model is used to estimate a biological process, it becomes implied that the system meets the assumptions of that model and the quality of any subsequent results will depend on this being (mostly) true (Clark et al. 1998). When selecting candidate models, established models can be used, or existing models can be modified to reflect the dynamics and conditions of the study system. The modification of existing models to fit the study system or the dynamics of interest can blur the line between using and creating theory, which is often a sign of effective integration of empirical and theoretical research (e.g., Duffy et al. 2005; Moeller et al. 2016).

The first way to use equations in empirical research is *model fitting* (aka "fitting models to data"). To do this, the empiricist identifies mathematical models that describe a process of interest, collects measurements of the response and predictor variables in these models, and then uses statistical techniques to estimate the values of *free parameters* (those whose values are unknown) that best match the

Box 3: How to interpret common figures in ecological theory articles

Here, we present five common types of figures in ecological theory (box fig. 1) and walk through their interpretation. Each panel shows a different way of representing the structure (A) or the outcome (B–E) of model simulations of the same model (eq. [1] in the main text).

Stock and flow diagram (box fig. 1A). These diagrams visually summarize a model by showing its components and how they interact. Box figure 1A shows one of many ways to draw a stock and flow diagram and follows conventions from Otto and Day (2007; see also Ogbunugafor and Robinson 2016). Here, circles are variables that can be thought of as “stocks” (e.g., the total amount of resources R and consumers C). Symbols within circles are variables, and symbols labeling the arrows are parameters. Arrows moving toward a circle are inflows that increase the amount of stock, while arrows moving away from a circle are outflows that decrease the amount of stock. Arrows moving from one type of stock to another show how those variables are interdependent and where one type of stock is converted into another (e.g., consumed resources converted into consumer growth). In this model, arrows between two stocks represent interspecific effects, arrows that feed back on themselves represent intraspecific effects, and arrows that point out of one stock without connecting to another stock represent flows out of the system (i.e., mC).

Time series (dynamic) plot (box fig. 1B, 1C). This type of figure shows how variables of interest change over time. They can be used to assess equilibria; for example, for a given combination of parameter values, one can see how long a system exhibits transient dynamics (i.e., an initial phase of instability) before it stabilizes. They can also be used to determine whether dynamics are static (i.e., population size remains constant in box fig. 1B) or oscillatory (box fig. 1C). Finally, they can be used to quickly assess ecological outcomes (e.g., which species persist over the long term) or how the dynamics of two variables are interrelated (i.e., synchronous dynamics vs. asynchronous dynamics).

Phase-plane (phase-portrait) diagram (box fig. 1D, 1E). These summarize the trajectories of variables in multi-variable models and serve as an alternative to time series plots. In these plots, the location of the tail of each arrow marks the value of each variable at the start of a time step, and the location of the head of the arrow is the value at the end of the time step. The length of the arrow represents the size of the change, and the arrow’s angle shows the relative magnitudes of change of one variable compared with the other. The isoclines (colored lines) represent the range of values at which the specified variable experiences no net growth if the value of the other variable were to be held constant (often not biologically plausible). The point at which the isoclines of the two species intersect is the two-species equilibrium. Here, the two-species equilibrium is stable when $e = 0.65$, as population sizes converge on these points. Note that variables’ trajectories could instead be shown as a vector field in which arrows point toward stable equilibria and away from unstable equilibria.

