RESEARCH ARTICLE

Defining model complexity: An ecological perspective

Charlotte A. Malmborg[1] | **Alyssa M. Willson**[2] | **L. M. Bradley**[3] |
Meghan A. Beatty[4] | **David H. Klinges**[5] | **Gerbrand Koren**[6] |
Abigail S. L. Lewis[7] | **Kayode Oshinubi**[8] | **Whitney M. Woelmer**[7]

[1]Department of Earth and Environment, Boston University, Boston, Massachusetts, USA

[2]Department of Biology, University of Notre Dame, Notre Dame, Indiana, USA

[3]Program in Population Biology, Ecology, and Evolution, Emory University, Atlanta, Georgia, USA

[4]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA

[5]School of Natural Resources and Ecology, University of Florida, Gainesville, Florida, USA

[6]Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands

[7]Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia, USA

[8]School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, Arizona, USA

Correspondence
Charlotte A. Malmborg, Department of Earth and Environment, Boston University, Boston, MA, USA.
Email: malmborg@bu.edu

Abstract

Models have become a key component of scientific hypothesis testing and climate and sustainability planning, as enabled by increased data availability and computing power. As a result, understanding how the perceived 'complexity' of a model corresponds to its accuracy and predictive power has become a prevalent research topic. However, a wide variety of definitions of model complexity have been proposed and used, leading to an imprecise understanding of what model complexity is and its consequences across research studies, study systems, and disciplines. Here, we propose a more explicit definition of model complexity, incorporating four facets—model class, model inputs, model parameters, and computational complexity—which are modulated by the complexity of the real-world process being modelled. We illustrate these facets with several examples drawn from ecological literature. Overall, we argue that precise terminology and metrics of model complexity (e.g., number of parameters, number of inputs) may be necessary to characterize the emergent outcomes of complexity, including model comparison, model performance, model transferability and decision support.

KEYWORDS

ecology, evaluation, forecasting, model development, modelling, prediction

1 | INTRODUCTION

In environmental and climatological research, **models** are increasingly used to understand changes in ecosystem services and their relationship with climate, define global policy goals, and plan and prioritize climate mitigation actions in the face of rapid climate change (Geary et al., 2020; Meehl et al., 2014). Transformative advances in computing and processing power have expanded our modelling capabilities, making it possible to integrate physical, chemical, and biological processes that both influence and respond to climate and biosphere dynamics at global scales (Bonan & Doney, 2018; McCrea et al., 2023; Yeager & Danabasoglu, 2014). These advancements have enabled quantitative environmental models to incorporate data from formerly disparate fields including climatology, hydrology, cryology, atmospheric sciences, marine sciences, ecology, biogeochemistry, and socioeconomics to simulate and predict the future state of our planet and its people (Dietze et al., 2018; Solé & Levin, 2022). Beyond improving our understanding of the earth system, model results also underpin major international environmental policy and decision-making efforts such as the UN's 17 Sustainable Development Goals and the Paris Climate Agreement (IPCC, 2023; The Sustainable Development Goals Report 2022, 2022). Despite the ubiquity of modelling in research, management, and decision-making, there is a lack of common terminology in how models are described. This represents a gap in understanding among the diverse interdisciplinary community that relies on model results and outcomes.

A notable example is the inconsistent use of the terms 'simple' or 'complex' to describe models across the current scientific literature. Typical definitions of model complexity often include some combination of the number of **parameters** or **inputs** to a model, the **class** of model being employed, the model's **computational** demand, and the complexity of the natural **processes** a model represents (Evans et al., 2013; Ward et al., 2014). However, despite the number of papers that mention model complexity, we currently lack a consistent terminology that can be used to make robust comparisons between models and studies, facilitate the transfer of models to new contexts, or communicate model results across disciplines. Moreover, there has been an understandably narrow focus on complexity as it relates to a model's final structure. Here, we provide a more holistic approach to define the complexity of a model's entire construction, including the model's mathematical structure and individual components (e.g. parameters and inputs), as well as its applications and the natural processes the model represents. As environmental modellers begin to reckon with the 'cost' of model complexity

TABLE 1 Examples of minimum metrics that may be reported or compared when analysing model complexity.

Recommendations for reporting model complexity by facet	
Model Class Complexity (2.1)	• Provide a detailed model description including (but not limited to) whether a model is mechanistic, statistical or hybrid, which parameters are being used to represent natural phenomena, and justification of selected model construction(s) where applicable • Link to a model description paper and share code through an open source software repository
Parameter Complexity (2.2)	• Report number of parameters used in the model • Report number of fitted parameters estimated for the model • Describe how model parameters were estimated • Publish parameter values and uncertainties, either within manuscripts or supplemental information
Input Complexity (2.3)	• Report number of inputs used in the model • Report type of inputs used in the model (e.g., 'raw' collected data, modelled or gridded data products, forecasts or ensemble products, etc.) • Make input data available in an open-source repository
Computational Complexity (2.4)	• Report model computation times and system specifications • Report computation times for estimating parameters and uncertainties • Report number of ensemble members and uncertainties when using ensemble approaches

throughout the research process (e.g., analysis time, model transferability, predictive capacity, etc.), the wide variety and vagueness of current definitions presents a barrier to collective understanding and inhibits our ability to address complexity during model development and application. Clear and consistent terminology for describing model complexity offers a way to characterize choices made during model development and a way to compare models for various applications or intended outcomes, from theory and hypothesis generation to prediction and forecasts.

Modellers commonly attempt to make generalizations about predictive performance and its relationship with complexity, especially in considering trade-offs between
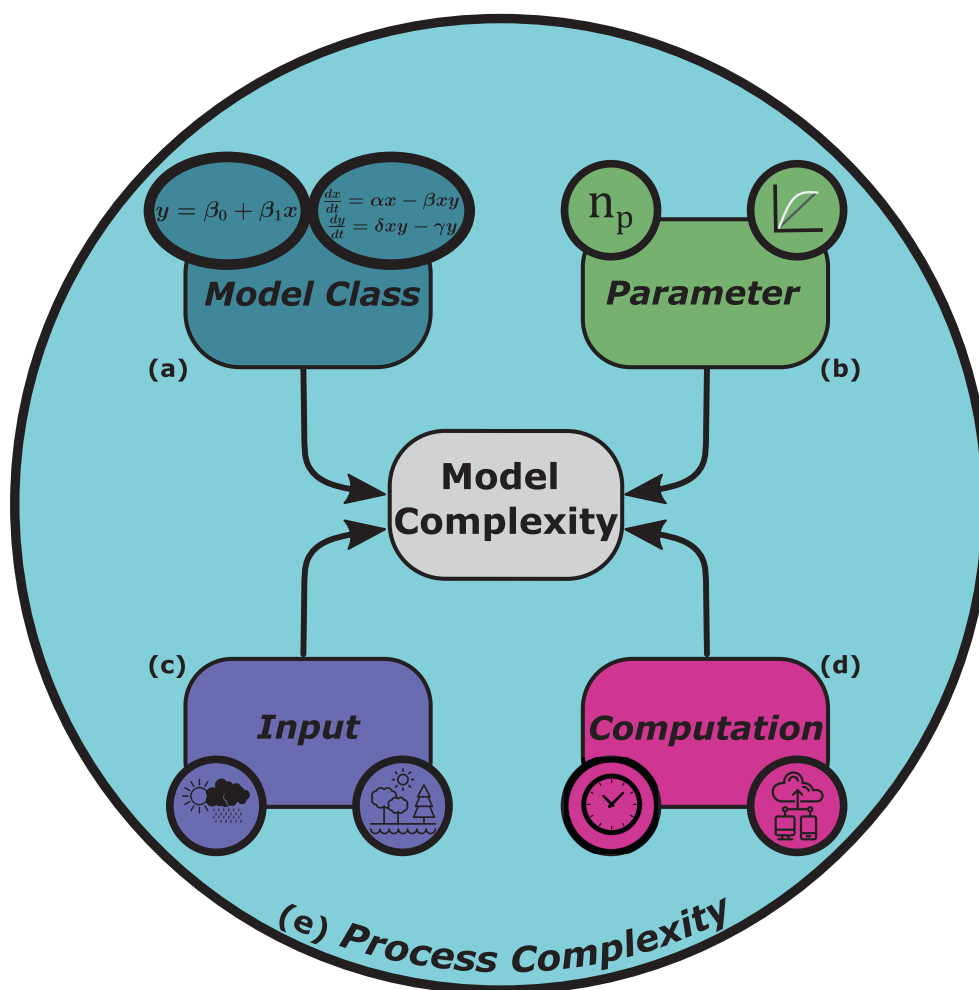
FIGURE 1 Model complexity can be decomposed into multiple components. (a) Model class (teal) complexity describes the complexity of the formulaic representation of ecological, chemical, climatological or other processes, including statistical models (left bubble, showing a linear model) and mechanistic models (right bubble, showing a Lotka–Volterra model). (b) Parameter complexity (green) comprises several components of complexity, including the number of parameters within a model (left bubble) and the nature of the relationship between driver and response variables (right bubble). (c) Input complexity (purple) defines the complexity of the variables functioning as inputs to the model, such as climatological drivers (left bubble) and initial ecosystem conditions in dynamical models (right bubble). (d) Computation complexity (pink) includes concepts such as the time required to complete a model simulation (left bubble) and the computing resources required to run the model, such as cloud computing resources (right bubble). (e) Process complexity (cyan) refers to the complexity of the system that is being modelled. While not a facet of model complexity, the underlying ecological process complexity defines and shapes the facets of model complexity.

