Writing Accessible Theory in Ecology and Evolution: Insights from Cognitive Load Theory

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Theories underpin science. In biology, theories are often formalized in the form of mathematical models, which may render them inaccessible to those lacking mathematical training. In the present article, we consider how theories could be presented to better aid understanding. We provide concrete recommendations inspired by cognitive load theory, a branch of psychology that addresses impediments to knowledge acquisition. We classify these recommendations into two classes: those that increase the links between new and existing information and those that reduce unnecessary or irrelevant complexities. For each, we provide concrete examples to illustrate the scenarios in which they apply. By enhancing a reader's familiarity with the material, these recommendations lower the mental capacity required to learn new information. Our hope is that these recommendations can provide a pathway for theoreticians to increase the accessibility of their work and for empiricists to engage with theory, strengthening the feedback between theory and experimentation.

Keywords: scientific writing, theory, mathematical models, cognitive load theory, pedagogy

Progress in science benefits from a healthy feedback between theoretical and empirical work. Although most ecologists and evolutionary biologists agree on the importance of this feedback for scientific progress, self-identified theoreticians and empiricists alike believe that, in practice, instances of these feedbacks are more of an exception than a rule (Haller 2014). One explanation for the divide is that theory articles, particularly those that rely on mathematical models, can feel daunting to nonpractitioners. As a result, theory in ecology and evolutionary biology is frequently misunderstood and sometimes even disregarded altogether (Caswell 1988, Hillis 1993, Keddy 2005, Fawcett and Higginson 2012, Scheiner 2013, Marquet et al. 2014, Servedio et al. 2014). Indeed, surveys have shown that even when theoretical papers are cited in empirical work, the authors of the theory papers often perceive these citations as incorrect, inappropriate, or too general (Servedio 2020). The development of theoretical and experimental biology as separate fields can come at the cost to either pursuit, and it can hinder our ability to develop the predictive models needed to address pressing societal challenges (Łomnicki 1988, Kareiva 1989, Keddy 2005, Marquet et al. 2014, Rossberg et al. 2019). The question of how to remove roadblocks that prevent the full integration of theoretical and empirical research is therefore of great interest to progress in the biological sciences.

Why does a lack of integration between theoretical and empirical work persist? Some authors argue that biology programs could benefit from increased formal mathematical training (Chitnis and Smith 2012, Rossberg et al. 2019), and it is true that, even though mathematics permeates biology, many students only find out about this later in their academic careers (Otto and Day 2007). But this gap is also driven by persistent communication barriers between theoreticians and empiricists (Servedio 2020). Communication is ultimately a matter of how well the reader decodes the presented information. The effectiveness of communication is therefore the responsibility of both the transmitter and the receiver of information. Viewed this way, increasing mathematical training (Chitnis and Smith 2012, Rossberg et al. 2019) or providing guidelines for understanding theoretical work (Grainger et al. 2021) increases the adoption of theory by empowering empiricists with the mathematical background needed to effectively decode theory. But the converse is also true: Empiricists can better decode theory if it is communicated in a more accessible manner (Shoemaker et al. 2021). In this article, we use insights from cognitive load theory to propose recommendations for communicating

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theory in a more accessible manner, thereby bridging the communication gap between theoreticians and empiricists.

Cognitive load theory, which is focused on impediments to knowledge acquisition, serves as a rigorous evidence-based reference from which we can draw guidelines to assist in the effective presentation of information (Sweller and Chandler 1994). We begin by reviewing, in brief, broad themes from cognitive load theory and how it can be applied to the writing of theoretical papers. We then provide specific recommendations that pertain to the type of cognitive load (i.e., burdens on working memory) that are imposed when interpreting theory. Specifically, these types of load include those that relate to the details of a mathematical model (i.e., mathematical approach, notations, and graphical representations) and those that relate to the intuition and reasoning behind the conceptual theory (i.e., abstractions, narratives, and assumptions). As a group of theoreticians and empiricists working in ecology and evolutionary biology, our intention is neither to castigate nor to dictate which writing practices are right or wrong; we recognize that there are no hard and fast rules when it comes to communication. Rather, we aim to provide suggestions to help theoreticians communicate more effectively with empiricists.

Every learning or problem-solving task imposes a mental demand on the learner or problem solver. Although the perceived demand can be subjective and influenced by context (e.g., how tired or distracted the learner is; Kantowitz 1987, MacDonald 2003), there are objective characteristics of the task, known as *cognitive load*, that can affect learning outcomes (Plass et al. 2010). Built on the understanding of the capabilities and limitations of how humans process information (e.g., encoding, storing, and modifying information, also known as *human cognitive architecture*), cognitive load theory provides a rich body of knowledge and a toolkit of principles that can be applied broadly to enhance learning outcomes. Therefore, we can draw insights from cognitive load theory to address communication barriers between theoreticians and empiricists by providing suggestions to help the former communicate their work in a way that facilitates knowledge acquisition by the latter.

Cognitive architecture

The human cognitive architecture can be divided into two main memory systems: long-term memory and working memory (Baddeley 1992, Sweller et al. 1998). As its name suggests, long-term memory is stored indefinitely and has no known limits. In contrast, the capacity of the working memory is limited, and information is stored only temporarily. Examples of long-term memory include unconscious cognitive activities, such as the ability to read familiar words without carefully reading every letter. The processing of new vocabulary goes through the working memory; the reader may have to consciously verbalize each syllable and pay attention to the structure of the word (e.g., affixes, morphemes) in order to get a sense of its pronunciation and meaning.

Experts and novices can be distinguished by whether they are able to effectively organize knowledge stored in long-term memory; this is the idea of having intuition in the colloquial sense. In other words, experts categorize information systematically, according to its use and subject matter, into coherent clusters called *schemata* (Chi et al. 1982). Schemata enable experts to efficiently process information because they bypass the limited capacity of the working memory and allow organization of knowledge contained in long-term memory. To facilitate schema acquisition, cognitive load theory identifies distinct types of cognitive load in the working memory and recommends specific interventions for overcoming each type (Sweller et al. 1998, 2019).