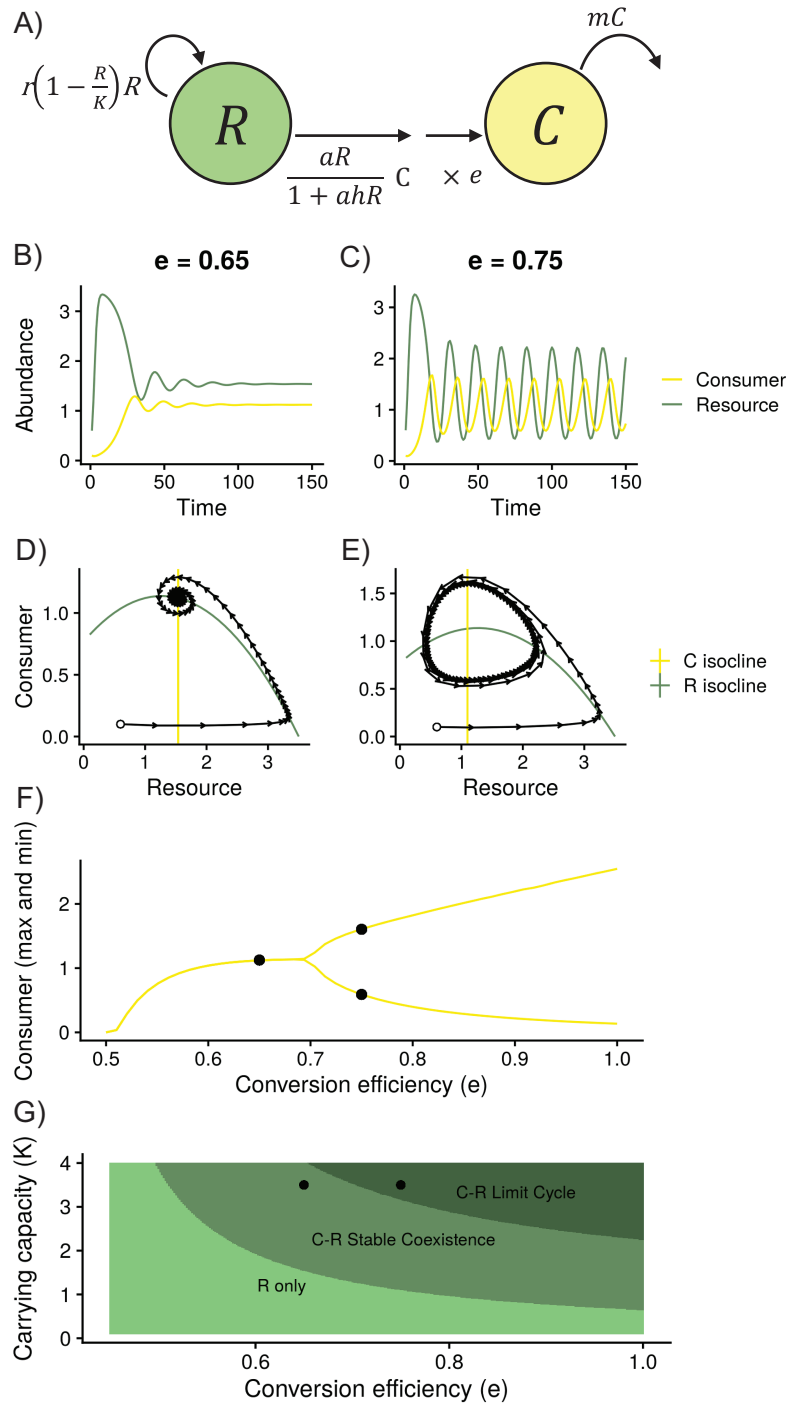
Bifurcation plot (box fig. 1F). These are useful for visualizing where the nature of the dynamics changes, for example, between having a single stable value to having unstable values or to something more variable. A bifurcation point is the value of a given parameter where such changes in the model’s dynamical behavior occurs. In box figure 1F, for example, a conversion efficiency of 0.65 leads to stable dynamics (a single consumer density over time), whereas a conversion efficiency of 0.75 causes oscillations (a range of consumer densities over time; minimum and maximum values of the oscillation are denoted on the plot). For this model, the range of abundances after the bifurcation is shaped like a tuning fork because as conversion efficiency increases, the amplitude (or the range of values covered) of the oscillating dynamics increases.

Summary plots (box fig. 1G). These show how changing multiple parameters at once affects an outcome of interest, for example, the type of population dynamics observed (e.g., stable limit cycles), and show the parameter values where transitions between outcomes occur. Here, each axis is a different parameter in the model, and the shading indicates which outcome is observed. They can also show whether the effect of one parameter on an outcome of interest depends on the value of other parameters. Parameters that are not explicitly shown on the axes are assigned fixed values that are often specified in figure captions (see box fig. 1 caption).

relationship observed in the data (Bolker 2008; table S1). Each of the free parameters represents a biological process or property of interest. An example of this approach is using a functional response model to estimate two parameters—the space clearance rate (aka attack rate) and handling time

in a predator-prey interaction—by inputting data from an experiment that quantifies the number of prey consumed (response variable, y) when different numbers of prey are available (predictor variable, x) (West and Post 2016). To fit a model, the empiricist provides candidate models (e.g., Ricker