being overly simplistic or unnecessarily complicated when representing the broad range of real-world processes and their myriad interactions (e.g., weather and climate forecasting in Scher and Messori (2019); ecological processes in Evans et al., 2013; Ward et al., 2014). This trade-off between overfitting and underfitting (e.g., the bias–variance trade-off) likely has important implications for the generalizability of models (Belkin et al., 2019; Briscoe & Feldman, 2011; Geman et al., 1992). In ecology, for instance, an increasing body of literature suggests that 'simple' models may perform as well as or better than more complex, highly parameterized models, particularly

when predicting future conditions (Chevalier & Knape, 2020; Merow et al., 2014; Ward et al., 2014). 'Complex' models can be overfit to existing data at the expense of predictive power and may be worse at predicting novel conditions (Evans et al., 2013; Yates et al., 2018). Conversely, simple models may fail to encompass some variation in the response variable, altering model-driven insight and resulting in worse predictions (Boettiger, 2022). However, a lack of terminology for defining models as simple or complex prevents a robust analysis of the impact of the bias–variance trade-off on the generalizability and predictability of models.

In this paper, we identify multiple facets of model complexity, discuss how more explicit terminology regarding model complexity may benefit the broader scientific modelling community and offer recommendations for incorporating more precise definitions of model complexity into model descriptions and comparisons (Table 1). The taxonomy we propose will be useful in two ways: (1) it provides a structure to describe choices made during model development and (2) it introduces consistent language for comparing model complexity across studies and intended applications. In practice, we view our proposed facets as a way to improve technical coherence so that researchers and practitioners may communicate effectively about different sources of model complexity and address their accompanying challenges. We outline four facets of model complexity (Figure 1) that together form a conceptual framework to facilitate a systematic assessment of a given model's complexities and outputs. While we delineate between these facets of model complexity, we also separately consider how the complexity of the natural process being modelled itself influences how complex a model needs to be to adequately represent reality. By doing so, we distinguish between complexity derived from the model itself, in which decisions about parameters, inputs, data, or structure are weighed by modellers and complexity derived from the process being modelled, which the modeller cannot influence. Further, we provide examples from the ecological literature associated with each facet as well as a case study (Box 2) to illustrate how different types of complexity impact model development and interact with one another. While model complexity is relevant to the whole of the scientific modelling community, we approach this topic from the perspective of quantitative ecology, a field that offers a wide variety of examples contrasting 'simple' and 'complex' models. Finally, we offer a brief set of recommendations to continue building upon this foundation.

2 | FACETS OF COMPLEXITY

Model complexity is often treated as a static, singular property despite arising from multiple sources during model development. These sources include model class (e.g., mechanistic vs. statistical), parameters, inputs and computation, all of which are moderated by the underlying complexity of the natural process being modelled. We maintain that each of these sources, which we describe as 'facets', introduces complexity to a model as a result of choices and trade-offs made during model development. A model's complexity, therefore, can be defined through these facets both individually and by the way they

interact with one another. Though our list of facets is not exhaustive, our aim is that the sources of complexity outlined here will spark greater discussion in the scientific community about how we define, confront, and communicate about model complexity. We define each facet in more detail below.

2.1 | Model class complexity

One key facet of model complexity is **model class** (Figure 1a), which we define as the mathematical 'scaffolding' that determines a model's overall structure and shapes how a model's parameters and inputs interact. The choice of model class entails trade-offs of generality, realism, and precision (Box 1), which are interlinked with how complex we perceive a model to be (Levins, 1966). Two general classes of model structure are **statistical models** (also colloquially interchanged with the terms *correlative*, *data-driven*, *empirical*, *phenomenological* or *pattern-based* models) and **mechanistic models** (colloquially interchanged with the term *process-based*): see Box 1 for definitions (Bolker, 2008). Statistical models seek to best quantify correlations between inputs and outputs within the domain of provided data, which may or may not be indicative of causal relationships between variables. Mechanistic models intend to mathematically represent, at least in an abstracted sense, the hypothesized processes occurring in nature, with state variables and parameters corresponding to the measures of traits and rates as they exist in the physical world. Here, we describe model class complexity to introduce how the model class may be associated, and potentially conflated, with other facets of complexity.

While model class is often referenced as a major determinant of model complexity, neither statistical nor mechanistic models are inherently more simple or complex. Some environmental scientists have posited that statistical models offer a more 'simple' alternative to heavily parameterized mechanistic models, and that the perceived added complexity when using mechanistic models (e.g., quantifying associated ecological traits and rates beyond the target variable) can decrease predictive capacity (Fordham et al., 2018; Perretti et al., 2013; Ward et al., 2014). The choice of statistical approach is vital, as some statistical models may provide linearized (i.e., 'simplified') estimates of relationships, which may have highly non-linear, idiosyncratic structures in reality or anticipate a highly non-linear (i.e., 'complex') relationship between variables that could be neatly approximated with more straightforward representations (Merow et al., 2014). Yet the legacy of ecology is also rich in mechanistic models that fall under the many definitions

BOX 1   Definitions of important terms. Definitions are consistent with (Dietze, 2017)

- **Model**: A model is a simplified representation of a system or process. Here, we specifically consider quantitative models, which represent the system or process via one or more equations with a quantitative set of inputs and outputs. Models may be stochastic, deterministic, or intermediate and may be **statistical**, **mechanistic**, or intermediate (see below).
- **Parameter**: Parameters describe the relationship between inputs and outputs of a model. When performing model fitting, parameters are the quantities that are being estimated.
- **Input**: Inputs are variables that are supplied to a model. When a model is used for prediction, the inputs are supplied to the model to predict the outputs. Inputs can be broadly divided into two classes: **drivers** and **initial conditions**. **Drivers** (also called **boundary conditions**) are variables that are considered outside of the system being modelled. For example, climatic variables are drivers of ecosystem function. **Initial conditions** are states that must be mathematically defined in the case of dynamic models. Typically, initial conditions are the value of the output variable of interest for the first time step in dynamical systems.
- **Model class**: Model class refers to whether a model is statistical or mechanistic or a hybrid incorporating features of each. **Statistical models**, such as linear regression, aim to capture correlative relationships between inputs and outputs without describing the physical or environmental processes underlying the relationship. When we refer to 'statistical' models, we also include machine learning and deep learning, as much like traditional statistical models, they employ a data-driven approach that does not attempt to capture underlying processes. **Mechanistic models**, such as many Earth system models (e.g., CESM, MIROC-ESM), mathematically imbed our knowledge of the physical or ecological system into a set of equations describing the mechanisms giving rise to observed relationships.
- **Natural process**: The naturally occurring processes that are being represented in a model.

While not a component of model complexity, real-world processes that are influenced by many earth system components or emerge from interactions between different components may lead to higher parameter, input, model class and/or computational complexity.

of 'simple' (e.g., few parameters or inputs, as detailed below; Levene, 1953; Macarthur & Wilson, 1967). Additionally, statistical models are not inherently 'less' complex, as they span many types of phenomenological modelling techniques and inputs. Thus, we contend that statistical models cannot be generally described as more complex than mechanistic models, or vice versa. For example, Coelho et al. (2019) proposed that while mechanistic models are often colloquially thought of as more complex, this can block the advancement of theory development in ecology and evolution.

Certain modelling approaches have also blended elements of both statistical and mechanistic models to form 'hybrid' approaches that leverage both abundant empirical data and established quantitative theory (Buckley et al., 2011; Peterson et al., 2015; Read et al., 2019), further muddying the typical distinction between these two model types. Mechanistic and statistical models can also be linked together in a hierarchical structure (Laubmeier et al., 2020), or a mechanistic model can be updated or calibrated using new information from statistical models (Fer et al., 2018; LeBauer et al., 2013). Hybrid approaches have been proposed as a means for efficiently capturing real environmental processes (Buckley et al., 2023; Tourinho & Vale, 2023; Zurell et al., 2016) without the high parameterization of purely mechanistic models, which may add complexity (see 'Parameter Complexity').