Types of cognitive load

The cognitive load associated with a given task determine the efficiency with which an individual understands the material. These types of load can be classified into three distinct types: intrinsic load, extraneous load, and germane load. *Intrinsic load* refers to the complexity inherent to the problem at hand. Some materials are inherently more difficult because they contain more elements that must be considered simultaneously in order to be comprehended (figure 1; Maybery et al. 1986, Sweller and Chandler 1994). In contrast, an *extraneous load* is not unique to the specific task, but rather, it is influenced by the way in which the material is presented (figure 1; Sweller and Chandler 1994). Finally, *germane load* refers to the mental resources that are devoted to organizing new knowledge into schemata (i.e., relating new ideas to previously existing knowledge into coherent clusters of information; figure 1). Because intrinsic load is a property inherent to the material and, therefore, cannot be altered, instructional interventions based on cognitive load theory work by altering the other two types of cognitive load (Sweller et al. 1998). Specifically, the efficiency of instructional design is optimized by reducing the extraneous load and increasing the germane load. An overview of the three types of cognitive load and how each relates to learning and to schema acquisition is illustrated in figure 1.

Recommendations

In the following sections, we provide recommendations for how theoreticians can reduce communication barriers that are inspired by pedagogical interventions suggested in cognitive load theory. We organize these recommendations into two broad categories: those that increase germane load by helping the reader organize new information into preexisting or novel schemata (i.e., relating new ideas to preexisting knowledge in a coherent way) and those that reduce extraneous load by reducing the amount of mental effort it takes to understand new concepts. This organization is practical, but it should not be considered absolute, because some of our suggestions blur the distinction between the two categories (and, when followed effectively, may both increase germane load and reduce extraneous load).

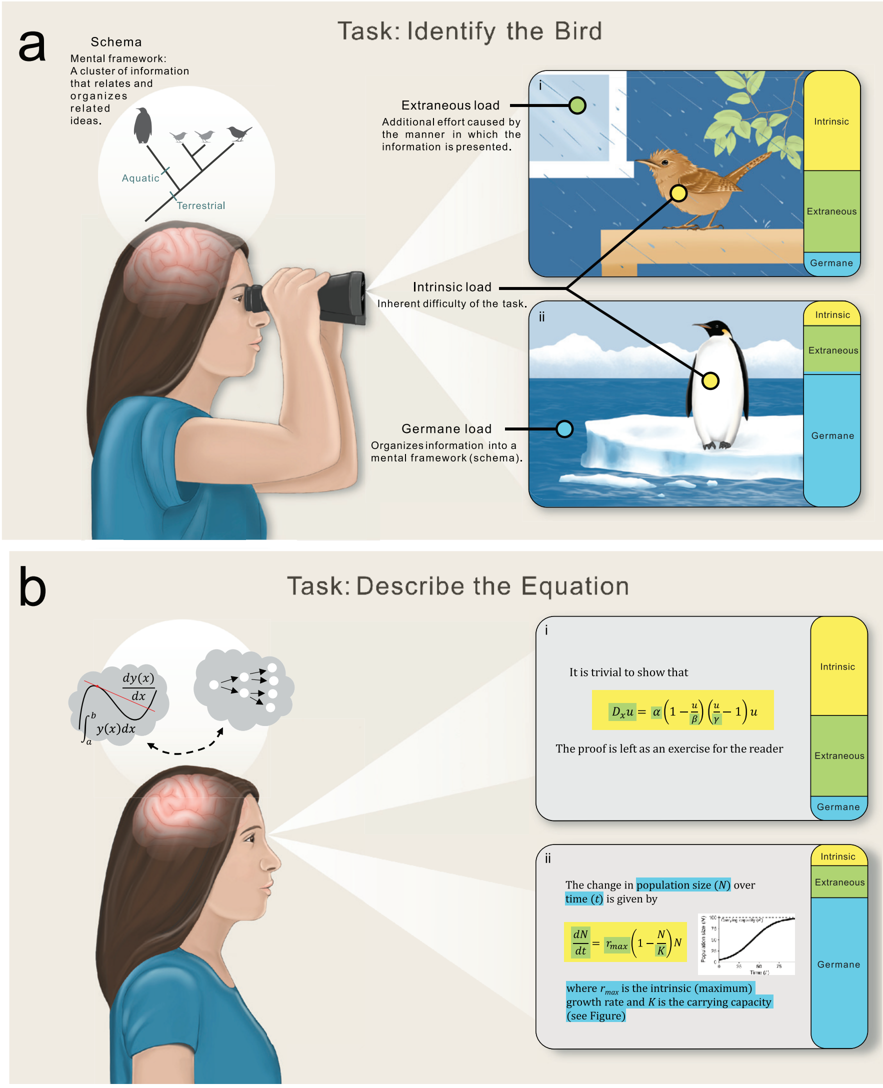

Figure 1. Schematic illustration of cognitive load. (a) Julie is an amateur birder with a basic understanding of bird taxonomy. She categorizes birds according to their evolutionary relationships and their characteristics—for example, what environments they inhabit. This is her schema: the organizing framework through which she understands avian diversity (represented by the fictional phylogeny). She is presented with the task of identifying a bird in two different scenarios in subpanels (ai) and (aii). The two scenarios are associated with very different levels of intrinsic, extraneous, and germane load, as was shown in the meters on the right. In subpanel (ai), intrinsic load is high because the bird is a house wren (a plain brown bird, often quick, hard to see, and easy to mistake for other species). Extraneous load is also high because the rain makes the wren hard to see. Germane load is close to nonexistent; there is nothing about the situation that relates the task to Julie's preexisting schema (e.g., there are no environmental cues because the bird is in a human-made habitat). In contrast, subpanel (aii) has a low intrinsic load because a penguin has very distinct characteristics. Extraneous load in this scenario is negligible because there are few distractions that are irrelevant to identifying the bird. Germane load is high because the bird is presented in its natural habitat, which Julie can relate to her preexisting knowledge that penguins are aquatic birds (part of her schema). Pedagogical interventions should aim to reduce extraneous load and increase germane load. The same concepts apply to mathematical learning tasks. In (b), Julie is learning about mathematical models of population growth. She has a schema for elementary calculus and a schema for population growth, but the two schemata are not yet strongly connected. Although the tasks presented in bi and bii both concern differential equations for population growth, bi is a harder task because of the additional Allee effect term (higher intrinsic load), unfamiliar notations (higher extraneous load), and being presented with no context whatsoever (lower germane load). In contrast, the population growth equation in bii is simpler (lower intrinsic load) and it is written in notations that are familiar to Julie (lower extraneous load). The presentation in bii also provides all the necessary definitions of terms and visuals, which allow Julie to connect her knowledge about population biology to her knowledge about calculus (high germane load).