Box 3 (Continued)



Box Figure 1: Five types of figures that are commonly encountered in theory articles: a stock and flow diagram (A), time series plots (B, C), phase plane diagrams (D, E), a bifurcation plot (F), and a summary plot (G). All panels are based on a modified Rosenzweig-MacArthur model of consumer-resource interactions (eq. [1]). B-F are parameterized as follows: $r = 1$, $K = 3.5$, $a = 1.3$, $h = 0.8$, $m = 0.5$. Two values of conversion efficiency (e) are contrasted in B-E and are represented by dots in F and G. Parameters and code to reproduce this figure are available at <https://mabarbour.github.io/foodweb-theory/rosenzweig-macarthur.html>.

model, Beverton-Holt model, a new model) that each propose a different relationship between x and y (e.g., straight line, hump shaped), along with the data for the variables in the model (e.g., x and y). Then statistical methods such as maximum likelihood are used to estimate the attributes (parameters) of that relationship (e.g., the y -intercept, the slope, and the curvature) of the model with the highest probability of explaining the observed data. These statistical methods usually quantify the deviation between the model expectation and the data and then iteratively alter the parameters to make the deviations smaller until the best-fitting model is found (Bolker 2008). The outputs of model fitting and model comparison are estimates of the parameters, their uncertainties (errors), and relative support for the different candidate models. The empiricist may be interested in these parameter values themselves (e.g., determining the space clearance rate of a given predator on a specific prey) or how they change with an experimental manipulation (e.g., determining how space clearance rates vary with temperature, as in DeLong and Lyon 2020).

A second way to use equations in empirical research is to collect data that can simply be plugged into an equation as predictor variables in order to calculate the response variable. In this case, the collected data are the variables and parameters on the right-hand side of the equation, and the variable on the left-hand side of the equation is the value of interest that is calculated. Examples of this approach include estimating maximum sustainable yield in fisheries from population growth rate and carrying capacity (Schaefer 1954) and estimating the spread rate of invading organisms from dispersal and population growth rates (Kolmogorov 1937; Andow et al. 1990). To do this, the empiricist collects the necessary data and enters them as predictor variables into the equation. The estimated outputs that are generated can then be used in subsequent analyses, for example, determining how species spread rates are affected by habitat type (Andow et al. 1990). One issue to be aware of with this approach is that collected data will have error surrounding them, and determining the proper way to carry this error through to the final estimated data can require careful consideration (e.g., Terry et al. 2021).

Approach 4: Test the Model Assumptions

A final way that empiricists can use theory is to directly test the assumptions that underlie theoretical models (fig. 1; box 2). This type of empirical research has a strong link to theory and is often conducted with the express purpose of informing future theoretical work (Price et al. 2012; Servidio et al. 2014). This type of research has the potential to make a major impact in the field, particularly when the tested assumptions are widely invoked. For example, empirical research that challenged the widespread assumptions that evo-

lution is slower than ecology (Reznick et al. 1990; Losos et al. 1997) and that interspecific niche differences play a major role in structuring ecological communities (Hubbell 2001) has inspired major bodies of research. Looking forward, many of the simplifying assumptions of the metabolic theory of ecology have not been adequately verified by empirical research (Price et al. 2012), and the widely adopted assumption that pairwise interactions can adequately capture community dynamics, which underlies much of coexistence research, remains largely untested (Levine et al. 2017).

How to do it. The first step in testing model assumptions is to identify assumptions that are likely to have significant impacts on the conclusions drawn in a field but are not yet well supported by empirical research. This can be achieved through a broad reading of both the theoretical and empirical work in the field, and widely applied assumptions may be particularly likely to come to light during a literature review or meta-analysis. Assumptions that have substantial effects on model outcomes will hopefully be identified explicitly in theoretical articles (see box 2) and can also be explored using the techniques for understanding equations provided below (particularly tip 4, “Achieve a working understanding of equations”). The next step is to collect the data required to support or refute the assumption. For example, while classic foraging theory assumes that per capita predator feeding rates are independent of predator density (Holling 1966), empirical data on feeding rates across predator densities have refuted this assumption and prompted revised models (Vucetich et al. 2002; DeLong and Vasseur 2011; Novak et al. 2017).