As a result, neither mechanistic nor statistical models are universally more complex than the other; rather, the complexity of both model classes should be evaluated based upon the set of facets unique to each model, described below. Mechanistic and statistical models differ in structure, which influences how other facets jointly determine complexity: these two classes differently shape how parameters and inputs are related, which in turn determines the computational capacity necessary for the model to run. Since model class dictates a model's overall structure, though not necessarily the total number or type of parameters or inputs in a model, we consider it a separate facet of model complexity from the others we define. Comparisons of models of different classes instead should be grounded in how statistical, mechanistic, and hybrid models yield accurate predictions or generate knowledge of underlying processes (Tourinho & Vale, 2023).

2.2 | Parameter complexity

Another common criterion by which models are classified as either simple or complex is the number and nature of parameters represented within a model (Figure 1b; Chevalier & Knape, 2020; Gerber & Kendall, 2018). Here, we define a parameter as a model value that can be estimated from data or prior knowledge and is used to quantify (in part or fully) the relationship between a driver and a response (Box 1). When classifying model complexity, the number of parameters included in a model is considered most often. For example, a statistical model such as a linear regression has at least two parameters: an intercept and a slope. Model complexity increases with each additional parameter (either including more covariates or representing interactions between covariates), up to hundreds (e.g., general circulation models predicting global climate patterns; Dunne et al., 2012) or even millions of parameters (e.g., >10 million parameters in large language models and other deep learning models; Hirn et al., 2022; Rostami et al., 2023). In one application of parameter complexity, Clark et al. (2020) used the number of parameters to demonstrate that a model of intermediate complexity (i.e., an intermediate number of parameters) produced the best out-of-sample predictions of species abundances within a grassland plant community. Similarly, Chevalier and Knape (2020) used increasing parameter number (i.e., adding environmental covariates and random site effects to a linear model) as a means to compare the complexity of different forecasts of bird abundance and found that the simplest model, an intercept-only model, where the intercept is a summation of climate effects on the bird populations, produced, on average, the most accurate forecast across species, sites and years.

Increasing the number of parameters has several important implications for a model's complexity. It does so directly, by increasing the potential for overfitting, and indirectly, by increasing the number of sources of uncertainty associated with these parameter values. Consequently, several reviews use the number of parameters to describe model complexity when highlighting the risk of overfitting models to data (Dietze, 2017; Geary et al., 2020; Merow et al., 2014; Rastetter, 2017). Parameter number is relevant for traditional model fitting as model comparison metrics often penalize statistical models based on the number of fitted parameters through degrees of freedom or likelihoods. However, users of process-based models often fit only a subset of all available parameters based on model sensitivity or data availability. As a result, many parameters may remain as constants or may be constrained by outside data, making analogous methods for penalizing based on the number of parameters difficult (although methods exist for reducing process-based model complexity using emulation; Ratto et al., 2012). In addition, the number of parameters being fit, as opposed to left as constants, in process-based models is often not reported, which can have implications for parameter identifiability and complexity. For example, when parameters are correlated with each other, multiple possible combinations of values of parameters can lead to an equally good fit, leading to equifinality (Luo et al., 2009). Altogether, these factors render comparisons of parameter complexity across model classes difficult without explicit documentation of parameter complexity.

These concepts have also appeared in empirical comparisons of model performance. For example, Rostami et al. (2023) compared the predictive accuracy of 12 deep learning models trained to classify images of pollen grains to their respective species. The authors found that when sufficiently large datasets are available, models with larger numbers of parameters (which they defined as more complex) had higher prediction accuracy than simpler models. However, when fewer data are available, the authors note that the extreme number of parameters in their most complex models (20–80 million parameters) would increase the risk of overfitting and reduce predictive accuracy.

Beyond the total number of parameters included in a model, the estimability of parameters can also influence model complexity. Estimating parameters from dynamic time series data—such as parameters for growth rates or extinction likelihoods of populations—can be difficult given that modelled process variation and unmodelled noise may operate at different temporal scales or experience time lags (Holmes et al., 2007; Lindley et al., 2003). For example, a complex model could be one with a noisy lag structure in the data that are difficult to estimate (Merow et al., 2014). Additionally, the parameter distributions (e.g., linear, exponential, quadratic) and drivers selected during estimation can modulate a model's overall complexity. For example, linear relationships tend to be the most simple to identify and evaluate, as the rate of change between variables does not depend on the value of either variable (Ruel & Ayres, 1999). In contrast, models may be more sensitive to parameters that govern non-linear relationships, increasing the ability to overfit data. A more detailed example of these considerations can be found in Box 2. While a simple definition of parameter complexity may be elusive, reporting metrics of parameter complexity can provide a more accurate and robust understanding of the implications of parameter complexity (Table 1).

MALMBORG ET AL.

Meteorological Applications
Science and Technology for Weather and Climate
Open Access

RMetS

7 of 16

2.3 | Input complexity

Another facet of model complexity concerns the model inputs (Figure 1c). Model inputs include drivers and initial conditions (Box 1), along with any other information that must be provided to the model in order for it to generate estimates of the state variable(s) and parameters. Input complexity touches on a diverse range of aspects, relating to the origin (e.g., models or observations) and nature of the input variables. Input complexity is related to parameter complexity in that an increase in the number of drivers will typically entail an increase in the number of parameters (Box 2). However, we separate input complexity from parameter complexity since the nature of given inputs places demands on modellers that necessarily increase complexity. For instance, some data may be challenging to collect due to physical constraints (i.e., effort or time required for collection) or complexity of the natural process being measured (see Section 3.4 Ecological Processes). As a result, estimating these inputs may require specialized methods or calibration, require representation by proxy rather than direct measurement or the input itself may be modelled or forecasted rather than directly measured, necessitating inclusion of specified uncertainties (Chadwick et al., 2023). For example, snow leopards (*Panthera uncia*) are elusive and difficult to monitor, and therefore proxies such as ungulate biomass have been tested in combination with camera-trap data to estimate home range size (Mccarthy et al., 2008). Often, model complexity is defined partially in terms of the number of drivers in a model (Perretti et al., 2013; Wood et al., 2020), but the complexity of the inputs themselves is often overlooked. Some input variables can be physically measured in the field or the lab (e.g., current air temperature), whereas others are necessarily from models (e.g., historical 2-m air temperature from climate reanalyses). Key features of input data are the spatial and temporal resolution, which can range across orders of magnitude. Higher spatial or temporal resolution usually entails higher complexity by representing more heterogeneity in space and time and requiring increased storage, memory, and/or computational power (see 'Computational Complexity'). This in turn may demand more time from researchers to process and analyse larger volumes of data (Jain et al., 2022). For specific cases, new methods are being introduced to effectively handle large datasets (Fer et al., 2018).

Other practical complexities relate to the infrastructure to read input files. Ideally, input data that conform to community standards (e.g., CF-conventions for NetCDF-files, or more specifically for ecological forecasting the EFI community standards, Dietze et al., 2023) can reduce the complexity of required data processing or curation. Also, the different licenses of data can

---

BOX 2 Facets of model complexity illustrated via an eco-epidemiological case study

Chronic wasting disease (CWD) is a contagious prion disease affecting animals within the family *Cervidae* (e.g., deer), causing irreversible and fatal neurological damage. It can only be diagnosed during autopsy, posing real-time challenges for disease and wildlife ecologists when building forecasts to evaluate different management intervention scenarios. The ecological processes driving CWD transmission are notoriously complicated to describe accurately (Ladeau, 2010), as they depend on animal traits (e.g., age and sex), spatial aggregation and transmission events occurring even after host death (Miller & Conner, 2005).

Beyond the underlying ecological process complexity, modelling CWD transmission and forecasting outbreaks across space and time is technically difficult from a modelling workflow perspective. This historically led to debate among researchers and managers on how to select contextually appropriate levels and layers of model complexity, as highlighted in a 2010 *Ecology* forum (Heisey et al., 2010a, 2010b; Hodges, 2010; Ladeau, 2010; Lavine, 2010; Lele, 2010; Waller, 2010). Below, we include where we believe our proposed model complexity facets might have improved clarity and allowed for important nuance to emerge, which are important for tackling the challenges from a multidisciplinary approach. The forum focused on the value of model complexity in CWD research and management, spurred by a 'complex' model first published by Heisey et al. in *Ecological Monographs* (2010) that used a hierarchical Bayesian semiparametric nested model approach. The forum broached both gritty technical details and philosophical discourse to critique Heisey et al.'s article, with the forum's other authors making arguments about the validity of each layer of complexity in the model. While this forum was extremely informative, many of the arguments for or against model complexity discussed were not mutually exclusive and could have potentially led to more emergent discussion if the model complexity had been defined more explicitly via partitioning into distinct facets.

