PERSPECTIVE

Methods in ecological forecasting



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The power of forecasts to advance ecological theory

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Abstract

- 1. Ecological forecasting provides a powerful set of methods for predicting short- and long-term change in living systems. Forecasts are now widely produced, enabling proactive management for many applied ecological problems. However, despite numerous calls for an increased emphasis on prediction in ecology, the potential for forecasting to accelerate ecological theory development remains underrealized.
- 2. Here, we provide a conceptual framework describing how ecological forecasts can energize and advance ecological theory. We emphasize the many opportunities for future progress in this area through increased forecast development, comparison and synthesis.
- 3. Our framework describes how a forecasting approach can shed new light on existing ecological theories while also allowing researchers to address novel questions. Through rigorous and repeated testing of hypotheses, forecasting can help to refine theories and understand their generality across systems. Meanwhile, synthesizing across forecasts allows for the development of novel theory about the relative predictability of ecological variables across forecast horizons and scales.
- 4. We envision a future where forecasting is integrated as part of the toolset used in fundamental ecology. By outlining the relevance of forecasting methods to

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ecological theory, we aim to decrease barriers to entry and broaden the community of researchers using forecasting for fundamental ecological insight.

KEYWORDS

ecological forecast, ecological theory, forecast cycle, forecast synthesis, hypothesis testing, modelling, predictability, transferability

1 | INTRODUCTION

Ecological forecasting combines ecological theory with recent revolutions in data availability and computing power (Jones et al., 2006; Keitt & Abelson, 2021; Reichman et al., 2011) to test specific, quantitative hypotheses about future ecosystem states (Box 1). Over time, the rate of forecast publication has increased, and ecological forecasts have now been produced for marine, freshwater and terrestrial ecosystems spanning all seven continents (Lewis et al., 2021; Payne et al., 2017). By enabling anticipatory action (Bradford et al., 2018), ecological forecasts are transforming decision-making processes for numerous applied ecological problems, from near-term drinking water management to long-term biodiversity conservation planning (e.g. Carey et al., 2021; Gaydos et al., 2019; Henden et al., 2020; Liu et al., 2018).

The growth and development of ecological forecasting parallels an increased emphasis on prediction in fundamental ecological research (Carpenter, 2002; Clark et al., 2001; Dietze, 2017; Dietze et al., 2018; Evans, 2012; Evans et al., 2013; Hilborn & Mangel, 1997; Houlahan et al., 2017; Maris et al., 2018; Petchey et al., 2015). Ecology has arguably lagged behind related disciplines (e.g. evolutionary biology) in the development and repeated testing of disciplinary theories (Scheiner, 2013), which we broadly define here as overarching, repeatable rules and principles (Box 1). Increased emphasis on prediction has the potential to energize and accelerate

ecological theory development, as prediction requires researchers to crystallize broad theories into specific, quantitative hypotheses that can be tested with data. Furthermore, some have argued that prediction is the *only* way to demonstrate scientific knowledge, thereby assessing the validity of existing theories (Houlahan et al., 2017). While prediction has often been interpreted to include historical modelling (Houlahan et al., 2017; Mouquet et al., 2015), forecasting is a particularly robust approach to testing theory as it ensures preregistration and protects against post hoc overfitting. Likewise, as climate change continues to disrupt and change ecosystem function across all levels of biological organization, forecasting is essential to understand future ecological function (Dietze et al., 2018).

Despite rapid increases in forecast development and the need for a stronger emphasis on prediction in fundamental ecological research, the potential for forecasting to contribute to ecological theory development remains underrealized. There has been little discussion outlining how forecasting can contribute to developing and advancing ecological theory, likely limiting the adoption of forecasting methods (but see Dietze, 2017). To fill this gap, we describe how ecological forecasting can shed new light on existing theory (Sections 2 and 3) while also allowing researchers to ask and answer novel theoretical questions about predictability (Section 4). We conclude by presenting a vision and roadmap for the integration of forecasting and theory in ecology (Section 5). By outlining the relevance of forecasting

BOX 1 Glossary of forecasting terminology in the context of ecological the	BOX 1	y of forecasting terminology in the context of ecological the	ory
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Term	Definition
Ecological forecast	A specific, quantitative prediction about a future ecological state, preferably including an uncertainty estimate
Ecological theory	An overarching, repeatable rule or principle in ecology
Process-based model	A mathematical representation of a hypothesized causal relationship between dependent and independent variables
Empirical model	A statistical representation of a correlative relationship between dependent and independent variables
Transferability	The relative performance of a model, preferably including uncertainties, when applied outside of the system in which the model was developed (e.g. new location, temporal or spatial scale, biological system)
Uncertainty	A probabilistic statement about the imprecision in our knowledge of a quantity or process of interest
Forecast skill	The proficiency of an existing model for predicting future ecological states (forecast skill can only be assessed retroactively, after data have been collected)
Predictability	The extent to which a future ecological state may be predicted based upon current and historical data
Forecast horizon	The length of time into the future for which forecasts are made

methods to ecological theory, we aim to broaden the community of researchers using ecological forecasting and identify research directions to further the implementation of this methodological approach.

2 | FORECASTING HARNESSES PREDICTION TO RAPIDLY ADVANCE THEORY

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Ecological forecasting provides a rapid and quantitative demonstration of the scientific method (Dietze et al., 2018). First, researchers formulate a hypothesis about an ecological process and represent that process in a model, which may fall anywhere on the spectrum from empirical to process based (Box 2). Next, a specific, quantitative prediction is made about the future (unobserved data) based upon that hypothesis, preferably including quantified uncertainty. Finally, the forecast is tested with data, allowing researchers to evaluate and refine their hypothesis. This process can be iterated in a forecast cycle as new data are collected, providing repeated tests of the underlying ecological hypothesis.