One consideration when designing this type of experiment is how broadly the results can be applied. If the goal is to assess whether the assumption is met in the type of system to which this theory is most often or most appropriately applied, then testing in a representative system makes sense (e.g., Bernhardt et al. 2018). If the goal is to make a broad statement about whether an assumption is met, in general, then data from multiple systems may be needed (e.g., DeLong and Vasseur 2011). Ideally, the final step for empirical research that tests model assumptions will be that the results of such experiments will feed back to inform and improve subsequent theoretical work.

A Tool Kit for Understanding Equations

So far, we have described how theory is created and have highlighted several ways that empiricists can integrate theory into their research to attain a better understanding of nature. However, many theories in ecology are expressed in the language of math, and in order to effectively use mathematical theory, empiricists must be able to understand it. A helpful first step toward understanding mathematical theory is to determine, generally, what type of model one is dealing

with by answering some basic questions (box 1). The next step is likely the biggest hurdle most empiricists face: understanding equations. We tackle this challenge by providing concrete tips for visualizing functions, interpreting common symbols and figures, and deciphering their biological meanings. For readers looking for a more comprehensive treatment of these topics, we also provide a list of textbook sections that cover these topics in much greater depth (table S1).

To anchor our discussion, we begin by presenting a modified Rosenzweig-MacArthur consumer-resource model where both the consumer (with density represented by the variable C) and the resource (with density R) grow and impact each other (Rosenzweig and MacArthur 1963):

$$\frac{dR}{dt} = \underbrace{\underbrace{r}_{\text{parameter}} \underbrace{R}_{\text{variable}} \left(1 - \frac{R}{K}\right)}_{\text{expression}} \underbrace{\underbrace{\frac{aR}{1 + ahR}}_{\text{term}}}_{\text{operator}} C, \quad (1)$$

$$\frac{dC}{dt} = e \frac{aR}{1 + ahR} C - mC. \quad (2)$$

Now, did you read the equations or skip past them? Our first piece of advice is to give the math a chance: spend five minutes trying to get to know it. The more time one spends with equations, the more familiar reading new equations becomes. Try not to get bogged down by new symbols (e.g., Greek lettering), as often the specific choice of symbols used is arbitrary or based on precedent. Here, C and R are the densities of individuals in each population, and dC/dt and dR/dt are the rates of change of each population's size; note that dC/dt represents a rate of change in continuous-time models, whereas discrete-time models are expressed as $C_{t+1} = f(C_t)$, which represents the value of a variable at the next time step (box 1). When $dC/dt > 0$, the value of C is increasing over time, whereas C is decreasing when $dC/dt < 0$. In equation (1), resources experience some maximum per capita growth rate in the absence of competition or consumers, denoted by r , and have carrying capacity K . In equation (2), a is the space clearance rate (aka attack rate; the area or volume cleared of prey per predator per prey unit time), h is the amount of time a consumer spends handling each prey item (e.g., time to kill, eat, digest, etc.) that would otherwise be spent searching for prey, e is the conversion rate of consumed resources into new consumer individuals, and m is the per capita rate of consumer death.

What is the best way to begin approaching these equations? We start by unpacking an equation's basic anatomy and considering the terminology that can be used to discuss different elements of equations. Each symbol in an equation

can be classified as a variable, a parameter, or an operator. As described above ("How Is Mathematical Theory Created?"), a *variable* is a quantity whose value changes either dependently (e.g., population size) or independently (e.g., time) of other variables. *Parameters* are fixed quantities that remain constant within a given equation (e.g., consumer death rate). *Constants* are numbers that enter equations according to some assumption made by the theoretician. For example, in equation (1), the 1 in $1 - R/K$ indicates that resources grow at 100% of their intrinsic growth rate if R is near zero. Sometimes, constants are called *coefficients* or *constant factors* when multiplying a variable (e.g., the coefficient rN in an equation of exponential growth represents the fact that every individual will produce r surviving offspring, on average). *Operators* describe how different quantities in equations interact with each other, including simple operations from algebra (i.e., addition, multiplication, etc.) and complex ones, such as those associated with set theory (e.g., \cap) or calculus (e.g., \int ; fig. 2).