8 of 16

Meteorological Applications
Science and Technology for Weather and Climate
Open Access

RMetS

MALMBORG ET AL.

Model class complexity

Heisey et al. (2010a) presented a predominantly mechanistic, hierarchical Bayesian model to forecast outbreaks and identify the driving ecological processes, arguing that CWD management requires a process-based approach to link relevant ecological traits to expected outcomes. However, the authors were criticized for selecting this process-rich, mechanistic model (often considered more complex) over statistical models that did not attempt to explain as many unobservable processes (Lele, 2010). One of the main conclusions that emerged from this back-and-forth discussion was that it is best to pick an approach that relies on the least number of untested assumptions about underlying processes (Ladeau, 2010) when balancing model class complexity and performance, and those hybrid models, or multi-model inference, are likely needed to reach parsimony (Waller, 2010).

The tension between mechanistic and statistical models is not unique to this forum, but the forum's take-home messages fall victim in a manner similar to the historical debates about model class complexity. If the forum had identified which mechanisms were *critical* to include for capturing the underlying ecological processes (i.e., perhaps through nested scenario modelling) and where simpler phenomenological patterns would suffice, this might have addressed the underlying concerns more effectively and mitigated much discussion. Heisey et al.'s hierarchical model approach is indeed well-suited for this type of selection since it marries different model classes, as noted by Waller. However, the discussion between model class and parameter complexity was understandably muddled at times, as they are intricately related. This detracted from the important distinction of how and where process and mechanism are best justified to model underlying ecological processes, and using distinct facets to guide discussion could have improved clarity.

Parameter complexity

One of the most controversial aspects of Heisey et al. (2010a) model was the seemingly high dimensionality of their parameter space, which was being fit to limited observational data. However, Heisey et al. noted in their article that identifying model complexity based on the number of parameters in their model was misleading, as not all of their parameters were independent due to spatial dependencies. Other forum authors challenged the underlying hypotheses/processes in the Heisey et al. model, arguing that since the model relied on potentially inestimable parameters, it would ultimately produce misleading predictions (Lele, 2010). Heisey et al. explained in their rejoinder that while using frequentist statistical methods they would have fixed, large parameter spaces to fit. Due to their hierarchical Bayesian approach, the parameter complexity of their model was not pre-determined and was simpler than the readers might have originally thought (Heisey et al., 2010b).

Heisey et al. and the other forum contributors had insightful discussions about the intricacies of parameter complexity and thoroughly explained the technical and philosophical reasoning behind decisions and critiques. This is not terribly surprising, given that reporting parameter complexity decisions is already integrated within model literature culture. However, using distinct facets of model complexity would have allowed the forum members (and the readers) to identify where trade-offs may be needed between these specific facets, as opposed to lumping all of the critiques mostly into parameter-focused discussions.

Input complexity

CWD transmission is difficult to forecast in large part due to the high-dimensional input data that spans gaps in space and time (Farnsworth et al., 2005). This is especially true for integrating spatial data of cervid demographics and temporal infection dynamics with minimized uncertainty (Heisey et al., 2010a). Heisey et al. point out that what must be modelled suffers from an 'inverse problem': the idea that the observed data (i.e., hunter harvest data) is used to extract the traditional model 'input' as a parameter. Essentially, a major barrier of this work is estimating latent transmission processes and rates, which they approached using their hierarchical Bayesian model framework. As both Heisey et al. and LaDeau discuss, the input data required for the model may be beyond the capabilities of the managers to collect. Thus, the complexity of the input data *practically* put the utility of the model in question for future applied use, which was eloquently captured by LaDeau: 'Are the efforts of designing models to more accurately characterize our understanding of processes and data mechanisms wasted if they cannot be used to manage the epidemic?'

However, much of the discussion did not center on this particular nuance and instead focused

on what amounts to critiques of parameter complexity. While important to discuss, distinguishing between parameter and input complexities would be particularly useful here. Doing so would separate the spatial processes associated with CWD and the statistical methods needed to model around the data gaps (Hodges, 2010) from issues around parameterization. Similar to the discussions on model class and parameter complexity, this supports how the facets relate to and interact with one another while allowing modellers to independently improve either or both without conflating the two.

Computational complexity

Heisey et al.'s model required significant computing power, which was acknowledged by (Hodges, 2010), who jokingly commented about the week-long run times. While discussed in the forum, it was the least critiqued facet of the model's complexity. However, the forum's authors approached this topic from a research standpoint, with little input from potential model end-users. Therefore, it is conceivable that practitioners with different priorities, such as managers using forecasts to apply CWD interventions, may be more concerned with computational complexity (due to constraints with time or personnel expertise). Additionally, if the model is altered by other research groups and becomes more complex, having access to appropriate computational power could be the difference between being able to use the model or not.

Overall, the importance of computational complexity is acknowledged in the forum, but the details of which are only briefly eluded to. Having space set aside to explicitly report and discuss this type of complexity would be especially beneficial for translation of this research to other fields of study or in applied settings in the future.

Conclusion

This case study exemplifies how these rigorous discussions about model complexity could be more informative for a broader swath of readers by implementing facets of model complexity as anchors for discussion. This strategy is not just beneficial to disease ecologists: similar discourse across disciplines, especially at the climate–environment interface, could benefit from compartmentalizing model complexity using the four facets we outline in this paper. This would allow researchers to identify trade-offs more clearly between different types of model complexity that are often conflated but are not mutually exclusive, improving our

fundamental understanding of nature and increasing model utility in applied settings.

complicate the use of certain datasets since data can be released under restrictive conditions that should be considered and respected.

A further complication related to input data is the distribution of data over time or space, which could be irregular. Gaps in time series or non-uniform spatial distribution, that are often resulting from the deployment of the measurement networks or malfunctioning of equipment, are typical examples that models are faced with. Gaps in time series require gap-filling strategies (e.g., Lucas-Moffat et al., 2022 show this for gas exchange measurements over vegetated surfaces), and the non-uniform distribution of measurement networks might require different weighting or extrapolation strategies. Specifically, gaps that are not randomly distributed (e.g., data on small-bodied organisms may be sparse relative to large-bodied organisms due to differences in detection ability) can be more accurately filled by modelling the relevant ecological process (Bowler et al., 2023; Taugourdeau et al., 2014). However, the inclusion of models and interpolation for gap-filling increases overall model complexity as both the number of steps required to estimate the data and the overall uncertainty in the data increase.

For input complexity, as in all facets of complexity, there are trade-offs between model complexity and usability. To help model developers and model users make sensible choices about which variables to include or not, sensitivity studies or feature importance analyses can provide useful information. Marolla et al. (2021) created near-term forecasts and explanatory models of rock ptarmigan population monitoring data from high-arctic Svalbard and found that including additional ecological input data substantially improved model performance. Similarly, Tramontana et al. (2016), who modelled carbon and energy exchange over ecosystems using a machine learning approach with remote sensing data, tested how model performance increases when adding meteorological data sets (including ERA-Interim, Dee et al., 2011). These examples illustrate how the input complexity can be systematically assessed, which can then inform selecting the appropriate input complexity level.

2.4 | Computational complexity

Another key aspect of model complexity is computational complexity (Figure 1d). This relates to the software

required to construct and execute a model, the cyberinfrastructure necessary to run it, and the amount of time needed for completion (Green et al., 2005). Such aspects of complexity are not always intrinsic to the model but may be defined by the data, the degree of rigour taken for model fitting and validation and how the model is employed. Nonetheless, computational needs have long been considered in ecology (Wiegert, 1975) and are an important consideration when evaluating trade-offs between models.

There are several aspects of a model workflow, which may determine the computational time. For statistical models, fitting relationships between parameters and response(s) can be time-consuming, especially when there are many parameters (or hyperparameters) to be fitted or relationships between predictors and responses are non-linear ('Parameter Complexity'). In some process-based models, parameters that are not defined by prior or current observations may require numerical solution ('guess-and-check') methods such as maximum likelihood estimation, which can be computationally costly. For instance, numerical weather prediction—a notoriously complicated set of procedures—has historically relied on numerical methods for estimating certain parameters in differential equations (Bauer et al., 2015). In other situations, state variable uncertainty estimation in process-based models is achieved via ensemble-based approaches (i.e., running the process model for hundreds or even thousands of independent simulations), which increases the computational complexity of the modelling workflow, but not of the model itself.