2.1 | Model improvement and comparison

Using the forecasting cycle to address ecological theory can be transformative in part because it emphasizes model improvement and

BOX 2 Both empirical and process-based models can be used to develop ecological theory

Ecological models exist on a spectrum from completely empirical models to highly parameterized process-based models (Box 1; Figure 1). Process-based models most directly represent ecological hypotheses that can be tested with incoming data. Because they incorporate ecological theory, processbased models are less constrained to the historic range of variability in the data used to fit the model, and they are generally preferred when forecasts extend into novel, outof-sample conditions (Cuddington et al., 2013; Evans, 2012; Mouquet et al., 2015; Rastetter, 2017; Tredennick et al., 2021). However, empirical models often have greater predictive power, particularly in the near term (e.g. Perretti et al., 2013). While empirical models do not directly represent mechanistic hypotheses for how ecological systems operate, they can be effective at identifying new potential drivers to inform future mechanistic hypotheses (see West & Brown, 2005). Many ecological models will not fall at either of these extremes, but instead will include both processbased and empirical aspects. We suggest that models across the spectrum of process representation can contribute meaningfully to the development of ecological theory.

comparison: forecasting requires researchers to not only posit the theoretical relationships among dependent and independent variables (e.g. X will affect Y), but also the functional forms and parameters governing these relationships (Houlahan et al., 2017). In other words, it forces us to be specific about the predictions that come from our hypotheses and to build on prior knowledge when testing theory.

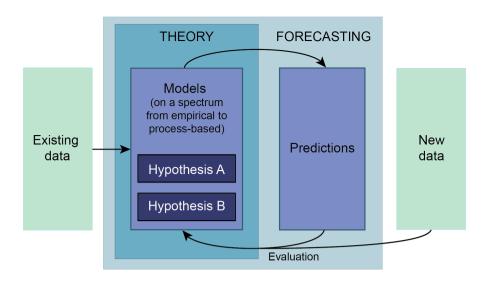
As one of many possible examples of where a forecasting approach could build upon the status quo, consider that terrestrial plant ecologists have been performing nitrogen addition experiments for well over 100 years and have consistently shown that net primary productivity (NPP) responds positively to nitrogen additions (LeBauer & Treseder, 2008). Building upon this evidence, researchers are well positioned to make anticipatory predictions about the magnitude of increase in NPP that would be expected with a given input of nitrogen, and common features of ecological forecasting can accelerate the testing and improvement of these predictions. Furthermore, forecasts that quantify specific sources of uncertainty (e.g. uncertainty in initial conditions, drivers and parameters of the model) can allow researchers to identify which components of the forecast are responsible for forecast error, thereby identifying gaps in current ecological knowledge that would be most productive to address. For example, error in NPP forecasts could result from uncertainty in the relationship between NPP and nitrogen addition, but also uncertainty in a number of other external drivers that influence NPP. Forecasts with quantified uncertainty are particularly effective at isolating each of these factors. Ultimately, emphasizing model improvement and comparison through a forecasting approach allows researchers to rapidly build upon existing theories regarding which drivers can predict an ecological quantity of interest and the magnitude of that effect.

2.2 | Increasing reproducibility

Creating specific, quantitative predictions that can be tested with incoming data is particularly important in the face of the ongoing reproducibility crisis across scientific disciplines (e.g. Freedman et al., 2015; Open Science Collaboration, 2015). Omission of nonsignificant results from publications, that is, publication bias, is common across ecology and evolutionary biology, as is the practice of researchers developing an explanation for their results retroactively and reporting this explanation as if it were their original hypothesis (Fraser et al., 2018). However, research practices like these can undercut the development of ecological theory by decreasing comparability and reproducibility between studies (Fraser et al., 2018). Ecological forecasts help address these issues by explicitly documenting a hypothesis before evaluating that hypothesis with data. As such, they function as a form of preregistration (sensu Nosek et al., 2018; Parker et al., 2019), increasing the validity and credibility of research findings.

Likewise, ecological forecasts increase reproducibility by avoiding spurious results that result from overfitting models to data (i.e. calibrating a model to closely match one dataset, at the expense of

FIGURE 1 Conceptual diagram describing how forecasts (on a spectrum from empirical to process based) contribute to ecological hypothesis development and refinement.



predictive power for new data), as can happen when all available data are used to fit a model. It is not possible to overfit a forecast, because data used to evaluate the model have not yet been collected when the forecast is generated. Thus, forecasts inherently provide out-of-sample validation. Forecasting new data can highlight model biases that might not be detected by any approach that uses an entire dataset for model selection, including cross-validation. Model evaluation using in-sample data will share any systematic errors, and a researcher using cross-validation may overfit the held-out data by modifying models post hoc after cross-validation. For example, Averill et al. (2021) found that out-of-sample validations for some forecasts of soil microbial taxonomic and functional groups were systematically biased due to small differences in measurement techniques. Ecological forecasts that successfully predict out-of-sample data often come from very simple models (Chevalier & Knape, 2020; Ward et al., 2014), in part because they cannot increase model fit simply by adding additional parameters and overfitting to data. Thus, forecasts provide a particularly rigorous test of ecological theory, highlighting which aspects of theory have real, predictive ability and uncovering previously unknown knowledge gaps.

2.3 | Iterative forecasts

Iterative forecasts—those that are made repeatedly, updating the forecast model through confrontation with new data—may be particularly useful for hypothesis testing and theory development. For example, when comparing multiple alternative auto-regressive models, testing short-term predictions and resetting conditions to the current state at the start of each forecast (rather than analysing model fit statistics over a longer interval) helps to overcome compounding structural biases in the model and reveal periods of time where each forecast model performs well (McClure et al., 2021). Iterative forecasts are also useful as a means of accelerating research because they can accommodate non-stationarity, or change in ecological processes over time, without requiring explicit nonstationary processes that initially may not be well represented in small

datasets (McClure et al., 2021). Consequently, generating repeated short-term predictions allows researchers to rapidly refine and compare hypotheses, rather than waiting until all data have been collected and analysing model performance post-hoc.