Increasing germane load

As was briefly introduced above (and as is illustrated in figure 1), *germane load* comprises the cognitive resources devoted to organizing new information into schemata. Recall that learning is most effective when intrinsic and extraneous load are low and when germane load is high. Increasing germane load means helping the reader understand new ideas by relating them to other known concepts. In this regard, learning theory can be particularly hard because the defining features of a theoretical model are often buried deep within the abstractness of mathematics. In this section, we first discuss why mathematical abstractions are useful in science and why they may be particularly hard to learn. We then provide recommendations on how to help the reader maximize germane load, including how one might go about addressing the obscurity of abstractions.

The utility of mathematics in scientific research stems from its ability to form abstractions of natural phenomena. Forming abstractions means generalizing beyond the particulars of a given observation, by identifying structures, patterns, or properties that are common to many other observations or even to different types of natural phenomena (Ferrari 2003, Marquet et al. 2014, Servedio et al. 2014). However, the utility of abstractions can come at the cost of clarity, especially when complex symbolic expressions are used to represent them (Ferrari 2003). Moreover, high levels of abstraction can conceal the connection to real-world phenomena and cause misunderstanding or misinterpretations. For novices, abstract concepts may be particularly hard to learn because their generality creates the additional task of differentiating the scenarios where the abstract concept applies and where it does not. This additional task of differentiating may create a high mental load for novices (Sweller and Sweller 2006). In fact, theoretical expertise is often built by stretching the limits of a model's applicability (e.g., by finding counterexamples or solving for boundary conditions).

As a concrete example of how abstraction can be useful while simultaneously creating challenges to interpretation, consider the concept of Shannon entropy. Although originally developed as a means of quantifying information, the concept's high level of abstraction makes it broadly applicable in fields as diverse as cryptography, data compression, probability theory, and ecology. In ecology, Shannon entropy provides a measure of species diversity that incorporates both species richness (number of elements) and evenness (relative proportions). This measure is often misused because the resulting value of the function is an *index* of species diversity (as a result of its abstraction) rather than species diversity per se (Jost 2006). For example, if hypothetical communities A and B have a Shannon entropy of 4.4 and 4.6, respectively, a naive (hypothetical) ecologist may conclude that the two communities are similar in species diversity. However, after conversion to the proper units, community B (99 species) actually contains 17 more “equally common” species than community A (81 species). This is because Shannon entropy scales proportionally to the natural log of the number of species. This scaling relationship might seem insignificant, but statistical estimates of effect size and significance on raw entropy indices may result in incorrect inferences of species diversity (Jost 2006). As this example illustrates, abstractions (often expressed through mathematical formulations) provide versatility but can impede understandability. In the following section, we provide recommendations for how theoreticians can make abstractions more concrete in order to increase the accessibility of their research to empiricists.

Using metaphors and analogies. Making analogies is core to human cognition (Gentner et al. 2001). By mapping relationships between disparate domains on the basis of relational similarity, making analogies allows us to transfer knowledge across contexts (Gentner 1983, Holyoak et al. 1984). Research in cognitive psychology has demonstrated that abstract concepts are understood via mental simulations of physical actions (Barsalou 1999). By conceiving of one thing in terms of another, through analogies, an author can communicate meaning in terms of something previously experienced and concrete to its readers. In this way, analogies can enhance germane load by serving as scaffolds that facilitate the mental modeling process and the acquisition of schemata (Goldin-Meadow et al. 2001, Lee 2007, Cheon and Grant 2012, Niebert and Gropengiesser 2015, Sweller et al. 2019). This, at least in part, explains why metaphors (an implicit analogy; Hsu 2006) have played a prominent role in the advancement and communication of science (Lakoff and Johnson 1980, Thibodeau and Boroditsky 2011). In ecology and evolutionary biology, metaphors such as environmental filtering, molecular clock, Red Queen, and evolutionary tinkering are so powerful for communicating ideas because they associate otherwise abstract concepts with mental images of familiar objects or processes (Olson et al. 2019). More importantly, these metaphors help convey ideas not only between researchers within disciplines but also across disciplines, because they instill images of our everyday experiences. As such, we recommend the use of metaphors and analogies in general, to help facilitate the creation of mental models and enhance interpretability of abstract ideas whenever possible.

When writing theory, one can consider its mechanistic similarities to other known mechanisms in the literature. For example, the storage effect (Chesson and Warner 1981) in coexistence theory can be thought of as niche partitioning in time (or space). *Storage effect* might be a term familiar only to practitioners of coexistence theory, but the concept of niche partitioning is likely familiar to anyone who has taken any introductory course in ecology and evolution. As a word of caution, we recognize that metaphors themselves may be vague and lead to misunderstandings (Jacob 1977, Kaplan 2008); however, careful selection of metaphors and being explicit and transparent about limits to the metaphor's applicability can help maximize its utility (Olson et al. 2019).

Providing narrative context. Scientific discoveries and endeavors often originate from observations of real-world phenomena.

To explain these phenomena, theoreticians and empiricists draw from their preexisting knowledge to develop mental models or verbal hypotheses. In empirical work, these mental models are tested by devising experiments and gathering data. Analogously, in theoretical work, they are tested by creating a mathematical model capable of generating precise predictions that can be compared with verbal predictions (Servedio et al. 2014). In this way, the lines of reasoning, or narratives, that seek to explain observations precede the development of theoretical models (Otto and Rosales 2020) just as much as they precede experiments. These narratives do not rely on mathematics and logical axioms but, rather, on mental simulations of probable scenarios (Johnson-Laird 2010); they are highly contextual and have a great influence on how models are built. They also influence the conclusions and inferences that one draws from models after they are created (Otto and Rosales 2020). Differences in narrative reasoning can matter so much as to cause disputes in the development of a field. For example, the debate over the relative importance of density-dependent and density-independent mechanisms for population regulation can be partially attributed to the different inferential methods (field observations versus controlled lab experiments), or narrative context, applied by the supporters of each camp (Hutchinson 1957). In evolutionary biology, conflicting interpretations about the effect of sexual reproduction on rates of adaptation arise from whether a finite population size is assumed, an assumption made on the basis of narrative reasoning by the investigator (Otto and Rosales 2020).