Similarly, the posterior distribution of hierarchical models often must be approximated numerically via Markov Chain Monte Carlo (MCMC) algorithms or advanced techniques such as inverse nested Laplace approximation. For all of these model fitting procedures, the number of observations used to fit the model can influence computation time, with larger numbers of observations leading to longer computation times (Guihenneuc-Jouyaux & Rousseau, 2005), although nested Laplace approximation has the potential to reduce computational burden (Rue et al., 2009). Model validation can also be resource intensive, especially when model predictions need to be tested separately across spatial and temporal domains (e.g., via leave-one-out cross-validation, Cho et al., 2020). For the case of forecasting species abundance in an ecosystem, Perretti et al. (2013) describe the potentially lengthy computation time of highly parameterized mechanistic models as one reason to instead try a model-free forecasting method.

In some cases, the computational complexity can be controlled by the model user by switching certain modules on or off (Smallman et al., 2021), or by adjusting the number of ensembles in a forecasting model. In such a setting, the larger number of ensembles typically increases execution time and thus the model complexity. In some cases, parallelization is a possibility, but this might involve the use of additional libraries (e.g., Dask, MPI, OpenMP) and thereby introduce additional complexity. Being able to adjust a model's settings such as the number of ensemble members provides the modeler control over the computational complexity, but having to make this decision each time in itself also contributes to a model's complexity from the user perspective.

3 | ECOLOGICAL PROCESSES

Models serve as simplified representations of real-world processes (Box 1), and the real-world complexity of the **natural process** (i.e., ecological process) being modelled has implications when drawing conclusions about model complexity. For example, consider a hypothetical case where the population of an R-selected species, tadpoles in a lake, depends exclusively upon two factors: reproductive rate and water temperature. In this case, a model that *also* includes a third driver (e.g., fish density) may be overly complex. Conversely, in a case where fish populations and aquatic vegetation play important roles in determining tadpole populations, a model that only includes reproductive rate and water temperature could instead be overly simple.

In reality, quantifying *all* relevant inputs and parameters for any real-world ecological process is impossible, or nearly so. Consequently, efforts have been made to generalize the real-world complexity of the variable being modelled in other ways. Literature across economics, meteorology and, more recently, ecological forecasting suggests that variables that are aggregated over larger spatial, temporal, or taxonomic scales may be more predictable (Hoffmann et al., 2015; Levin, 1987; Lewis et al., 2023; McLeod & Leroux, 2021; Noda, 2004; Wedi, 2014 and references therein). That is, models perform better when they predict a 'simpler' variable that averages across the variability of sub-components (e.g., total phytoplankton biomass rather than the biomass of an individual species of phytoplankton). Additionally, some attempts have been made to describe different *types* of variables as generally being simpler or more complex (Soares & do Carmo Calijuri, 2021). For example, does complexity increase hierarchically from physical variables to chemical variables to biological variables, which are shaped in part by physics, chemistry, and ecology? To more quantitatively analyse the complexity of time series data, statistical entropy metrics have been developed (e.g., permutation entropy, multiscale

entropy) that define complexity as the extent to which patterns re-appear in data (Bandt & Pompe, 2002). Ultimately, these continued efforts to identify axes of variation that characterize the complexity of ecological data highlight the important role that real-world ecological complexity can play in the interpretation and formulation of model complexity.

4 | CONCLUSION

Across a broad range of ecological studies, the concept of model complexity is commonly used to guide decisions about model development and selection and explain model outcomes and performance. Yet definitions of model complexity are inconsistent, preventing the scientific community from making direct comparisons between models or effectively communicating and acting on model outcomes. Given that consistent terminology is critical for advancing research directives across disciplines (Lélé & Norgaard, 2005; Robinson et al., 2016), defining model complexity may be particularly important within ecology and climatology, where interdisciplinary collaboration is increasingly the norm (Goring et al., 2014).

Delineating between different aspects of model complexity provides several benefits to the environmental modelling community. First, we aim for our definitions to assist hypothesis generation. Models represent our current understanding of how ecosystems function and are explicit representations of quantifiable scientific hypotheses (Dietze et al., 2013; Lewis et al., 2023). Therefore, additional nuance describing model complexity may help guide the hypotheses we make, as well as help us reject or reimagine unsupported hypotheses. While our ideas on this topic are shaped by the authors' perspectives from predictive modelling in ecology, models used for theoretical and phenomenological approaches may have different relationships with complexity. For instance, Edmonds (2017) encourages modellers to think of models as tools for specific applications and lays out five model purposes (prediction, explanation, theoretical exposition, description and illustration) with different motivations and associated needs for development. In thinking of models as tools for each of these purposes, we anticipate that these distinctions will also enable us to pinpoint common sources of complexity that arise when using particular methods or when working within specific ecosystems. Instead of asking 'is this model simple or complex?' the more comprehensive distinctions of model complexity outlined here allow us to ask questions about which types of models or which natural processes are more likely to be associated with each facet of complexity and how we might address those complexities. The categories we have

specified, while distinct from one another, are also interrelated, whereby increased complexity in one class may propagate to additional complexity in another facet (e.g., higher input resolution requiring more computational power). Identifying patterns in these relationships will enable us to tackle the broader fundamental questions about predictability and generality in ecology.

Second, more unified definitions of complexity, whether arising from the number of parameters, type of input data used, computational costs, or chosen model help us better navigate the model selection process. By evaluating model complexity in a holistic fashion, we are more likely to be aware of our models' flaws or shortcomings, helping us to settle for 'good enough' models rather than continuing towards an unachievable 'perfect' model. Identifying aspects of model complexity in competing models is an opportunity to examine pros and cons of using different models in different contexts (Rostami et al., 2023) and provides additional metrics by which to evaluate trade-offs when deciding which models to use. As such, these facets of complexity act as a way to discern where additional complexity may be useful or may be mitigated during model development.

Beyond choosing a model for a single application, patterns in model complexity may also help make models more transferable when adapting an existing model to a species, ecosystem, geographic region, or management context. Indeed, it has been proposed that, structurally, simpler models (e.g., models of a particular class or models with fewer parameters) may be more transferable than highly parameterized models, since those more complex models are more likely to include time- or location-specific information (Lewis et al., 2023; Wenger & Olden, 2012). For out-of-sample predictions, process-based models are thought to perform better than empirical models (Lewis et al., 2023), but these models may come at the cost of additional parameter, input or computational complexity, and it remains unknown how model class and other aspects of model complexity interact to influence the transferability of various ecological models. Being aware of which aspects of complexity are present or that arise when adapting existing modelling frameworks to new applications may facilitate these transfers to new contexts, revealing relationships between model complexity and performance, as well as showing how 'good enough' models may be improved for different scenarios.

Lastly, these distinct facets could make translation of models and their results more approachable across the systems or fields in which they are employed. When engaging in coproduction or interdisciplinary research, it is critical to develop shared concepts and goals that can span a team's respective disciplines to avoid the barriers

introduced by linguistic divides (Dietze et al., 2018; Eigenbrode et al., 2007; Read et al., 2016). Shared terminology offers us a foundation from which to better communicate model outcomes and trade-offs, particularly when moving models from initial development to application. A common lexicon for model complexity may also serve to confront underlying assumptions about 'simplicity' and 'complexity' held by researchers from different disciplines, easing collaboration among scholars who may typically use different types of models or models with different applications in mind.

Our attempt to refine our notions of model complexity is not exhaustive, but we hope that this initial discussion of the facets of complexity prompts an ongoing, informed conversation on how we describe and compare models in the future. We have taken care not to imply a hierarchy among our defined facets of complexity. Though appealing, we feel that establishing a hierarchy may not be generalizable and, depending on the specific case or modelling approach, may be challenging or even impossible. Indeed, it is likely that any hierarchy that arises may only be evaluated based on the scientific questions or aims of a given project. Ultimately, we strove to provide a framework that is more generalizable and holistic to reduce collective uncertainty about how complexity is defined or derived when using models and reporting their outcomes.