When developing iterative forecasts, researchers are able to conduct targeted sampling to resolve uncertain model processes or states, developing a more complete and accurate understanding of the ecological process (Redmond et al., 2019). Changing the data collection strategy in response to forecasts is a unique opportunity that forecasting offers in comparison with retrospective analysis, and is transformative as a means of distinguishing between competing hypotheses (Coelho et al., 2019). For example, imagine we have three alternative hypotheses/models that are all equally compatible with past observations. If we collect data at times and places where the models continue to predict the same thing (which we may be likely to do under conventional sampling designs), it remains impossible to distinguish between the hypotheses. However, if we instead use forecasts to predict forward and identify the times and places where the models make different predictions, we can then adapt monitoring to more efficiently collect the data required to differentiate between the models. Any time forecasts diverge, observations are going to refute at least one of the models.

3 | FORECAST TRANSFERABILITY EVALUATES THE GENERALITY OF ECOLOGICAL FUNCTION ACROSS LOCATIONS, VARIABLES AND SCALES

While the term 'forecast transferability' (Box 1) may be new to many ecologists, understanding the generality of ecological theories has long been a central goal for the field. Questions like *Do the same macroecological patterns apply to microorganisms and macroorganisms, and are they caused by the same processes?* and What are the generalities in ecosystem properties and dynamics between marine, freshwater and terrestrial biomes? are essentially questions about the transferability of ecological models. Both of these questions appear in

the list of 100 fundamental questions in ecology from Sutherland et al. (2013). While not all forecasts involve model transfers, here we consider any model transfer to new conditions (e.g. time, location, species) to be forecasts.

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By transferring models to new ecological conditions, researchers can empirically assess the generality of ecological structure and function, thereby identifying overarching rules and patterns in ecology. As an example, consider the case where we already have forecast models for k species within a clade and want to know how well we can constrain a forecast for another species in the group (species k+1). Can we predict what drivers and functional forms should be used? Can we put prior constraints on parameters for modelling the out-of-sample species? How much can we further constrain these choices using across species knowledge, including but not limited to phylogenetic constraints, functional traits, life-history trade-offs, biomechanical constraints, trophic position and physical environmental conditions? Understanding how models transfer across species, locations and times is transformative by explicitly identifying when, where and why a theory breaks down.

While assessment of model transferability using ecological forecasts is only just beginning, emerging research has identified at least two general patterns. First, many studies suggest that transferability is governed by ecological novelty: relative model performance decreases most when the magnitude and character of environmental variation differs between the original and transferred conditions (Kleiven et al., 2018; McClure et al., 2021; Qiao et al., 2018; Sequeira et al., 2016). For example, we would predict that a model built for one species will perform better for a closely related species than one that is more distantly related. Second, model structure likely modulates transferability: simple models (e.g. models with few parameters) may be more transferable than complex models, as complex models are more likely to incorporate particularities of an individual time or location (Wenger & Olden, 2012), and process-based models are thought to be better at predicting out-of-sample conditions than empirical models (Box 2). However, more precisely characterizing patterns in transferability will require both technical advances (e.g. standardized metrics of transferability) and a significant increase in the frequency with which ecological modelling studies assess model transferability (Yates et al., 2018).

4 | NEW FRONTIERS OF ECOLOGICAL RESEARCH: UNDERSTANDING THE LIMITS TO PREDICTABILITY

In addition to providing an effective means of refining existing ecological theories, forecasting allows for the development and testing of novel theories regarding the predictability of ecological variables. Understanding ecological predictability (Box 1) has long been an implicit goal in ecology. For example, the classic question of whether plant communities are primarily characterized by climax communities (Clements, 1936) or individualistic responses

(Gleason, 1926) is fundamentally a question of ecological predictability. Recent efforts have been made to explicitly discuss (e.g. Godfray & May, 2014; Houlahan et al., 2017; Sutherland et al., 2013) and analyse (Dietze, 2017; Lewis et al., 2021; Petchey et al., 2015; Ward et al., 2014) the relative predictability of ecological variables. These advances, alongside growth in the practice of ecological forecasting (Lewis et al., 2021), make now an ideal time to develop testable hypotheses about patterns of ecological predictability.

Ecological predictability presents an exciting, synthetic lens through which to view ecological theory. To date, only a few studies have analysed predictability across scales and variables (Lewis et al., 2021; Rousso et al., 2020; Ward et al., 2014). These studies have found that forecast skill consistently decreases over 1- to 30day forecast horizons, forecasts created with greater historical data have superior forecast skill, and taxonomically similar systems have similar forecast skill. Given these initial results, we suspect that there are seemingly distinct phenomena (e.g. algal blooms, epidemics, invasive species) that show congruent patterns of predictability across scales (e.g. forecast horizon, grain or extent). Analysing the patterns of predictability for phenomena like these may provide a means of addressing new problems and new situations without starting from scratch each time. In doing so, we can harness sub-disciplinary progress to advance a broader understanding of ecology across scales and variables.

Quantifying ecological predictability may also help to identify gaps in existing theory that could be addressed to efficiently advance our knowledge of ecological processes. If we can understand the limits to predictability and isolate the extent to which those limits are due to irreducible factors versus imperfect knowledge, we could prioritize research in areas with low current forecast skill and high potential predictability; these are areas where increased knowledge has high value of information (see Bolam et al., 2019) for increasing forecast skill. These same areas, when they involve natural resources, could also be high priorities for investment in improved ecological forecasts to inform management decisions. However, characterizing the limits to predictability will require a significant body of research, and current hypotheses are insufficient to describe how ecological predictability differs across variables and horizons.

Advancing theory about predictability in ecology will require the development and repeated testing of hypotheses. To begin this process, we propose two hypotheses below about the relationships that govern ecological predictability. For each hypothesis, we briefly describe the state of current evidence using forecasting to test these hypotheses. Here, we are using forecast skill as a metric of predictability (Box 1); while errors in model structure and uncertainty in parameters also affect forecast skill, forecast skill is likely correlated with intrinsic predictability, which cannot be measured directly (Pennekamp et al., 2019). Our consideration of forecast skill as a measure of predictability differs from previous studies that have quantified predictability as the improvement in forecast skill relative to a null model (e.g. a model that predicts the next observation will be the same as the last observation), which removes any predictability that results from autocorrelation (Ward et al., 2014). While

null model comparisons are beneficial when quantifying what factors contribute to the skill of an ecological model, considering such autocorrelated processes holistically with forecast skill facilitates comparisons of overall ecological predictability between sites, variables and scales, making it useful for advancing theoretical ecology.