Collections of symbols also have their own terminology. A *term* is a set of variables and/or parameters that are multiplied or divided together or placed inside parentheses. There are two terms on the right-hand side of equation (2): $e(aRC)/(1 + ahR)$ and mC . These terms may be composed of multiple *factors* that multiply together to give the term (e.g., m times C). An *expression* is the full set of terms contained on the same side of the equal sign. Any one equation can be rearranged, or "expressed," in different ways, resulting in different expressions that maintain the equivalence between the left-hand side and the right-hand side of the equation (sometimes abbreviated to LHS and RHS in theory articles, respectively). Clearly, there is a specific terminology associated with different elements of equations that should not be used interchangeably (i.e., variable \neq parameter, term \neq expression).

Now, let's get into some concrete tips.

Tip 1: Align the Math with the Biology

Math provides an abstraction of nature, but backtranslating math into biology can help make equations interpretable and can make it easier to identify the model's assumptions. In the equations above, notice that the population growth of resource R depends on the population size of consumers C and vice versa (i.e., R and C appear in both equations). This interdependence makes intuitive biological sense because the consumer population relies on resources to produce offspring, and as consumers consume resources, the resource population is depleted. Also notice that in these equations, the resource can exist without the consumer (if $C = 0$ in eq. [1], the growth of R reverts to logistic growth), but the consumer cannot persist without the resource (if $R = 0$ and $C > 0$ initially in eq. [2], C will decline to

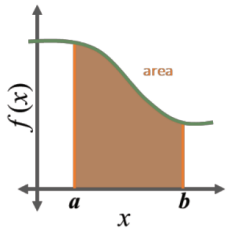
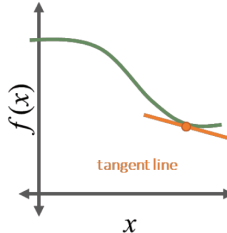
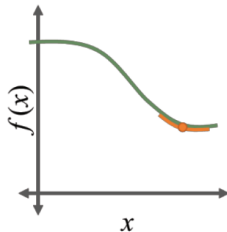
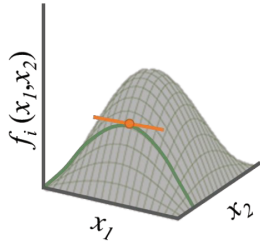
Typical notation	Context/description	Operator	Realm	Mathematical definition	Example of use in ecology	Visual representation
\int	$\int_a^b f(x)dx$	Integral	Calculus	The area under a function $f(x)$ for the range of x values between a and b .	Total amount of resources consumed by consumer, with a gradient of resource types (e.g., seeds of different sizes) (Roughgarden 1971).	
d	$\frac{df}{dx}$ or $f'(x)$	Derivative	Calculus	The slope of a function evaluated for any value of x . Equals the rise/fall in the function for a very small change in x .	Used to address rates of change of population size over time and the stability of equilibria.	
d^2	$\frac{d^2 f}{dx^2}$ or $f''(x)$	2 nd -degree derivative	Calculus	The derivative of a derivative indicating how fast the slope changes (i.e., acceleration) for any value of x .	Used to describe whether fitness is stabilizing ($\frac{d^2 W}{dx^2} < 0$) or disruptive ($\frac{d^2 W}{dx^2} > 0$) for trait x .	
∂	$\frac{\partial f}{\partial x}$	Partial derivative	Calculus	When a function has more than one variable, say x and y , a partial derivative assesses the slope in one direction, say x at a specific (underived) value of y .	Change in population size over time at a particular point in space (Okubo and Levin 2013)	
A or A_{ij}	Uppercase, bold Roman symbol	A matrix. If unbolded and italicized (i.e., A_{ij}), refers to a single cell in the matrix.	Matrix algebra	An i (row) by j (column) matrix. For square matrices, i and j vary from 1 to n , the number of dimensions.	A Leslie matrix contains information on fecundity and survival of different life stages.	$\mathbf{A} = \begin{bmatrix} A_{1,1} & A_{1,2} \\ A_{2,1} & A_{2,2} \\ A_{3,1} & A_{3,2} \end{bmatrix}$
v or v_i or \vec{v}	Lowercase, Roman symbol	A list or vector if bold, a single element if unbolded	Matrix algebra	A vector	A vector representing population sizes of different life stages or species	$\mathbf{v} = [v_1, v_2, v_3, v_4]$

Figure 2: Common theoretical notations.