By emphasizing the narrative reasoning behind new models, theoreticians can provide context to readers and resolve any ambiguities they may encounter along the way. Narratives provide the reader with a verbal motivation for the choice of methods and interpretation of the results. It is the narrative, rather than the equations themselves, that imbues models with meaning (Otto and Rosales 2020). To do this, a theoretician can inform the readers of the whole conceptualization process of the theoretical model. In the introduction, instead of simply stating the knowns and unknowns in current literature, a theoretician can speculate possible reasons for how and why the focal field of research has developed the way that it has. They can remind the reader of the empirical phenomenon being modeled, discuss the theoretical approaches that have been taken, but also elaborate on why those particular approaches were taken. Although it is important that the mathematics is accurate, it is also important that the narrative reasoning on which models are built and interpreted is sound and effectively communicated.

To give a concrete example of a theory sparked by empirical observation, narrative reasoning, and abstractions, consider the famous anecdote of Newton's falling apple as recalled by William Stukeley (1752): "Why should [the apple] not go sideways, or upwards? But constantly to the Earth's centre? Assuredly, the reason is, that the Earth draws it. There must be a drawing power in matter." When Newton was questioning the apple's motion, he was really asking why anything would fall toward Earth. More generally, he was really questioning what laws of motion were at play. Through abstraction, he was able to make general inferences about the laws of motion: the apple and the Earth as hypothetical spherical objects with a given mass. Questioning why the apple fell downward and not sideways or upward was his narrative reasoning about the origin of the forces. He applied what he knew about the mass scaling of spherical objects (preexisting schema) and inferred that the attraction must be proportional to the masses of the two objects and their squared distances. Although his mental model was that of an apple, the theory and mathematical model he developed were general in the sense that they could be applied to explain the attraction of any bodies of mass, including that of celestial bodies.

Stating assumptions and explaining their purpose. A famous Lewis Carroll passage describes a fictional map that had "the scale of a mile to a mile" (Carroll 1893). When asked how frequently the map was used, one of the characters replies, "it has never been spread out yet" because "the farmers objected: They said it would cover the whole country and shut out the sunlight! So now we use the country itself, as its own map, and I assure you it does nearly as well." Models, like maps, are useful only inasmuch as they simplify nature (Levins 1966; see also Orzack and Sober 1993, Levins 1993), otherwise the resulting equations would have too many parameters and be impossible to solve or interpret. Therefore, all models make simplifying assumptions, ideally in a way that preserves the essential features of a problem (Levins 1966). Despite its importance, the exercise of making constraining assumptions is the step of the model-building process that poses one of the greatest cognitive difficulties to those who are unfamiliar with modeling (Fortus 2009). The ability to conceive, select, and apply subjective assumptions is not developed in conventional education settings (Seino 2005), even at the undergraduate level and in quantitative disciplines such as physics (Fortus 2009) or engineering (Peters 2015). Readers who are less familiar with modeling might not have the conceptual schemata that allow them to understand which assumptions are relevant and why (Peters 2015), according to cognitive load theory; therefore, clearly stating model assumptions and their purpose increases germane load. It is therefore not only important for theoretically inclined readers who may want to follow the mathematical details, but for empiricists as well. It helps readers understand how a real-world problem gets converted to a well-defined model, which, in turn, allows them to see what natural systems the model applies to, how it can be tested, and which parts of the model are most relevant for its qualitative behavior. All of this is necessary if empiricists are to attempt to validate model predictions and establish connections between theory and empirical studies (Servedio 2020).

It is critical to not only clearly state *what* was assumed but also *why*. Broadly speaking, assumptions are made for one of three reasons: critical, exploratory, or logistical (Servedio et al. 2014, Servedio 2020). In the present article, we first describe each kind of assumption and then describe how to avoid misunderstandings that may arise when making them. *Critical assumptions* are those that are essential for modeling a given biological process or asking a particular question. Without those assumptions, the model does not accurately describe the process it purports to study. For example, if studying the probability of genetic rescue during environmental change, one *has to* assume that such environmental change has a detrimental effect on fitness. *Exploratory assumptions* are those decisions that are not essential, but that we have to make in order to limit the full range of possibilities. They provide a point of entry into the analysis. Building further on our evolutionary rescue example, for instance, we can assume that the environmental change happens gradually and continuously at some constant velocity, or alternatively, we may assume a discrete change between different environmental states. Making alternative exploratory assumptions would provide additional insight but is not always feasible. Finally, *logistical assumptions* are made merely to simplify the model and allow for mathematical tractability. For example, when calculating the fitness of an individual at some distance to the environmental optimum, we may assume that higher-order terms can be safely ignored. In a theory paper, if assumptions are not stated or properly justified, the reader may justifiably think the conclusions are valid outside their range of applicability. Conversely, they may also disregard the results because of a belief that logistical assumptions made for the sake of convenience are actually critical to the reported results.

What can the author do to reduce misunderstandings? It depends on the type of assumption. When making exploratory assumptions, one could be clear that alternative possibilities exist, and even, if possible, make educated speculations regarding their potential consequences. When making logistical assumptions, one could, as much as possible, explain their biological implications. To return to the example from the previous paragraph: Ignoring higher-order terms may be equivalent to assuming weak selection. One could also clarify when the purpose of these assumptions is to reduce complexity, rather than to mimic nature. If possible, it is important to try to ensure that logistical assumptions have no qualitative effect on the results. If one has no good reason to suppose that the results are robust to a logistical assumption, then one can transparently acknowledge the potential consequences of relaxing it. Critical assumptions are less likely to induce misunderstandings, but it is helpful to provide a clear link between the mathematical form of the model and the biological process it is meant to represent.

The type and extent of assumptions one makes are related to the goals of the model. Because models have different purposes, one does not always need to ensure that all assumptions are realistic; models can be valuable even when their aim is not to closely represent nature. However, when assumptions are not realistic, it is especially important to explain why they were made. In some cases, there may be no empirical knowledge to help guide the choice of assumptions. In other cases, assumptions may be made with the explicit purpose of demonstrating that they have important qualitative consequences (proof of concept models; Servedio et al. 2014). This may in turn motivate empirical work to verify such assumptions. For example, Charlesworth and colleagues (1997) performed numerical simulations to demonstrate “the qualitative effects” of mutation rate on population differentiation. They freely admit that they “did not choose biologically plausible values” of mutation rate, but rather “values that would produce clear-cut effects” (Charlesworth et al. 1997). The assumptions were not meant to be realistic, but the model still provided proof of concept that background selection can affect differentiation. This theoretical paper then motivated further research to check whether the pattern actually holds in realistic scenarios, using empirically derived recombination maps (Matthey-Doret and Whitlock 2019).