4.1 | Hypothesis 1: The rate of decline in predictability over increasing forecast horizons differs across variables and scales

As forecasts extend further into the future, numerous sources of uncertainty in the forecast (e.g. initial conditions, parameters, external forcing; Dietze, 2017) can compound, decreasing the potential predictability of an ecological state. Consequently, we hypothesize that predictability decreases with increasing forecast horizons (Box 1) across all variables and scales. However, due to differences in the nature of ecological processes (e.g. the extent to which a process is governed by chaotic dynamics), we anticipate that the rate of decline in predictability likely differs across variables and scales (Dietze, 2017).

Several published studies provide support for the hypothesis that ecological forecast skill decreases with increasing forecast horizon through the analysis of simulated data (Petchey et al., 2015) and meta-analyses of published forecasts (Lewis et al., 2021; Rousso et al., 2020). However, these studies only describe forecast skill for a relatively small subset of ecological variables. How the relationship between predictability and forecast horizon differs across scales and variables remains comparatively uncharacterized. That being said, existing theory provides a suite of predictions about how different sources of uncertainty (e.g. initial conditions, parameters, drivers, random effects, process error) may affect the rate at which forecast proficiency declines within an ecological forecast and creates differences in predictability across scales and variables (Dietze, 2017).

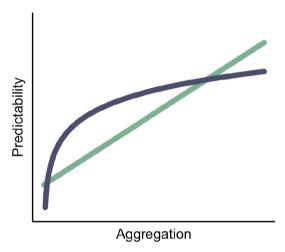
A synthesis of near-term forecasts published from 1932 to 2020 provides support for our assertion that the pattern of decline in predictability over increasing forecast horizons may be an ecologically relevant means of assessing similarities and differences in ecological dynamics across systems (Lewis et al., 2021). Analysing forecast skill across four variables and 29 papers, Lewis et al. (2021) found that the rate of decline in skill (i.e. predictability) with increasing forecast horizon appeared to be very similar for closely related variables (e.g. the biomass of individual phytoplankton taxa and chlorophyll, an aggregate measure of phytoplankton biomass) but significantly different for variables that were somewhat further removed (e.g. pollen and evapotranspiration). However, at the time of that analysis, data were only available to analyse the decline in predictability for four variables (chlorophyll, phytoplankton biomass, pollen, evapotranspiration) over 1- to 7-day forecast horizons. Determining the factors that control rates of decline in predictability over increasing forecast horizons will require the development and comparison of forecasts for many more ecological variables and at a wide range of forecast horizons.

Through increased forecast development and comparison, ecologists will be able to determine whether there are congruent

patterns of predictability across variables and scales, synthesizing sub-disciplinary theoretical developments to develop a broader understanding of patterns in ecology.

4.2 | Hypothesis 2: Predictability increases with biological and ecological aggregation

Ecological states can be conceptualized with varying levels of aggregation (e.g. temporal, spatial and phylogenetic aggregation; Figure 2). In general, forecasting research across multiple fields (e.g. economics, meteorology) suggests that increasing levels of aggregation typically increase predictability (Hoffmann et al., 2015; Levin, 1987; McLeod & Leroux, 2021; Noda, 2004; Wedi, 2014). However, these relationships remain poorly characterized in ecology. In line with cross-disciplinary research, we hypothesize that increasing biological and ecological aggregation increases predictability and aggregation



Ward et al. (2014)

- Species maximum age (fish)
- Species trophic level (birds)
 Species maximum length (fish)

Other metrics of aggregation:

? Spatial scale Temporal scale Taxanomic scale Community size

FIGURE 2 Ward et al. (2014) quantified the relationship between forecast skill and several metrics of ecological aggregation. They found that predictability increased linearly with species trophic level for bird populations and with species maximum length for fish populations. Conversely, predictability increased nonlinearly with species maximum age for fish populations. These relationships are plotted here as general, non-quantitative patterns. Predictability likely increases across many other axes of ecological aggregation; however, the specific parameters of these relationships (e.g. do we expect a linear relationship? Logarithmic? Exponential?) for each axis remain unknown.

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is consequently a useful axis along which to begin comparing the predictability of ecological variables.

Previous research analysing several metrics of biological and ecological aggregation provides initial support for our hypothesis that aggregation increases ecological predictability. For example, Ward et al. (2014) suggest that populations of longer-lived, larger and higher trophic-level species—which integrate some variability in their environment (Apollonio, 2002)—may be more predictable than shorter-lived species (Figure 2). Likewise, numerous phytoplankton forecasts have found that aggregate measures of phytoplankton biomass (e.g. chlorophyll) may be more predictable than the abundance of an individual species or functional group (e.g. Kakouei et al., 2022; Page et al., 2018). Averill et al. (2021) found that the predictability of soil microbial community composition increases with spatial and taxonomic aggregation, and in the spatial ecology realm, recent studies have demonstrated that species responses to habitat change can be better predicted by focusing efforts at larger spatial and temporal scales (Banks-Leite et al., 2022; Brodie et al., 2021). Still, these are broad, general predictions (X increases Y) and give little indication as to the specific parameters governing this general relationship (Figure 2). For example, is this always a linear relationship? Exponential? Logarithmic? Does the nature of the relationship between aggregation and predictability differ depending on the axis of aggregation considered? Increased forecast development and comparison across multiple levels of aggregation will be essential to characterizing these relationships.

5 | CONCLUSION: ROADMAP FOR INCREASED USE OF FORECASTING TO DEVELOP AND REFINE ECOLOGICAL THEORY

5.1 | Vision

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We envision a future where forecasting is fully integrated as part of the suite of research methods used in ecology. As forecast development increases, we expect that forecasts will shed light on a wide range of existing ecological theories and will aid in developing new theories about ecological predictability. Along the way, we anticipate that increased use of forecasts in ecology at large will accelerate their integration into proactive ecological management, and that harnessing the power of forecasting for both fundamental and applied ecological research will help strengthen connections between ecological theory and practice. Thus, we envision that integration of ecological forecasting into the toolset of fundamental ecology could rapidly energize and advance ecological research.