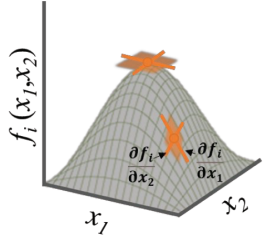
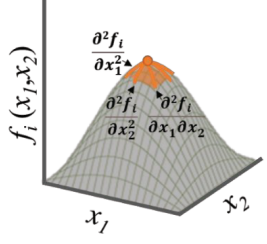
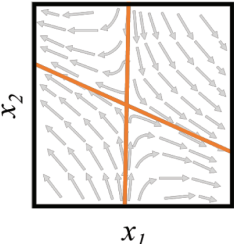
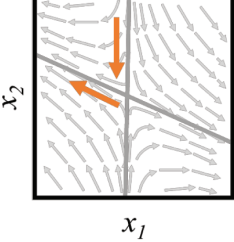
Mathematical term	Realm	Mathematical definition	Example of use in ecology	Visual representation
Jacobian matrix	Matrix calculus	A square matrix of derivatives describing linear approximations of function $f_i(x_1, x_2, \dots, x_n)$ for each equation i , with $\frac{\partial f_i}{\partial x_j}$ as the entry in row i column j .	The Jacobian matrix describes the rate of change of each function with respect to each variable. Used in linear stability analyses, where the functions describe how each variable changes over time.	 A 3D surface plot of a function $f_i(x_1, x_2)$. The vertical axis is labeled $f_i(x_1, x_2)$. The horizontal axes are labeled x_1 and x_2 . The surface is a smooth, rounded peak. At the top of the peak, there are three small arrows representing partial derivatives: $\frac{\partial f_i}{\partial x_1}$, $\frac{\partial f_i}{\partial x_2}$, and $\frac{\partial f_i}{\partial x_3}$.
Hessian matrix	Matrix calculus	A square matrix of second-order derivatives describing the curvature of function $f_i(x_1, x_2, \dots, x_n)$, with $\frac{\partial^2 f_i}{\partial x_j \partial x_k}$ as the entries in row j and column k .	Describes the local curvature of a function with many variables. Can be helpful in identifying critical points of a function (e.g., local maxima). Used in evolution to determine evolutionarily stable strategies (ESS).	 A 3D surface plot of a function $f_i(x_1, x_2)$. The vertical axis is labeled $f_i(x_1, x_2)$. The horizontal axes are labeled x_1 and x_2 . The surface is a smooth, rounded peak. At the top of the peak, there are three small arrows representing second-order partial derivatives: $\frac{\partial^2 f_i}{\partial x_1^2}$, $\frac{\partial^2 f_i}{\partial x_2^2}$, and $\frac{\partial^2 f_i}{\partial x_1 \partial x_2}$.
Eigenvector	Linear algebra	A vector associated with a square matrix which, when multiplied with the matrix, does not change its direction.	The dominant eigenvector (with the largest eigenvalue) of the Leslie Matrix is the stable age distribution of a population.	 A phase plane plot with horizontal axis x_1 and vertical axis x_2 . The plot shows a vector field of small arrows representing the direction of change. A prominent orange line passes through the origin, representing the stable age distribution eigenvector. The arrows generally point towards this line.
Eigenvalue	Linear algebra	A unique real number associated with an eigenvector which represents how much the eigenvector gets scaled when multiplied by the square matrix.	Describes the direction and speed of change. The largest eigenvalue of the Leslie Matrix represents the long-term growth rate of the population.	 A phase plane plot with horizontal axis x_1 and vertical axis x_2 . The plot shows a vector field of small arrows representing the direction and speed of change. A prominent orange line passes through the origin, representing the stable age distribution eigenvector. The arrows generally point towards this line, and their length indicates the speed of change.

Figure 2: (Continued)

extinction [i.e., $C = 0$] over time because $dC/dt < 0$). Again, this intuitively makes sense (see tip 4 for tips on how to understand any equation), and it illustrates how models often build on previous models (here adding a consumer to a model of resource growth). Notice also that the equation for resource population growth includes a carrying capacity (K), which causes population growth to slow as the value

of R (resource density) approaches K (i.e., R/K approaches 1, causing the quantity in the parentheses to approach zero). This indicates that in this particular set of consumer-resource equations, the resource R is biological and is itself limited by density-dependent competition. This equation for R thus fits the behavior of a plant but not an abiotic resource that enters and exits the system in a density-independent fashion

(i.e., sunlight). Try picturing two organisms that adhere to the biological assumptions above in order to make the abstract math more tangible. Last, if the consumer spends relatively little time handling a resource relative to the time it takes to find and attack that resource (so $h \approx 0$, e.g., a sessile filter feeder), then the rate of resource consumption by each consumer increases linearly with the population size of the resource (because the denominator in eq. [2] equals 1). If, by contrast, substantial time is spent handling resources (i.e., $h \gg 0$, e.g., carnivores that hunt large prey), then the rate of resource consumption saturates when more resources are present than the consumer has time to consume.