Defining terms and describing their biological meaning. Even when mathematical notation is consistent and familiar, it is critical to define every term and describe its biological interpretation. This helps the reader build intuition and categorize novel information into relevant schemata, which increases germane load and allows a broader readership to understand one’s results (even if only qualitatively).

By itself, a mathematical expression is meaningless; it gains explanatory power only when all the parameters and variables are defined. For example, many ecologists are familiar with the equation for logistic growth,

$$\frac{dx}{dt} = rx\,(1 - x),$$

and may think that it is unnecessary to define r as the intrinsic growth rate and x as the population size. Evolutionary biologists, however, may assume that x represents allele frequency and r represents the selection coefficient, and they may reasonably conclude that the equation describes response to selection rather than logistic growth (Otto and Rosales 2020). A table summarizing the description and value of parameters (and their units, if applicable) can also be helpful and can reduce the load associated with remembering a large number of symbols.

In addition to defining the parameters, it is helpful to provide a description of their biological meaning. *Biological meaning* is the translation between the mathematical effect of a parameter and its biological interpretation. Take the effect of interspecific interactions in a Lotka–Volterra competition model, often represented as α. A simple sentence such as “$\alpha > 0$ represents competitive interactions, whereas $\alpha < 0$ represents facilitative interactions” can greatly aid understanding. Providing biological meaning also includes describing a parameter’s units (when applicable) or explaining the biological interpretation and reasonable range of dimensionless quantities.

Apart from parameters, it is also useful to provide biological interpretations for entire equations and for important results. Consider, for example, Holling's disc equation (Holling 1959):

$$f(R) = \frac{aR}{1 + ahR},$$

where $f(R)$ denotes a consumer's intake rate given resource density R. In this equation, a is the rate at which the consumer encounters resources per unit of resource density (attack rate) and h is the average time spent processing a resource item (handling time). Even though all the parameters have been defined in clear biological terms, the way in which these parameters interact is not necessarily evident. To make the equation's biological meaning transparent, we could point out that, for a given population size of predators, the intake rate increases with resource density when resources are not abundant but levels off at high resource densities. This makes sense because at very high resource densities consumers find resources easily but are limited by their capacity to process them, for example, because of satiation.

Providing links to empirical research. Beyond communicating theory effectively, a healthy feedback between theoretical and empirical work ultimately depends on how knowledge gained from one can guide knowledge acquisition of the other. To increase the adoption of theory in empirical work we recommend that theoreticians explicitly state the types of experiments that can be conducted to validate their theory. What are the variables that need to be collected? Are they straightforward to measure, or will empiricists need to find proxies? How can the models be fitted to the data? What kind of evidence is required for inference (e.g., qualitative trends or specific parameter values)? For instance, the metabolic theory of ecology not only predicts a sublinear relationship between metabolism and body size but also makes the specific prediction that it scales to the power of ¾ (West et al. 1997). In this case, the theory can be validated by measuring body size and metabolism of various organisms, the compiled data set can then be fitted to a power law model and be statistically tested to see whether the estimate deviates significantly from the theoretical value of ¾. In some cases, empirical validation of theoretical models might require development of new tools or technologies (e.g., faster algorithms, new instruments, or statistical frameworks). Even stating obstacles that one might need to overcome before empirical work can be conducted can be a good starting point, highlighting which areas still need work. Importantly, these statements not only can increase adoption of theory but can also solidify understanding by casting the theory in terms that are relevant to an empiricist. In other words, it helps relate the theory to previously existing categories of information (i.e., schema acquisition).

Reducing extraneous load

As is illustrated in figure 1, *extraneous load* refers to the additional mental effort that is generated by the manner in which information is presented to a learner (Sweller and Chandler 1994). Reducing extraneous load means avoiding burdening the reader with superfluous details or distractions or with an unnecessarily complicated presentation.

Adjusting the level of mathematical detail to the target audience. Fawcett and Higginson (2012) showed that, in top journals specializing in ecology and evolution, papers receive 28% fewer citations overall for each additional equation per page in the main text. Although citation rates are not necessarily an indication of quality (Fernandes 2012), and reducing the number of equations could in some cases decrease intelligibility, one important message from this finding is that the amount of mathematical detail in the main text could be calibrated to the target audience. In some journals (e.g., *The American Naturalist*) equations actually increase citation rate (Gibbons 2012); furthermore, equation-dense papers tend to be cited more frequently by other theoretical papers (Fawcett and Higginson 2012). If, on the other hand, the target audience consists mostly of scientists specializing in empirical research, there are several approaches that allow an author to reach more readers without sacrificing rigor.

One approach is to decrease equation density by adding more explanations between each equation, to ensure that readers understand the notation, assumptions, biological meaning, and purpose of the mathematical methods being employed. This can include a step-by-step explanation of each term in an equation (for a good example, see Thompson et al. 2020). It can also include explanations ahead of the technical sections that "kill the suspense" by revealing the purpose of each section and flagging important parts of the argument. Because close to half of empiricists reportedly skip technical sections in papers (Haller 2014), this kind of signposting may help readers decide for themselves which sections to pay attention to and which sections they can skim or skip.

An alternative (and complementary) approach is to minimize the mathematical details in the main text and move them to an appendix. When using this approach, the main text would describe the model in general terms and convince readers that the mathematics provides new insights that would not be obvious otherwise, whereas the appendix would show the readers how they can recreate the results from the main text. Importantly, the text in the appendix should not take mathematical deduction as common sense, and should instead show readers all the intermediate steps. One can provide an intuitive road map of the calculations so that readers know where they are stuck and can move forward even if they do not understand a particular step. Offering the reader a reproducible notebook (e.g., a *Mathematica* notebook or equivalent) may be desirable.