5.2 | Roadmap

Achieving our vision (Section 5.1, above) will require broadening the community of researchers that use ecological forecasts in their

research. Increased production of forecasts across a wide range of variables and sites would not only help to refine specific existing theories, but is essential to building the database of forecast studies needed to analyse patterns in ecological transferability and predictability.

For ecologists considering using forecasting in their research, barriers to entry can be theoretical (e.g. 'what are the most productive ways of incorporating forecasts in my work?") as well as technical. Throughout this paper (Sections 2 and 3, above), we suggest at least three areas of 'low-hanging fruit' for incorporating forecasting into existing research projects: forecasting the results of an experiment to quantify the accuracy of existing theory, using forecasts to test competing hypotheses through model selection and assessing transferability of ecological forecasts to quantify generality in ecology. We acknowledge that a forecasting approach is certainly not the most effective means of answering every ecological question. For example, in cases where driver uncertainty is high, historical modelling may be more effective than forecasting at identifying how well varying model functional forms recreate patterns in data. Forecasts are likely to be most beneficial when incorporated as one of the many forms of inference used in ecology, and the research directions we suggest above are areas we believe will be fruitful for ecologists interested in adding forecasting into their repertoire of approaches.

Another potential barrier for individual researchers may be a perceived lack of the technical and mathematical experience necessary to develop ecological forecasts. One response to this concern is that forecasts do not need to be elaborate to be useful. Indeed, very simple models (e.g. predicting that the future state will be the same as the last observation) currently often have greater forecast skill than their more complex counterparts (Chevalier & Knape, 2020; Ward et al., 2014). Furthermore, forecasts do not need to be perfect to be helpful in developing theory; learning occurs most quickly when the forecast is wrong, as this identifies where existing theory is insufficient. Still, we acknowledge that some technical expertise is important when developing forecasts. Many educational and training materials are already available and helpful for those interested in starting to forecast. For example, the Ecological Forecasting Initiative (EFI)—an interdisciplinary consortium aimed at building a community of practice around the development and implementation of ecological forecasts-maintains a database of over 100 educational resources related to ecological forecasting and adjacent skills (e.g. coding in R; Willson & Peters, 2021). Resources in the database, include course material, videos, code repositories, modules and online textbooks, and are categorized as introductory, intermediate or advanced. The EFI community continues to identify gaps in available resources and develop new material and resources available for anyone interested in ecological forecasting. To further increase the accessibility of these methods, researchers may consider forming interdisciplinary collaborations (e.g. with statisticians and computer scientists) and delegating tasks outside of their expertise to experts in these relevant areas (Carey et al., 2021).

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Open-access code and reproducible examples can provide helpful resources for the development of new forecasts and further advance the pace of theory-driven ecological research (Lowndes et al., 2017). Promisingly, the use of open science practices in ecological forecasting (e.g. data publication and forecast archiving) is already increasing over time, providing a wealth of examples that can be used as a foundation for new forecasting projects (e.g. Lewis et al., 2021, Dietze, Boettiger, et al., 2021; Dietze, Thomas, et al., 2021). The U.S. National Ecological Observatory Network (NEON) Ecological Forecasting Challenge, which promotes the development and comparison of multiple forecasts for a range of NEON data streams, includes reproducible examples of forecasting workflows, including null models, multiple aspects of ecology and a single shared cyberinfrastructure, and is freely available online (Thomas et al., 2021). Through these and other open science efforts, it is becoming easier to build upon previous work and rapidly advance the use of ecological forecasting.

Several technological developments have the potential to further lower barriers to entry for using forecasting in ecology, though adoption of these technologies is predicated on the accessible learning opportunities described above. Forecasting can be computationally intensive and may require large data storage/computing facilities to deal with the vast amounts of data (e.g. from satellites) used in some forecasting projects (e.g. NOAA Coral Reef Watch, Liu et al., 2018). Increasing the development and accessibility of such facilities could increase adoption of forecasting as a methodological approach. Similarly, improved cloud infrastructure with the capacity for intensive computation and data sharing across decentralized scientific collaborations can increase the accessibility of research collaborations, decreasing barriers to entry for individual researchers (Farley et al., 2018; Lowndes et al., 2017; Reichman et al., 2011). Both resources are essential for building the capacity of ecological forecasting and making it an accessible tool for developing and advancing ecological theory.

A community-wide effort will be required to fully realize the potential of forecasting to inform questions about the limits of ecological predictability or the generality of ecological function. In particular, it is critical that we increase our ability to compare across ecological forecasts. Doing so will require standardized conventions for forecast documentation, among other developments, and efforts to create such resources are in progress, with support from organizations like EFI. For example, EFI has developed community standards and an R package for archiving forecast output and metadata (Dietze, Boettiger, et al., 2021; Dietze, Thomas, et al., 2021). These standards and associated R package facilitate comparing and analysing variables such as model structure, forecast horizon and quantified uncertainty, across forecasts of varying skill, facilitating future comparative analyses that could test the hypotheses outlined in Sections 4.1 and 4.2. Likewise, forecast challenges, where many forecasts are developed by separate teams of researchers with different models and approaches (see Hyndman, 2020) provide another means of encouraging rapid forecast development and comparison.

As forecasting becomes integrated into the suite of methods used in fundamental ecology, forecast standards and challenges will be impactful as means of ensuring that researchers are able to harness individual forecasting projects to develop broader theory about the predictability and transferability of ecological forecasts.

Amid increases in forecast development and numerous calls for increased emphasis on prediction in ecological research (e.g. Dietze, 2017; Evans et al., 2013; Houlahan et al., 2017; Levin, 1987), ecological forecasting provides a powerful class of methods for the development and testing of theory. The future is bright for forecast-driven insights into fundamental ecological theory.