Tip 2: Think in Terms of Stocks and Flows

On a basic level, equations describe how variables grow or shrink in response to other variables. The *stock* is the amount of a given variable that exists at any point in time (e.g., population size), whereas *flows* are inflows (i.e., individuals added by birth) and outflows (i.e., individuals being removed by death) that affect the amount of stock and its rate of change. It can help to keep track of which parameters represent inflows compared with outflows. Drawing out a *stock and flow diagram* (box fig. 1A) by linking stocks (typically represented by circles) and flows (arrows) can be helpful, especially when multiple terms cause any one variable to shrink or grow or when multiple variables are linked. Although the conventions for stock and flow diagrams vary across the literature, we use a recommended approach that maximizes connections between the equations and the diagram (Otto and Day 2007; see also Ogbunugafor and Robinson 2016).

Tip 3: Verbally Summarize Complex Terms

Some mathematical terms are complex and involve many symbols. For example, the term $eaRC/(1 + ahR)$ is the consumer birth rate, but it can be broken into three main parts: the number of consumers (C), the foraging rate per consumer ($aR/(1 + ahR)$), and the number of consumers produced per resource eaten (e). By breaking down multisymbol terms in this way, we can see which mechanisms are being invoked (here, individual-level foraging, satiation, reproduction) to generate higher-order phenomena (here, population-level growth). Thus, although complex, we can simplify equation (2) to read as just two parts: individuals added via birth due to consumption minus individuals lost via death. These simplifications can be written out in words, as we have done in our description of $eaRC/(1 + ahR)$, or can be shown by annotating the equations to reflect the summarized descriptions. Doing so reduces the number of specific symbols that need to be tracked. Note that some parameters in equations may themselves be a simplification made by the author. For

example, parameter h in equation (2) is a consumer's handling time, but h can be expanded further to include time spent subduing a resource, time spent consuming it, and time spent resting after consumption. Rearranging equations to build new expressions (while maintaining left-hand-side and right-hand-side equivalence) can produce more biologically intuitive descriptions of terms (e.g., dividing both sides of eq. [2] by C in order for the left-hand side to be expressed as a per capita rate).

Tip 4: Achieve a Working Understanding of Equations

Well enough is better than not at all, but what level of understanding is sufficient to be useful? For example, one may not need to know at what exact value of a variable a function reaches an inflection point, but understanding whether the function is saturating or nonsaturating is still useful. One trick is to think in terms of what happens to a dependent variable when the independent variable takes on a particular value, especially an extreme value. For example, consider what happens in an equation if a variable is zero or a large number: perhaps an asymptote is reached, or the function may become undefined (e.g., division by zero), meaning that the value chosen is outside the *domain* (set of possible values) of the function. Solving equations with arbitrary values of variables also can help determine whether a function is linear or nonlinear or whether relationships between variables are negative or positive. This is a plug-and-play approach where plug = input value and play = calculate output value. This approach can be used to understand the relationship between two variables for some specific combination of parameter values or to explore how different parameter values change the relationship between variables.

Tip 5: Visualize Functions Precisely by Plotting Them

Tip 4 described how to generally understand what a function looks like. For some purposes, though, this is not sufficient. Although a theoretician's ideal solution to this problem would be to find analytical solutions, doing so may require expert knowledge and may not be feasible for some complex equations. For someone trying to better understand a theory, another option is to input equations in a spreadsheet (e.g., Excel) or a programming application (e.g., R) and use plotting to explore the consequences of changing different parameter values or the initial value of variables on the dynamics of the state variable itself (e.g., N_t). This is essentially a simple numerical analysis. A worked example of how to explore equations using simple numerical analysis can be found in chapter 3 of Bolker (2008). Alternatively, interactive applications for exploring certain models can be found online (e.g., Shiny apps; see McGuire et al. 2021).