Adjusting the level of mathematical detail goes beyond judicious use of equations. Mathematical jargon or specialized terminology plays a similar dual role: It may increase rigor and facilitate communication between theoreticians, but it may also decrease accessibility with respect to other readers. Just as with equations, extensive use of jargon correlates with decreased citation numbers (Martínez and Mammola 2021). Although this does not mean authors should avoid jargon altogether, Martínez and Mammola (2021) recommended that jargon be restricted to appropriate sections of the paper. In the case of articles describing theoretical models, this could be the methods section or the appendix. Alternatively, authors can provide accessible definitions (or at least intuitions) for the meaning of jargon terms. We suggest that the appropriate level of jargon, much as the appropriate amount of mathematical detail, should depend on the target audience.

Using consistent, intuitive notation. The use of mathematical notation can improve communication by increasing precision and efficiency relative to prose. Equations are also often simpler and more straightforward than equivalent verbal statements, especially when the verbal form is long and convoluted, which imposes substantial extraneous cognitive load (Leung et al. 1997). However, some styles of mathematical notation can also hinder communication when it is hard to decipher. Equations with nonstandard or unnecessarily complex notation impose heavy extraneous load, forcing the reader to search and assimilate semantic meanings for unfamiliar symbols (Dee-Lucas and Larkin 1991, Leung et al. 1997). By employing careful notation and providing biological interpretations, theoreticians can improve the reader's understanding. Below, we provide some guidelines on the use of mathematical notation in biological modeling; for a more extensive treatment of the same topic, see Edwards and Auger-Méthé (2019).

Careful notation is consistent. The meaning of a symbol should not change throughout the article and, conversely, the same concept should always be represented by the same symbol. For instance, the derivative (with respect to x) of a function $f(x)$ is conventionally represented as $f'(x)$ (Lagrange's notation) or as df/dx (Leibnitz's notation), but one should not alternate between them within the same article.

Ideally, although this is not always possible, one could also strive for semantic consistency—that is, using related symbols for related concepts. A familiar example of semantic consistency is the use of Greek letters to denote population parameters (such as the population mean μ and the population standard deviation σ) and Roman letters for their sample counterparts (sample mean $\bar{x}$, sample standard deviation s). Another common example is the use of contiguous letter sequences to indicate quantities that follow an ordinal sequence—for example, x, y, z to represent the first, second, and third spatial coordinates or i, j for the first and second indices of a matrix. Consistency can extend to font styles as well. For instance, it is common to use roman lowercase boldface letters to represent vectors and roman uppercase boldface letters to represent matrices. It would be confusing to denote some matrices with uppercase variables and other matrices with lowercase variables.

Finally, notation should ideally also be consistent with the conventions of one's field as well as with broader mathematical conventions. In ecology, N or n is often used to represent population size, t represents time, and r represents growth rates. Understanding the equation for exponential growth rate, $n(t) = n_0\ exp(rt)$, where n_0 is the initial population size, is straightforward partly because it abides by these conventions. Familiarity with the symbols carries across articles, decreasing the extrinsic load faced by the reader when encountering a new equation. If we replaced these symbols by unfamiliar alternatives (e.g., δ for population size, X for growth rate, and f for time), interpretation would be considerably more difficult: $\delta(f) = \delta_0\ exp(Xf)$.

Providing programs or scripts. Facilitated by the advent and utility of modern computers, programming has become a toolkit of many modern-day biologists (Touchon and McCoy 2016, Lai et al. 2019). This provides a unique opportunity for theoreticians to communicate their mathematical models in the form of source code—a written set of instructions that specify the actions to be performed by a computer. Although the accessibility of source code may differ between programming languages, high-level programming languages that are popular among the scientific community (e.g., Julia, Python, and R) incorporate natural language elements (i.e., words such as *while*, *if*, or *function*). This renders instructions for the computer into worked examples that readers can break apart into constituent parts to facilitate learning (Sweller and Cooper 1985, Paas et al. 2003). Furthermore, because readers may be more familiar with programming than with mathematical notation, providing code can greatly reduce the amount of items in a reader's working memory, enabling them to focus their attention on the main findings instead of mathematical nuances. For example, an empiricist unfamiliar with mathematical notation may take several minutes to recognize that y and x in the equation

$$y_i = \sum_{k=1}^{i} x_k,\ for\ i = \{1, 2, \ldots, N\}$$

are vectors and might take a few more minutes to realize that the equation represents the cumulative sum function (Edwards and Auger-Méthé 2019). In contrast, a biologist with programming experience will have no trouble recognizing the same function in the form of R code:

```
y <- cumsum (x)
```

Importantly, this approach relies on the reader being familiar with the particular language being employed. Because programming languages fall in and out of favor over time, Edwards and Auger-Méthé (2019) caution against providing only the code as a substitute for mathematical equations.

Providing code is becoming increasingly common and is now required in many journals, particularly for simulation-based studies. However, even if readers have some familiarity with programming, the complexity of an analysis or model can be so complicated that the code is effectively inaccessible to the reader. For this reason, good coding practices can go a long way (Wilson et al. 2014, 2017). Because human working memory is limited, pattern recognition is fine-tuned, and attention spans are short (Wilson et al. 2014), having human-readable scripts that are well commented throughout can greatly reduce extraneous load and allow readers to easily pick up on the main functions of the program and their relation to the models presented. This is particularly important for reproducibility in another programming language because readers might not be familiar with an author's choice of programming language (Tiwari et al. 2021). Moreover, following good coding practices—for example, consistent naming conventions for variables (camelCase or pothole_case)—can enhance accuracy and reduce the time it takes for readers to interpret computer programs (Letovsky 1987, Binkley et al. 2019). We limit our recommendations of good coding practices in the main text, because this subject has been discussed extensively elsewhere (e.g., Wilson et al. 2014, 2017, Tiwari et al. 2021).

Not all readers are able to read code, or read code from specific programming languages. Building interactive apps (e.g., Shiny apps) can overcome this problem and provide another option for readers to play with and visualize models; for an example, see http://mmosmond.shinyapps.io/criticalsplines, which is a companion app to Osmond and Klausmeier (2017). Finally, we also recognize that implementing good coding practice and reproducible code is another skill that takes time to master. However, authors should not hesitate to publish code even if the quality is not perfect; the act of making code accessible alone is enough to enable others to better engage with theory (Barnes 2010).