5 | RECOMMENDATIONS

We conclude this paper with recommendations to build upon the foundation we provide for describing model complexity (Table 1). First, we suggest researchers and model developers describe their model in terms of multiple facets of complexity where possible. Specifically defining multiple facets of complexity, rather than terming a model 'simple' or 'complex', will enable readers to better understand the model's behaviour, outputs, advantages, and limitations. For applications beyond research, we assert that identifying model complexities explicitly will allow practitioners to make better judgements about which models to use for different applications or management scenarios, streamlining the model development to model implementation pipeline. Second, we recommend that researchers report metrics associated with each facet of complexity where applicable. At a minimum, this should include reporting a description of the model class (e.g., maximum entropy machine learning model), the number and source of inputs (e.g., whether inputs are themselves modelled data products), the number of parameters in the model, the computational time required to fit or run the model, along with specifications

of the hardware on which the model was run (computer processor, central processing unit or graphics processing unit set-up, RAM per node and parallelization; Tredennick et al., 2016). Computationally expensive models or models with many parameters or inputs may require appropriate expertise or infrastructure to run, and reporting on computational times and capacities required for using individual models will allow modellers to account for trade-offs when deciding between different methods. We also suggest that researchers publish code, model data, and metadata in open source repositories (e.g., GitHub, the Environmental Data Initiative repository, etc.) and use consistent conventions when doing so (e.g., using Ecological Metadata Language (EML), Ecological Forecasting Initiative community standards, etc.). These recommendations align with efforts that address the ongoing reproducibility crisis in science, mirroring suggested best practices for managing and reusing datasets and code, such as providing clear documentation and metadata (Goodman et al., 2014; Wilkinson et al., 2016). Lastly, we hope that the community continues to refine the distinctions we have provided, especially with perspectives from fields beyond ecology that reflect the diverse community developing and engaging with models.

The historical lack of formal definitions of model complexity is a barrier to model comparison, transferability, and operationalization. In particular, as research teams broaden participation to tackle interdisciplinary projects, a unified understanding of modelling terms and ideas that are descriptive and approachable will prove essential. While we approached this task from the perspective of quantitative ecology, we see these distinct facets of model complexity as applicable broadly among modellers. In opening this conversation to other model developers and users, we hope to draw attention to the missing ideology in climate and environmental modelling and create opportunities for more discussions on this topic.

AUTHOR CONTRIBUTIONS

Charlotte A. Malmborg: Conceptualization (equal); supervision (lead); writing – original draft (equal); writing – review and editing (equal). **Alyssa M. Willson:** Conceptualization (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **L. M. Bradley:** Conceptualization (equal); writing – original draft (lead); writing – review and editing (equal). **Meghan A. Beatty:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **David H. Klinges:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Gerbrand Koren:**

Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Abigail S. L. Lewis:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Kayode Oshinubi:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Whitney M. Woelmer:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal).

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

ORCID

Charlotte A. Malmborg https://orcid.org/0000-0001-6407-3637

REFERENCES

Bandt, C. & Pompe, B. (2002) Permutation entropy: a natural complexity measure for time series. *Physical Review Letters*, 88(17), 4. Available from: https://doi.org/10.1103/PhysRevLett.88.174102

Bauer, P., Thorpe, A. & Brunet, G. (2015) The quiet revolution of numerical weather prediction. *Nature*, 525(7567), 47–55. Available from: https://doi.org/10.1038/nature14956

Belkin, M., Hsu, D., Ma, S. & Mandal, S. (2019) Reconciling modern machine-learning practice and the classical bias– variance trade-off. *Proceedings of the National Academy of Sciences*, 116(32), 15849–15854. Available from: https://doi.org/10.1073/pnas.1903070116

Boettiger, C. (2022) The forecast trap. *Ecology Letters*, 25(7), 1655–1664. Available from: https://doi.org/10.1111/ele.14024

Bolker, B.M. (2008) *Ecological models and data in R*. Princeton, NJ: Princeton University Press. Available at: http://press.princeton.edu/titles/8709.html [Accessed 30th October 2019]

Bonan, G.B. & Doney, S.C. (2018) Climate, ecosystems, and planetary futures: the challenge to predict life in earth system models. *Science*, 359(6375), eaam8328. Available from: https://doi.org/10.1126/science.aam8328

Bowler, D., Boyd, R., Callaghan, C., Robinson, R., Isaac, N., Pocock, M. (2023) Treating gaps and biases in biodiversity data as a missing data problem. Available at: https://ecoevorxiv.org/repository/view/6122/ [Accessed 8th February 2024]

Briscoe, E. & Feldman, J. (2011) Conceptual complexity and the bias/variance tradeoff. *Cognition*, 118(1), 2–16. Available from: https://doi.org/10.1016/j.cognition.2010.10.004

Buckley, L.B., Carrington, E., Dillon, M.E., García-Robledo, C., Roberts, S.B., Wegrzyn, J.L. et al. (2023) Characterizing biological responses to climate variability and extremes to improve biodiversity projections. *PLOS Climate*, 2(6), e0000226. Available from: https://doi.org/10.1371/journal.pclm.0000226

Buckley, L.B., Waaser, S.A., MacLean, H.J. & Fox, R. (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology*, 92(12), 2214–2221. Available from: https://doi.org/10.1890/11-0066.1

Chadwick, F.J., Haydon, D.T., Husmeier, D., Ovaskainen, O. & Matthiopoulos, J. (2023) LIES of omission: complex observation processes in ecology. *Trends in Ecology & Evolution*, 39, 368–380. Available from: https://doi.org/10.1016/j.tree.2023.10.009

Chevalier, M. & Knape, J. (2020) The cost of complexity in forecasts of population abundances is reduced but not eliminated by borrowing information across space using a hierarchical approach. *Oikos*, 129(2), 249–260. Available from: https://doi.org/10.1111/oik.06401

Cho, D., Yoo, C., Im, J. & Cha, D.H. (2020) Comparative assessment of various machine learning-based bias correction methods for numerical weather prediction model forecasts of extreme air temperatures in urban areas. *Earth and Space Science*, 7(4), e2019EA000740. Available from: https://doi.org/10.1029/2019EA000740

Clark, A.T., Ann Turnbull, L., Tredennick, A., Allan, E., Harpole, W.S., Mayfield, M.M. et al. (2020) Predicting species abundances in a grassland biodiversity experiment: trade-offs

between model complexity and generality. *Journal of Ecology*, 108(2), 774–787. Available from: https://doi.org/10.1111/1365-2745.13316

Coelho, M.T.P., Diniz-Filho, J.A. & Rangel, T.F. (2019) A parsimonious view of the parsimony principle in ecology and evolution. *Ecography*, 42(5), 968–976. Available from: https://doi.org/10.1111/ecog.04228

Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S. et al. (2011) The ERA-interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society*, 137(656), 553–597. Available from: https://doi.org/10.1002/qj.828

Dietze, M.C. (2017) Prediction in ecology: a first-principles framework: a. *Ecological Applications*, 27(7), 2048–2060. Available from: https://doi.org/10.1002/eap.1589

Dietze, M.C., Fox, A., Beck-Johnson, L.M., Betancourt, J.L., Hooten, M.B., Jarnevich, C.S. et al. (2018) Iterative near-term ecological forecasting: needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences*, 115(7), 1424–1432. Available from: https://doi.org/10.1073/pnas.1710231115

Dietze, M.C., Lebauer, D.S. & Kooper, R. (2013) On improving the communication between models and data. *Plant, Cell & Environment*, 36(9), 1575–1585. Available from: https://doi.org/10.1111/pce.12043

Dietze, M. C., Thomas, R. Q., Peters, J., Boettiger, C., Koren, G., Shiklomanov, A. N., & Ashander, J. (2023) A community convention for ecological forecasting: Output files and metadata version 1.0. *Ecosphere*, 14(11), e4686. https://doi.org/10.1002/ecs2.4686

Dunne, J.P., John, J.G., Adcroft, A.J., Griffies, S.M., Hallberg, R.W., Shevliakova, E. et al. (2012) GFDL's ESM2 global coupled climate–carbon earth system models. Part I: physical formulation and baseline simulation characteristics. *Journal of Climate*, 25(19), 6646–6665. Available from: https://doi.org/10.1175/JCLI-D-11-00560.1

Edmonds, B. (2017) Different modelling purposes. In: Edmonds, B. & Meyer, R. (Eds.) *Simulating social complexity: a handbook*. Cham: Springer International Publishing, pp. 39–58. Available from: https://doi.org/10.1007/978-3-319-66948-9_4

Eigenbrode, S.D., O'rourke, M., Wulfhorst, J.D., Althoff, D.M., Goldberg, C.S., Merrill, K. et al. (2007) Employing philosophical dialogue in collaborative science. *Bioscience*, 57(1), 55–64. Available from: https://doi.org/10.1641/B570109

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M. et al. (2013) Do simple models lead to generality in ecology? *Trends in Ecology & Evolution*, 28(10), 578–583. Available from: https://doi.org/10.1016/j.tree.2013.05.022