AUTHORS' CONTRIBUTIONS

A.S.L.L. wrote the manuscript, with support from all co-authors; A.S.L.L., A.J.A., J.A., S.B., E.C., J.A.P., N.R.R. and C.R.R. contributed to drafting figures; M.C.D., A.S.G., J.A.P. and C.R.R. made meaningful contributions through supervision and administration. All co-authors contributed to the conceptual development of this manuscript through participation in regular working group meetings, and all co-authors reviewed and edited manuscript drafts. After A.S.L.L. and C.R.R., author order is alphabetical by last name.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

- Apollonio, S. (2002). Hierarchical perspectives on marine complexities: Searching for Systems in the Gulf of Maine. Columbia University Press.
- Averill, C., Werbin, Z. R., Atherton, K. F., Bhatnagar, J. M., & Dietze, M. C. (2021). Soil microbiome predictability increases with spatial and taxonomic scale. *Nature Ecology & Evolution*, *5*(6), 747–756. https://doi.org/10.1038/s41559-021-01445-9
- Banks-Leite, C., Betts, M. G., Ewers, R. M., Orme, C. D. L., & Pigot, A. L. (2022). The macroecology of landscape ecology. *Trends in Ecology & Evolution*, 37, 480–487. https://doi.org/10.1016/j.tree.2022.01.005
- Bolam, F. C., Grainger, M. J., Mengersen, K. L., Stewart, G. B., Sutherland, W. J., Runge, M. C., & McGowan, P. J. K. (2019). Using the value of information to improve conservation decision making. *Biological Reviews*, 94, 629–647. https://doi.org/10.1111/brv.12471
- Bradford, J. B., Betancourt, J. L., Butterfield, B. J., Munson, S. M., & Wood, T. E. (2018). Anticipatory natural resource science and management for a changing future. Frontiers in Ecology and the Environment, 16(5), 295–303. https://doi.org/10.1002/fee.1806
- Brodie, S., Abrahms, B., Bograd, S. J., Carroll, G., Hazen, E. L., Muhling, B. A., Pozo Buil, M., Smith, J. A., Welch, H., & Jacox, M. G. (2021). Exploring timescales of predictability in species distributions. *Ecography*, 44(6), 832–844. https://doi.org/10.1111/ecog.05504
- Carey, C. C., Woelmer, W. M., Lofton, M. E., Figueiredo, R. J., Bookout, B. J., Corrigan, R. S., Daneshmand, V., Hounshell, A. G., Howard, D. W., Lewis, A. S. L., McClure, R. P., Wander, H. L., Ward, N. K., & Thomas, R. Q. (2021). Advancing lake and reservoir water quality management with near-term, iterative ecological forecasting. *Inland Waters*, 12(1), 107–120. https://doi.org/10.1080/20442041.2020.1816421
- Carpenter, S. R. (2002). Ecological futures: Building an ecology of the long now. *Ecology*, *83*(8), 2069–2083. https://doi.org/10.1890/0012-9658(2002)083[2069:EFBAEO]2.0.CO;2
- 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. https://doi.org/10.1111/oik.06401
- Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W. V.,

- Rose, K. A., Sala, O., Schlesinger, W. H., Wall, D. H., & Wear, D. (2001). Ecological forecasts: An emerging imperative. *Science*, 293(5530), 657–660. https://doi.org/10.1126/science.293.5530.657
- Clements, F. E. (1936). Nature and structure of the climax. *Journal of Ecology*, 24(1), 252-284. https://doi.org/10.2307/2256278
- 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. https://doi.org/10.1111/ecog.04228
- Cuddington, K., Fortin, M.-J., Gerber, L. R., Hastings, A., Liebhold, A., O'Connor, M., & Ray, C. (2013). Process-based models are required to manage ecological systems in a changing world. *Ecosphere*, 4(2), art20. https://doi.org/10.1890/ES12-00178.1
- Dietze, M. C. (2017). Prediction in ecology: A first-principles framework. *Ecological Applications*, 27(7), 2048–2060. https://doi.org/10.1002/eap.1589
- Dietze, M. C., Boettiger, C., Shiklomanov, A., Thomas, Q., & Peters, J. (2021). Ecological forecasting initiative: Community Standards R Package: v0.3. Zenodo, https://doi.org/10.5281/zenodo.4768741
- Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., Keitt, T. H., Kenney, M. A., Laney, C. M., Larsen, L. G., Loescher, H. W., Lunch, C. K., Pijanowski, B. C., Randerson, J. T., Read, E. K., Tredennick, A. T., Vargas, R., Weathers, K. C., & White, E. P. (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges. Proceedings of the National Academy of Sciences of the United States of America, 115(7), 1424–1432. https://doi.org/10.1073/pnas.1710231115
- Dietze, M. C., Thomas, R. Q., Peters, J., Boettiger, C., Shiklomanov, A. N., & Ashander, J. (2021). A community convention for ecological forecasting: Output files and metadata. *EcoEvoRxiv*, https://doi.org/10.32942/osf.io/9dgtq
- Evans, M. R. (2012). Modelling ecological systems in a changing world. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1586), 181–190. https://doi.org/10.1098/rstb.2011.0172
- Evans, M. R., Bithell, M., Cornell, S. J., Dall, S. R. X., Díaz, S., Emmott, S., Ernande, B., Grimm, V., Hodgson, D. J., Lewis, S. L., Mace, G. M., Morecroft, M., Moustakas, A., Murphy, E., Newbold, T., Norris, K. J., Petchey, O., Smith, M., Travis, J. M. J., & Benton, T. G. (2013). Predictive systems ecology. *Proceedings of the Royal Society B: Biological Sciences*, 280(1771), 20131452. https://doi.org/10.1098/rspb.2013.1452
- Farley, S. S., Dawson, A., Goring, S. J., & Williams, J. W. (2018). Situating ecology as a big-data science: Current advances, challenges, and solutions. *Bioscience*, 68(8), 563–576. https://doi.org/10.1093/biosci/biy068
- Fraser, H., Parker, T., Nakagawa, S., Barnett, A., & Fidler, F. (2018). Questionable research practices in ecology and evolution. *PLoS ONE*, 13(7), e0200303. https://doi.org/10.1371/journal.pone.0200303
- Freedman, L. P., Cockburn, I. M., & Simcoe, T. S. (2015). The economics of reproducibility in preclinical research. *PLoS Biology*, 13(6), e1002165. https://doi.org/10.1371/journal.pbio.1002165
- Gaydos, D. A., Petrasova, A., Cobb, R. C., & Meentemeyer, R. K. (2019). Forecasting and control of emerging infectious forest disease through participatory modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1776), 20180283. https://doi.org/10.1098/rstb.2018.0283
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53(1), 7–26. https://doi.org/10.2307/2479933
- Godfray, H. C. J., & May, R. M. (2014). Open questions: Are the dynamics of ecological communities predictable? *BMC Biology*, 12(1), 22. https://doi.org/10.1186/1741-7007-12-22
- Henden, J.-A., Ims, R. A., Yoccoz, N. G., Asbjørnsen, E. J., Stien, A., Mellard, J. P., Tveraa, T., Marolla, F., & Jepsen, J. U. (2020). Enduser involvement to improve predictions and management of populations with complex dynamics and multiple drivers. *Ecological Applications*, 30(6), e02120. https://doi.org/10.1002/eap.2120