Visualizing the model and the results. Abstract mathematical ideas are communicated to readers through so-called external representations: physical manifestations or symbols that can be perceived by the senses (Pape and Tchoshanov 2001). Common external representations include equations, tables, diagrams, and charts. Studies in the mathematics classroom context suggest that the simultaneous use of multiple representations facilitates the understanding of mathematical concepts (Brenner et al. 1997, Greeno and Hall 1997). Cognitive load theorists argue that visual and verbal information are processed by independent working memory systems. The use of multiple presentation modalities distributes load across systems, increasing the capacity of working memory (Kirschner 2002). On the basis of these considerations, we suggest that visual representations should play an important role in communicating mathematical models. This includes graphical representations of the model itself, graphical representations of key equations and results, and numerical illustrations of model dynamics.

A graphical representation of a dynamic model (figure 2) can take the form of a stock and flow diagram, which illustrates the interactions and relationships between variables (e.g., Ogbunugafor and Robinson 2016). In such a diagram, each variable is represented by a box (a stock). The value of the variable can increase via inflows (arrows moving toward the box) or be depleted via outflows (arrows moving away from the box). The arrows, which are typically labelled with corresponding rates, may connect different variables, highlighting their relationships and interdependencies (figure 2a, 2b). Another helpful graphical representation, useful for discrete-time models, is the life cycle diagram, which shows the order of events that occur during a single model time step. Figures such as stock and flow diagrams or life cycle diagrams provide schematic pictures of the model, allowing readers to understand the logic behind the corresponding differential or recursion equations or individual-based simulations. Models can also be illustrated with pictorial diagrams that explain the relationships between variables through drawings or cartoons of concrete biological objects (figure 2c, box 1). This is analogous to providing a visualization of a complex experimental design, as is common in empirical papers.

It is also helpful to provide graphical representations of complicated or important equations and results. Research suggests that, at least among college students, interpretation of mathematical relationships is more accurate when they are depicted in graphical form instead of symbolic form (Mielicki and Wiley 2016). Particularly helpful depictions show the effect of varying parameters. These range from plots showing multiple curves for increasing parameter values to more complex depictions of a system's dynamics (e.g., phase plane diagrams, pairwise invasibility plots) or statics (e.g., bifurcation diagrams). Figures showing the effect of parameters on summary estimates (e.g., slopes) can be harder to interpret, because these are often further removed from the raw variables. Nonetheless, summary estimates may have meaningful biological interpretations. In such cases, these figures may be useful, because they allow us to synthesize the results of a study. When using them, it is helpful to make the link between the summary estimates and the raw variables explicit, either verbally or visually (e.g., if the figure shows the effect of a parameter on the slope, the author

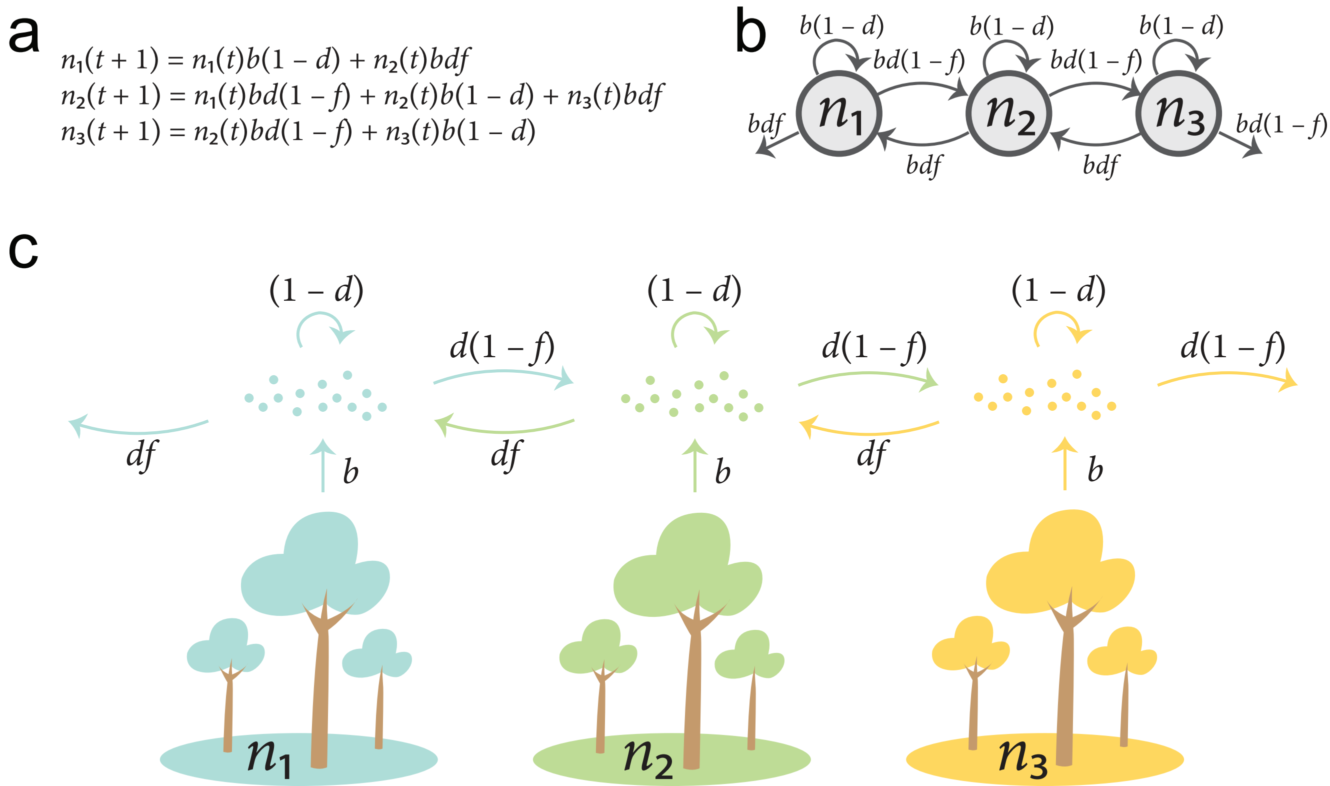

Figure 2. Different representations of the same model (see box 1 for more details). (a) A system of equations describing a model that keeps track of the number of individuals in an annual plant species that inhabits three island patches, arranged from west to east. Each generation, b seeds are produced, of which only a fraction d disperse, with the rest of the seeds remaining in the parental patch. Of the dispersing seeds, a fraction f disperse west and the remainder disperse east. No seeds that disperse outside the range survive. In the following year, all seeds that land on a patch grow into adults. Model adapted from Otto and Day (2007), with author permission. (b) A stock and flow diagram (which is equivalent to the system of equations) makes relationships between variables more obvious than simply writing out the equations. (c) A pictorial diagram that uses cartoons of trees to activate associations with prior knowledge of, and interest in, tree seed dispersal (also equivalent to the system of equations).

can provide small inset figures that show the raw variables with different slopes).