Farnsworth, M.L., Wolfe, L.L., Hobbs, N.T., Burnham, K.P., Williams, E.S., Theobald, D.M. et al. (2005) Human land use influences Chronic Wasting disease Prevalence in Mule deer. *Ecological Applications*, 15(1), 119–126. Available from: https://doi.org/10.1890/04-0194

Fer, I., Kelly, R., Moorcroft, P.R., Richardson, A.D., Cowdery, E.M. & Dietze, M.C. (2018) Linking big models to big data: efficient ecosystem model calibration through Bayesian model emulation. *Biogeosciences*, 15(19), 5801–5830. Available from: https://doi.org/10.5194/bg-15-5801-2018

Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Neto, D., Brown, S.C. et al. (2018) How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, 24(3), 1357–1370. Available from: https://doi.org/10.1111/gcb.13935

Geary, W.L., Bode, M., Doherty, T.S., Fulton, E.A., Nimmo, D.G., Tulloch, A.I.T. et al. (2020) A guide to ecosystem models and their environmental applications. *Nature Ecology & Evolution*, 4(11), 1459–1471. Available from: https://doi.org/10.1038/s41559020-01298-8

Geman, S., Bienenstock, E. & Doursat, R. (1992) Neural networks and the bias/variance dilemma. *Neural Computation*, 4(1), 1–58. Available from: https://doi.org/10.1162/neco.1992.4.1.1

Gerber, B.D. & Kendall, W.L. (2018) Adaptive management of animal populations with significant unknowns and uncertainties: a case study. *Ecological Applications*, 28(5), 1325–1341. Available from: https://doi.org/10.1002/eap.1734

Goodman, A., Pepe, A., Blocker, A.W., Borgman, C.L., Cranmer, K., Crosas, M. et al. (2014) Ten simple rules for the care and feeding of scientific data. *PLoS Computational Biology*, 10(4), e1003542. Available from: https://doi.org/10.1371/journal.pcbi.1003542

Goring, S.J., Weathers, K.C., Dodds, W.K., Soranno, P.A., Sweet, L.C., Cheruvelil, K.S. et al. (2014) Improving the culture of interdisciplinary collaboration in ecology by expanding measures of success. *Frontiers in Ecology and the Environment*, 12(1), 39–47. Available from: https://doi.org/10.1890/120370

Green, J. L., Hastings, A., Arzberger, P., Francisco, J.A., Cottingham, K. L., Cuddington, K., Davis, F., Dunne, J.A., Fortin, M-J., Gerber, L., Neubert, M. (2005) Complexity in ecology and conservation: mathematical, statistical, and computational challenges. *Bioscience*, 55(6), 501–510. Available from: https://doi.org/10.1641/0006-3568(2005)055[0501:CIEACM]2.0.CO;2

Guihenneuc-Jouyaux, C. & Rousseau, J. (2005) Laplace expansions in Markov chain Monte Carlo algorithms. *Journal of Computational and Graphical Statistics*, 14(1), 75–94.

Heisey, D.M., Osnas, E.E., Cross, P.C., Joly, D.O., Langenberg, J.A. & Miller, M.W. (2010a) Linking process to pattern: estimating spatiotemporal dynamics of a wildlife epidemic from cross-sectional data. *Ecological Monographs*, 80(2), 221–240. Available from: https://doi.org/10.1890/09-0052.1

Heisey, D.M., Osnas, E.E., Cross, P.C., Joly, D.O., Langenberg, J.A. & Miller, M.W. (2010b) Rejoinder: sifting through model space. *Ecology*, 91(12), 3503–3514. Available from: https://doi.org/10.1890/10-0894.1

Hirn, J., García, J.E., Montesinos-Navarro, A., Sánchez-Martín, R., Sanz, V. & Verdú, M. (2022) A deep generative artificial intelligence system to predict species coexistence patterns. *Methods in Ecology and Evolution*, 13(5), 1052–1061. Available from: https://doi.org/10.1111/2041-210X.13827

Hodges, J.S. (2010) Are exercises like this a good use of anybody's time? *Ecology*, 91(12), 3496–3500. Available from: https://doi.org/10.1890/10-0052.1

Hoffmann, H., Zhao, G., van Bussel, L., Enders, A., Specka, X., Sosa, C. et al. (2015) Variability of effects of spatial climate data aggregation on regional yield simulation by crop models. *Climate Research*, 65, 53–69. Available from: https://doi.org/10.3354/cr01326

Holmes, E.E., Sabo, J.L., Viscido, S.V. & Fagan, W.F. (2007) A statistical approach to quasi-extinction forecasting. *Ecology Letters*, 10(12), 1182–1198. Available from: https://doi.org/10.1111/j.1461-0248.2007.01105.x

IPCC. (2023) Climate change 2023: Synthesis report. In: Core Writing Team, Lee, H. & Romero, J. (Eds.) *Contribution of working groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change* (p. 184). IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647

Jain, S., Mindlin, J., Koren, G., Gulizia, C., Steadman, C., Langendijk, G.S. et al. (2022) Are we at risk of losing the current generation of climate researchers to data science? *AGU Advances*, 3(4), e2022AV000676. Available from: https://doi.org/10.1029/2022AV000676

Ladeau, S. (2010) Advances in modeling highlight a tension between analytical accuracy and accessibility. *Ecology*, 91(12), 3488–3492. Available from: https://doi.org/10.1890/09-2249.1

Laubmeier, A.N., Cazelles, B., Cuddington, K., Erickson, K.D., Fortin, M.J., Ogle, K. et al. (2020) Ecological dynamics: integrating empirical, statistical, and analytical methods. *Trends in Ecology & Evolution*, 35(12), 1090–1099. Available from: https://doi.org/10.1016/j.tree.2020.08.006

Lavine, M. (2010) Living dangerously with big fancy models. *Ecology*, 91(12), 3487. Available from: https://doi.org/10.1890/10-1124.1 3487; discussion 3514.

LeBauer, D.S., Wang, D., Richter, K.T., Davidson, C.C. & Dietze, M.C. (2013) Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs*, 83(2), 133–154. Available from: https://doi.org/10.1890/120137.1

Lélé, S. & Norgaard, R.B. (2005) Practicing interdisciplinarity. *Bioscience*, 55(11), 967–975. Available from: https://doi.org/10.1641/0006-3568(2005)055[0967:PI]2.0.CO;2

Lele, S.R. (2010) Model complexity and information in the data: could it be a house built on sand? *Ecology*, 91(12), 3493–3496. Available from: https://doi.org/10.1890/10-0099.1

Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *The American Naturalist*, 87(836), 331–333. Available from: https://doi.org/10.1086/281792

Levin, S.A. (1987) Scale and predictability in ecological modeling. In: Vincent, T.L. et al. (Eds.) *Modeling and Management of Resources under uncertainty*. Berlin, Heidelberg: Springer (Lecture Notes in Biomathematics), pp. 2–10. Available from: https://doi.org/10.1007/978-3-64293365-3_1

Levins, R. (1966) The strategy of model building in population biology. *American Scientist*, 54(4), 421–431.

Lewis, A.S.L., Rollinson, C.R., Allyn, A.J., Ashander, J., Brodie, S., Brookson, C.B. et al. (2023) The power of forecasts to advance ecological theory. *Methods in Ecology and Evolution*, 14(3), 746–756. Available from: https://doi.org/10.1111/2041210X.13955

Lindley, J.A., Reid, P.C. & Brander, K.M. (2003) Inverse relationship between cod recruitment in the North sea and young fish in the continuous plankton recorder survey. *Scientia Marina*, 67(S1), 191–200. Available from: https://doi.org/10.3989/scimar.2003.67s1191

Lucas-Moffat, A.M., Schrader, F., Herbst, M. & Brümmer, C. (2022) Multiple gap-filling for eddy covariance datasets. *Agricultural and Forest Meteorology*, 325, 109114. Available from: https://doi.org/10.1016/j.agrformet.2022.109114

Luo, Y., Weng, E., Wu, X., Gao, C., Zhou, X. & Zhang, L. (2009) Parameter identifiability, constraint, and equifinality in data assimilation with ecosystem models. *Ecological Applications*, 19(3), 571–574.

Macarthur, R.H. & Wilson, E.O. (1967) *The theory of Island biogeography*. REV-Revised. Princeton, NJ: Princeton University Press.

Available at: https://www.jstor.org/stable/j.ctt19cc1t2 [Accessed 20th October 2023].