- Hilborn, R., & Mangel, M. (1997). The ecological detective: Confronting models with data (MPB-28). In *The ecological detective*. Princeton University Press. https://doi.org/10.1515/9781400847310
- Hoffmann, H., Zhao, G., Van Bussel, L. G. J., Enders, A., Specka, X., Sosa, C., Yeluripati, J., Tao, F., Constantin, J., Raynal, H., Teixeira, E., Grosz, B., Doro, L., Zhao, Z., Wang, E., Nendel, C., Kersebaum, K. C., Haas, E., Kiese, R., ... Ewert, F. (2015). Variability of effects of spatial climate data aggregation on regional yield simulation by crop models. Climate Research, 65, 53–69. https://doi.org/10.3354/cr01326
- Houlahan, J. E., McKinney, S. T., Anderson, T. M., & McGill, B. J. (2017). The priority of prediction in ecological understanding. *Oikos*, 126(1), 1–7. https://doi.org/10.1111/oik.03726
- Hyndman, R. J. (2020). A brief history of forecasting competitions. International Journal of Forecasting, 36(1), 7–14. https://doi.org/10.1016/j.ijforecast.2019.03.015.
- Jones, M. B., Schildhauer, M. P., Reichman, O. J., & Bowers, S. (2006). The new bioinformatics: Integrating ecological data from the gene to the biosphere. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 519–544. https://doi.org/10.1146/annurev.ecolsys.37.091305.110031
- Kakouei, K., Kraemer, B. M., & Adrian, R. (2022). Variation in the predictability of lake plankton metric types. *Limnology and Oceanography*, 67(3), 608–620. https://doi.org/10.1002/lno.12021
- Keitt, T. H., & Abelson, E. S. (2021). Ecology in the age of automation. Science, 373(6557), 858-859. https://doi.org/10.1126/science.abi4692
- Kleiven, E. F., Henden, J.-A., Ims, R. A., & Yoccoz, N. G. (2018). Seasonal difference in temporal transferability of an ecological model: Near-term predictions of lemming outbreak abundances. *Scientific Reports*, 8(1), 15252. https://doi.org/10.1038/s41598-018-33443-6
- LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89(2), 371–379. https://doi.org/10.1890/06-2057.1
- Levin, S. A. (1987). Scale and predictability in ecological modeling. In T. L. Vincent, Y. Cohen, W. J. Grantham, G. P. Kirkwood, & J. M. Skowronski (Eds.), Modeling and management of resources under uncertainty (pp. 2-10). Springer. https://doi.org/10.1007/978-3-642-93365-3_1
- Lewis, A. S. L., Woelmer, W. M., Wander, H. L., Howard, D. W., Smith, J. W., McClure, R. P., Lofton, M. E., Hammond, N. W., Corrigan, R. S., Thomas, R. Q., & Carey, C. C. (2021). Increased adoption of best practices in ecological forecasting enables comparisons of forecastability. *Ecological Applications*, 32(2),e02500. https://doi. org/10.1002/eap.2500
- Liu, G., Eakin, C. M., Chen, M., Kumar, A., De La Cour, J. L., Heron, S. F., Geiger, E. F., Skirving, W. J., Tirak, K. V., & Strong, A. E. (2018). Predicting heat stress to inform reef management: NOAA coral reef Watch's 4-month coral bleaching outlook. Frontiers in Marine Science, 5, 57. https://doi.org/10.3389/fmars.2018.00057
- Lowndes, J. S. S., Best, B. D., Scarborough, C., Afflerbach, J. C., Frazier, M. R., O'Hara, C. C., Jiang, N., & Halpern, B. S. (2017). Our path to better science in less time using open data science tools. *Nature Ecology & Evolution*, 1(6), 1–7. https://doi.org/10.1038/s41559-017-0160
- Maris, V., Huneman, P., Coreau, A., Kéfi, S., Pradel, R., & Devictor, V. (2018). Prediction in ecology: Promises, obstacles and clarifications. Oikos, 127(2), 171–183. https://doi.org/10.1111/oik.04655
- McClure, R. P., Thomas, R. Q., Lofton, M. E., Woelmer, W. M., & Carey, C. C. (2021). Iterative forecasting improves near-term predictions of methane ebullition rates. Frontiers in Environmental Science, 9, 525. https://doi.org/10.3389/fenvs.2021.756603
- McLeod, A. M., & Leroux, S. J. (2021). Incongruent drivers of network, species and interaction persistence in food webs. *Oikos*, 130(10), 1726–1738. https://doi.org/10.1111/oik.08512
- Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G. J., Lavorel, S., Gall,