Finally, when applicable, one can consider illustrating model dynamics with numerical solutions or individual-based simulations (e.g., time series). Even when this is not the main analysis technique, simulating different model outcomes will help readers understand the different dynamics embedded in more complicated figures (such as phase plane diagrams). When numerical solution or stochastic simulation is the main technique, it is good to provide a range of parameter values over which one has simulated (or the figure should be indicative of the broad range covered by the results).

Conclusions

Irrespective of discipline, learning new information will always require mental effort. In the present article, we provided an inexhaustive list of recommendations and guidelines for communicating theory on the basis of cognitive load theory, which we hope can optimize the distribution of cognitive load within the constraints of the reader's working memory, enhancing learning and bridging the gap between theoretical and empirical work (summarized in table 1). Although our recommendations are organized into distinct sections, all of them work by maximizing one key element: familiarity. Whether it is using consistent notations, including additional modal representations (graphical versus verbal), or providing context to the scientific story, all of these work by finding a link (albeit subtle) between new information (i.e., the theoretical model) and something that is already familiar to the novice learner. We hope that the guidance presented in the present article offers a possible avenue toward increasing the accessibility of theory in ecology and evolutionary biology.

Box 1. Graphical representations of mathematical models.

Stock and flow diagrams or life cycle diagrams are nothing more than graphical representations of a system of equations (compare figure 2a with figure 2b). Examples of diagrammatic representations of equations abound. For instance, the population geneticist Sewall Wright (1918, 1934) introduced the use of diagrams to perform causal inference (a method called path analysis). Such graphical representations do not add any information to the system of equations; from a logical standpoint, they are redundant. But they illustrate systematic relationships, make evident the causal connections, enable hypothesizing, and assist in understanding (Griesemer and Wimsatt 1989, Taylor and Blum 1991).

Over the past decades, it has become increasingly clear that visualizations and diagrams help in explaining and learning scientific concepts (reviewed in Phillips et al. 2010, Vavra et al. 2011). Flow diagrams and visual displays facilitate learning by distilling a complex process or phenomenon into a single "big picture" (Holliday et al. 1977). This enables rapid recognition and inference, makes the most relevant information explicit and easily identifiable (Larkin and Simon 1987), and fosters the graphic reconstruction of knowledge (Eppler 2006).

Victor (2011) uses the concept of a "ladder of abstraction" to describe the process of understanding complex concepts using visual representations. The reader can climb "down" from a very abstract domain of equations to a slightly more familiar domain of visual diagrams. Climbing further down the ladder of abstraction, one can represent elements of the model in the form of pictorial representations: diagrams that use concrete drawings, pictures, or cartoons.

Pictorial representations have many advantages over both prose and abstract diagrams. One such advantage is that they can serve as mnemonic aids (Eppler 2006). In an experiment with high school students, subjects that learned a task with a pictorial aid were more adept at remembering how to solve the task on a delayed test (Hayes and Henk 1986). In another experiment, students were better at grasping and retaining information on cell structure/function relationships when provided with a pictorial analogy (Bean et al. 1990). Another advantage is that pictures draw attention and inspire curiosity (Eppler 2006). Pictorial diagrams are also versatile, because they are not bound by strict rules or conventions. Even though the example from figure 2c is formally equivalent to the system of equations in figure 2a, this is not in general necessarily the case. For examples of pictorial diagrams that help explain models in an accessible way, see the illustrations in McElreath and Smaldino (2015) and Thompson and colleagues (2020).

Perhaps the greatest advantage of pictorial representations relates to their role in activating prior knowledge—that is, triggering associations with information that the reader already has about the objects depicted (Eppler 2006). Prior knowledge is an important determinant in learning (Johnson and Lawson 1998). Learners use prior knowledge to determine what information is relevant in a graphic, and they combine new information with prior knowledge to develop mental models (Braune and Foshay 1983, Cook 2006). Incorporating prior knowledge is particularly important in developing mathematical competence (Brownell 1928, 1935) because arithmetic procedures are often understood by mentally linking them with real-world analogues, called *concrete manipulatives* (Resnick and Ford 1981). Concrete manipulatives are mental representations or metaphors that make it possible to think about new ideas in terms of objects with which the learner is already familiar (Fuson 1992, Hiebert and Carpenter 1992). The example depicted in figure 2c might activate associations with prior knowledge of (and interest in) seed dispersal or plant ecology, whereas the (formally equivalent) abstract diagram in figure 2b may be too generic to elicit such associations.

There are, however, some drawbacks of pictorial representations. figure 2c may be *too* concrete, emphasizing tree seed dispersal at the expense of other possible interpretations of the model (e.g., dispersal by other organisms); the diagram from figure 2b, in contrast, is much more general (further up in the ladder of abstraction). Pictorial representations may also sometimes be "theoretically superfluous" (Taylor and Blum 1991, Cook 2006). That is, they may include so many arbitrary or illustrative features that they overwhelm understanding. There is a danger that readers lacking relevant schemata may focus on surface features of the illustration to the detriment of the relevant information. For example: Many representations of DNA replication use color to distinguish between the original DNA strand and the new one. In a study (Patrick et al. 2005), novice learners noted the difference in color, but, lacking prior knowledge, did not have a starting point for interpreting its meaning. Therefore, when using pictorial representations such as cartoons, it is important to strike the right balance between the abstract and the concrete.

Table 1. Summary table of recommendations.

Cognitive load	Recommendation
Increase germane load	Use metaphors and analogies
	Provide narrative context
	State assumptions and explain their purpose
	Define terms and their biological meaning
	Provide links to empirical research
Decrease extraneous load	Adjust the level of mathematical detail and use signposting
	Use consistent and intuitive notation
	Provide scripts and programs
	Visualize models and results

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