Marolla, F., Henden, J.A., Fuglei, E., Pedersen, Å.Ø., Itkin, M. & Ims, R.A. (2021) Iterative model predictions for wildlife populations impacted by rapid climate change. *Global Change Biology*, 27(8), 1547–1559. Available from: https://doi.org/10.1111/gcb.15518

Mccarthy, K.P. et al. (2008) Assessing estimators of snow leopard abundance. *The Journal of Wildlife Management*, 72(8), 1826–1833. Available from: https://doi.org/10.2193/2008-040

McCrea, R., King, R., Graham, L. & Börger, L. (2023) Realising the promise of large data and complex models. *Methods in Ecology and Evolution*, 14(1), 4–11. Available from: https://doi.org/10.1111/2041-210X.14050

McLeod, A.M. & Leroux, S.J. (2021) Incongruent drivers of network, species and interaction persistence in food webs. *Oikos*, 130(10), 1726–1738. Available from: https://doi.org/10.1111/oik.08512

Meehl, G.A., Goddard, L., Boer, G., Burgman, R., Branstator, G., Cassou, C. et al. (2014) Decadal climate prediction: an update from the trenches. *Bulletin of the American Meteorological Society*, 95(2), 243–267. Available from: https://doi.org/10.1175/BAMS-D-12-00241.1

Merow, C., Smith, M.J., Edwards, T.C., Jr., Guisan, A., McMahon, S.M., Normand, S. et al. (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography*, 37(12), 1267–1281. Available from: https://doi.org/10.1111/ecog.00845

Miller, M.W. & Conner, M.M. (2005) Epidemiology of CHRONIC WASTING disease in free-ranging MULE deer: spatial, temporal, and demographic influences on observed PREVALENCE patterns. *Journal of Wildlife Diseases*, 41(2), 275–290. Available from: https://doi.org/10.7589/0090-3558-41.2.275

Noda, T. (2004) Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. *Population Ecology*, 46(2), 105–117. Available from: https://doi.org/10.1007/s10144-004-0184-x

Perretti, C.T., Munch, S.B. & Sugihara, G. (2013) Model-free forecasting outperforms the correct mechanistic model for simulated and experimental data. *Proceedings of the National Academy of Sciences of the United States of America*, 110(13), 5253–5257. Available from: https://doi.org/10.1073/pnas.1216076110

Peterson, A.T., Papeş, M. & Soberón, J. (2015) Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, 1(2), 28–38. Available from: https://doi.org/10.1515/eje-2015-0014

Rastetter, E.B. (2017) Modeling for Understanding v. Modeling for Numbers. *Ecosystems*, 20(2), 215–221. Available from: https://doi.org/10.1007/s10021-016-0067-y

Ratto, M., Castelletti, A. & Pagano, A. (2012) Emulation techniques for the reduction and sensitivity analysis of complex environmental models. *Environmental Modelling & Software*, 34, 1–4. Available from: https://doi.org/10.1016/j.envsoft.2011.11.003

Read, E.K., O'Rourke, M., Hong, G.S., Hanson, P.C., Winslow, L.A., Crowley, S. et al. (2016) Building the team for team science. *Ecosphere*, 7(3), e01291. Available from: https://doi.org/10.1002/ecs2.1291

Read, J.S., Jia, X., Willard, J., Appling, A.P., Zwart, J.A., Oliver, S.K. et al. (2019) Process-guided deep learning predictions of Lake

water temperature. *Water Resources Research*, 55(11), 9173–9190. Available from: https://doi.org/10.1029/2019WR024922

Robinson, T., Alexander, M.E., Simon, C.A., Griffiths, C.L., Peters, K., Sibanda, S. et al. (2016) Lost in translation? Standardising the terminology used in marine invasion biology and updating south African alien species lists. *African Journal of Marine Science*, 38(1), 129–140. Available from: https://doi.org/10.2989/1814232X.2016.1163292

Rostami, M.A., Balmaki, B., Dyer, L.A., Allen, J.M., Sallam, M.F. & Frontalini, F. (2023) Efficient pollen grain classification using pre-trained convolutional neural networks: a comprehensive study. *Journal of Big Data*, 10(1), 151. Available from: https://doi.org/10.1186/s40537-023-00815-3

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 71(2), 319–392. Available from: https://doi.org/10.1111/j.1467-9868.2008.00700.x

Ruel, J.J. & Ayres, M.P. (1999) Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, 14(9), 361–366. Available from: https://doi.org/10.1016/S0169-5347(99)01664-X

Scher, S., & Messori, G. (2019) Weather and climate forecasting with neural networks: using general circulation models (GCMs) with different complexity as a study ground. *Geoscientific Model Development*, 12(7), 2797–2809.

Smallman, T.L., Milodowski, D.T., Neto, E.S., Koren, G., Ometto, J. & Williams, M. (2021) Parameter uncertainty dominates C-cycle forecast errors over most of Brazil for the 21st century. *Earth System Dynamics*, 12(4), 1191–1237. Available from: https://doi.org/10.5194/esd-12-1191-2021

Soares, L.M.V. & do Carmo Calijuri, M. (2021) Deterministic modelling of freshwater lakes and reservoirs: current trends and recent progress. *Environmental Modelling & Software*, 144, 105143. Available from: https://doi.org/10.1016/j.envsoft.2021.105143

Solé, R. & Levin, S. (2022) Ecological complexity and the biosphere: the next 30 years. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 377(1857), 20210376. Available from: https://doi.org/10.1098/rstb.2021.0376

Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O. & Amiaud, B. (2014) Filling the gap in functional trait databases: use of ecological hypotheses to replace missing data. *Ecology and Evolution*, 4(7), 944–958. Available from: https://doi.org/10.1002/ece3.989

The Sustainable Development Goals Report 2022. (2022) United Nations.

Tourinho, L. & Vale, M.M. (2023) Choosing among correlative, mechanistic, and hybrid models of species' niche and distribution. *Integrative Zoology*, 18(1), 93–109. Available from: https://doi.org/10.1111/1749-4877.12618

Tramontana, G., Jung, M., Schwalm, C.R., Ichii, K., Camps-Valls, G., Ráduly, B. et al. (2016) Predicting carbon dioxide and energy fluxes across global FLUXNET sites with regression algorithms. *Biogeosciences*, 13(14), 4291–4313. Available from: https://doi.org/10.5194/bg-13-4291-2016

Tredennick, A.T., Hooten, M.B., Aldridge, C.L., Homer, C.G., Kleinhesselink, A.R. & Adler, P.B. (2016) Forecasting climate change impacts on plant populations over large spatial extents. *Ecosphere*, 7(10), e01525. Available from: https://doi.org/10.1002/ecs2.1525

Waller, L.A. (2010) Bridging gaps between statistical and mathematical modeling in ecology. *Ecology*, 91(12), 3500–3502. Available from: https://doi.org/10.1890/10-0432.1

Ward, E.J., Holmes, E.E., Thorson, J.T. & Collen, B. (2014) Complexity is costly: a meta-analysis of parametric and non-parametric methods for short-term population forecasting. *Oikos*, 123(6), 652–661. Available from: https://doi.org/10.1111/j.1600-0706.2014.00916.x

Wedi, N.P. (2014) Increasing horizontal resolution in numerical weather prediction and climate simulations: illusion or panacea? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 372(2018), 20130289. Available from: https://doi.org/10.1098/rsta.2013.0289

Wenger, S.J. & Olden, J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, 3(2), 260–267. Available from: https://doi.org/10.1111/j.2041-210X.2011.00170.x

Wiegert, R.G. (1975) Simulation models of ecosystems. *Annual Review of Ecology and Systematics*, 6(1), 311–338. Available from: https://doi.org/10.1146/annurev.es.06.110175.001523

Wilkinson, M.D., Dumontier, M., Aalbersberg, I.J.J., Appleton, G., Axton, M., Baak, A. et al. (2016) The FAIR guiding principles for scientific data management and stewardship. *Scientific Data*, 3(1), 160018. Available from: https://doi.org/10.1038/sdata.2016.18

Wood, C.M., Loman, Z.G., McKinney, S.T. & Loftin, C.S. (2020) Testing prediction accuracy in short-term ecological studies. *Basic and Applied Ecology*, 43, 77–85. Available from: https://doi.org/10.1016/j.baae.2020.01.003

Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S. et al. (2018) Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution*, 33(10), 790–802. Available from: https://doi.org/10.1016/j.tree.2018.08.001

Yeager, S. & Danabasoglu, G. (2014) The origins of late-twentieth-century variations in the large-scale North Atlantic circulation. *Journal of Climate*, 27(9), 3222–3247. Available from: https://doi.org/10.1175/JCLI-D-13-00125.1

Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D. et al. (2016) Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology*, 22(8), 2651–2664. Available from: https://doi.org/10.1111/gcb.13251