- L. L., Meslin, L., ... Loreau, M. (2015). REVIEW: Predictive ecology in a changing world. *Journal of Applied Ecology*, 52(5), 1293–1310. https://doi.org/10.1111/1365-2664.12482
- 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. https://doi.org/10.1007/s10144-004-0184-x
- Nosek, B. A., Ebersole, C. R., DeHaven, A. C., & Mellor, D. T. (2018). The preregistration revolution. *Proceedings of the National Academy of Sciences of the United States of America*, 115(11), 2600–2606. https://doi.org/10.1073/pnas.1708274114
- Open Science Collaboration. (2015). Estimating the reproducibility of psychological science. *Science*, 349(6251), aac4716. https://doi.org/10.1126/science.aac4716
- Page, T., Smith, P. J., Beven, K. J., Jones, I. D., Elliott, J. A., Maberly, S. C., Mackay, E. B., De Ville, M., & Feuchtmayr, H. (2018). Adaptive forecasting of phytoplankton communities. *Water Research*, 134, 74–85. https://doi.org/10.1016/j.watres.2018.01.046
- Parker, T., Fraser, H., & Nakagawa, S. (2019). Making conservation science more reliable with preregistration and registered reports. Conservation Biology, 33(4), 747–750. https://doi.org/10.1111/cobi.13342
- Payne, M. R., Hobday, A. J., MacKenzie, B. R., Tommasi, D., Dempsey, D. P., Fässler, S. M. M., Haynie, A. C., Ji, R., Liu, G., Lynch, P. D., Matei, D., Miesner, A. K., Mills, K. E., Strand, K. O., & Villarino, E. (2017). Lessons from the first generation of marine ecological forecast products. Frontiers in Marine Science, 4, 289. https://doi.org/10.3389/fmars.2017.00289
- Pennekamp, F., Iles, A. C., Garland, J., Brennan, G., Brose, U., Gaedke, U., Jacob, U., Kratina, P., Matthews, B., Munch, S., Novak, M., Palamara, G. M., Rall, B. C., Rosenbaum, B., Tabi, A., Ward, C., Williams, R., Ye, H., & Petchey, O. L. (2019). The intrinsic predictability of ecological time series and its potential to guide forecasting. *Ecological Monographs*, 89(2), e01359. https://doi.org/10.1002/ecm.1359
- 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. https://doi.org/10.1073/pnas.1216076110
- Petchey, O. L., Pontarp, M., Massie, T. M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G. M., Altermatt, F., Matthews, B., Levine, J. M., Childs, D. Z., McGill, B. J., Schaepman, M. E., Schmid, B., Spaak, P., Beckerman, A. P., Pennekamp, F., & Pearse, I. S. (2015). The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters*, 18(7), 597–611. https://doi.org/10.1111/ele.12443
- Qiao, H., Feng, X., Escobar, L. E., Peterson, A., Soberón, J., Zhu, G., & Papes, M. (2018). An evaluation of transferability of ecological niche models. *Ecography*, 42, 521–534. https://doi.org/10.1111/ecog.03986
- Rastetter, E. B. (2017). Modeling for understanding v. modeling for numbers. *Ecosystems*, 20(2), 215–221. https://doi.org/10.1007/s10021-016-0067-y
- Redmond, M. D., Law, D. J., Field, J. P., Meneses, N., Carroll, C. J. W., Wion, A. P., Breshears, D. D., Cobb, N. S., Dietze, M. C., & Gallery, R. E. (2019). Targeting extreme events: Complementing near-term ecological forecasting with rapid experiments and regional surveys. Frontiers in Environmental Science, 7, 183. https://doi.org/10.3389/fenvs.2019.00183
- Reichman, O. J., Jones, M. B., & Schildhauer, M. P. (2011). Challenges and opportunities of open data in ecology. *Science (New York, N.Y.)*, 331(6018), 703–705. https://doi.org/10.1126/science.1197962
- Rousso, B. Z., Bertone, E., Stewart, R., & Hamilton, D. P. (2020). A systematic literature review of forecasting and predictive models for cyanobacteria blooms in freshwater lakes. Water Research, 182, 115959. https://doi.org/10.1016/j.watres.2020.115959
- Scheiner, S. (2013). The ecological literature, an idea-free distribution. *Ecology Letters*, 16, 1421–1423. https://doi.org/10.1111/ele.12196

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Sequeira, A. M. M., Mellin, C., Lozano-Montes, H. M., Vanderklift, M. A., Babcock, R. C., Haywood, M. D. E., Meeuwig, J. J., & Caley, M. J. (2016). Transferability of predictive models of coral reef fish species richness. *Journal of Applied Ecology*, 53(1), 64–72. https://doi.org/10.1111/1365-2664.12578

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- Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., ... Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101(1), 58-67. https://doi.org/10.1111/1365-2745.12025
- Thomas, R., Quinn, C., Boettiger, C., Carey, M., Dietze, A., Fox, M., Kenney, A., Laney, C. M., McLachlan, J. S., Peters, J., Weltzin, J. F., Woelmer, W. M., Foster, J. R., Guinnip, J. P., Spiers, A., Ryan, S., Wheeler, K. I., Young, A. R., Johnson, L. R., ... Yule, K. (2021). Ecological forecasting initiative: NEON ecological forecasting challenge documentation V1.0 (v1.0). Zenodo. https://doi.org/10.5281/zenodo.4780155
- Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102(6), e03336. https://doi.org/10.1002/ecy.3336
- 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. 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. 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. https://doi.org/10.1111/j.2041-210X.2011.00170.x
- West, G. B., & Brown, J. H. (2005). The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology*, 208(9), 1575–1592. https://doi.org/10.1242/jeb.01589
- Willson, A., & Peters, J. (2021). Ecological forecasting repository of online educational eesources. *QUBES Educational Resources*, https://doi.org/10.25334/XAW7-JW16
- Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., Fielding, A. H., Bamford, A. J., Ban, S., Barbosa, A. M., Dormann, C. F., Elith, J., Embling, C. B., Ervin, G. N., Fisher, R., Gould, S., Graf, R. F., Gregr, E. J., Halpin, P. N., ... Sequeira, A. M. M. (2018). Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution*, 33(10), 790–802. https://doi.org/10.1016/j.tree.2018.08.001

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