Tip 6: Identify Common Signposts

In reading theory articles, one might notice a range of symbols of various script types (e.g., Roman, Greek) and typefaces (e.g., bolding, capitalization, cursive script). Although any one symbol may be used to denote entirely different variables in different articles or, even worse, different symbols may be used to denote the same biological process in different articles entirely at the discretion of the author, some symbols are used consistently and have a specific meaning (Edwards and Auger-Méthé 2019). When these types of symbols appear in theory articles to symbolize complex operations or data structures, they are rarely defined because they are considered common knowledge. Not knowing what these symbols represent, or even which symbols are specific to that article and which hold some generally accepted meaning, can be a major barrier to understanding equations. In figure 2, we present a list of common symbols/typefaces, describe what they mean mathematically, and provide an example of their use in a biological context. Although we cannot cover every symbol that will be encountered in theory articles, simply knowing that undefined symbols and specific typefaces often hold specific meaning should help you recognize when and what to ask of a search engine (most symbols can be copied and pasted into search engines). We also cover some commonly encountered mathematical objects and operations (e.g., Jacobian matrices) in figure 2.

Tip 7: Consider the Fact That Some Information Might Be Missing, Presented Unclearly, or Incorrect

In some instances, confusion on the part of the reader may stem from the presentation of the material itself (e.g., undefined terms, unclear units) rather than the reader's knowledge. We hope that our discussion of some of the barriers to empiricists understanding theory will encourage theoreticians to present their work in a way that can be more easily interpreted by a nonexpert. And while we have focused our discussion on tests of theory that do not involve determining whether the math is correct, it may also be helpful for empiricists to keep in mind that theory is not infallible and that in some instances the math may indeed be incorrect. We suggest that empiricists, after putting in some effort to understand a theory article and arriving at unresolved uncertainties, contact the authors for clarification.

Conclusion

We hope that by demystifying theoretical work, the perspectives presented here will help break down current barriers to the integration of and feedback between theoretical and empirical research in ecology. We particularly hope that this

article is valuable to early-career empiricists starting out in the field. Charles Elton (1935, p. 149), when reviewing Alfred Lotka's book on the mathematics of populations, famously critiqued, "Like most mathematicians, [Lotka] takes the hopeful biologist to the edge of the pond, points out that a good swim will help [their] work, and then pushes [them] in and leaves [them] to drown." Unfortunately, nearly a century later, hopeful empiricists are still regularly being left to flail around in the murky waters of theory. Here, we offer a life raft and encourage empiricists to dip into the shallow waters of theory and to slowly gain the confidence, capability, and curiosity to venture deeper.

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Statement of Authorship

T.N.G. and R.M.G. conceived of the idea for the article and wrote the manuscript; A.S., P.-J.K., and M.A.B. helped make the figures and boxes; and all authors provided feedback and revisions on manuscript drafts.

Data and Code Availability

Annotated code for box figure 1 is publicly available on GitHub (<https://github.com/mabarbour/foodweb-theory/releases/tag/v2.0>), and we also provide a more user-friendly website to view the code (<https://mabarbour.github.io/foodweb-theory/rosenzweig-macarthur.html>). This code has also been archived with Zenodo (<https://doi.org/10.5281/zenodo.5154139>).

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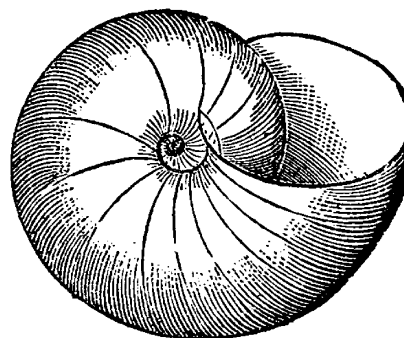
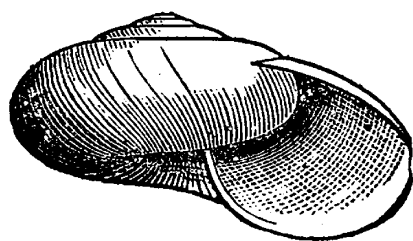
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“**HELIX FULIGINOSA** Binney. [Figured.] Shell thin, flattened above, nearly chestnut-color, sometimes a greenish horn-color. . . . This species occurs in nearly all the States east of the Rocky Mountains. It is extremely rare in New England, having been found only in the extreme western limits.” From “The Land Snails of New England (Continued)” by Edward S. Morse (*The American Naturalist*, 1867, 1:313–315).