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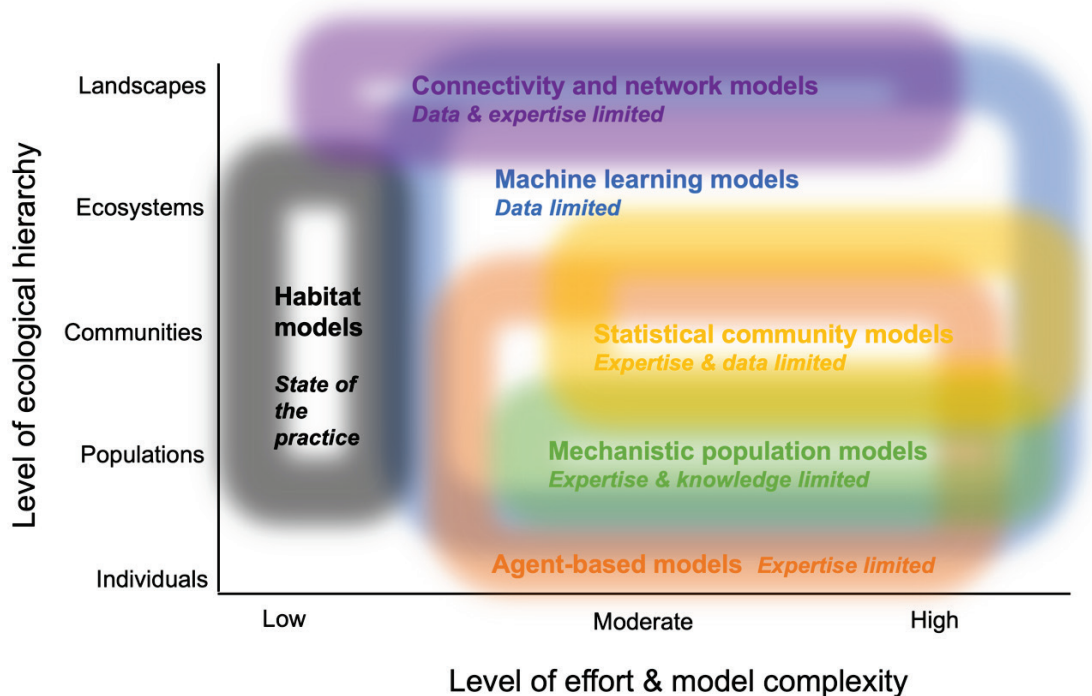
Ecosystem Management and Restoration Research Program

Updating Ecological Modeling Within the US Army Corps of Engineers (USACE)

Exploring Innovative Approaches and Implementation Strategies

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and S. Kyle McKay

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Abstract

The US Army Corps of Engineers (USACE) engages in the planning, design, construction, monitoring, and adaptive management of aquatic ecosystem restoration projects. Like many organizations, USACE uses ecological models to inform decisions regarding ecosystem restoration and management. Most ecological modeling to support ecosystem restoration is conducted using habitat and other index models. However, these approaches have changed little in decades, while the field of ecology has seen the rapid growth of new modeling techniques with an array of applications. More advanced ecological models have the potential to align more closely with aquatic ecosystem restoration project objectives, provide more accurate predictions, and improve the communication of restoration benefits. This overview of modern ecological modeling approaches highlights promising ways to increase the use of advanced ecological models to support ecosystem restoration. We describe the characteristics, benefits, and constraints of five ecological modeling families—agent-based models, population models, community models, connectivity/network models, and machine learning methods—and their applicability to ecosystem restoration projects. We also outline important considerations for selecting ecological models for a given scenario. Finally, we highlight promising avenues for increasing the use of contemporary modeling approaches, including the value of conducting targeted case studies, in light of project planning constraints.

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Preface

This study was conducted for the US Army Engineer Research and Development Center, Environmental Laboratory (ERDC-EL), Ecosystem Management and Restoration Research Program, under Funding Account Code U4405032, AMSCO Code 031342, SON 1570, “Emerging Approaches for USACE [US Army Corps of Engineers] Ecological Modeling.” The program manager at the time of publication was Dr. Brook D. Herman.

The work was performed by the Ecological Resources Branch of the Ecosystem Evaluation and Engineering Division of ERDC-EL. At the time of publication, Mr. Joseph B. Minter was branch chief, Mr. William Jones was division chief, and Dr. Jennifer Seiter-Moser was the technical director. The acting deputy director of ERDC-EL was Dr. Aimee R. Poda, and the acting director was Dr. Brandon J. Lafferty.

LTC Joshua M. Haynes was the commander, and Dr. Beth C. Fleming was the director of ERDC.

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1 Introduction

1.1 Background

The 1986 Water Resources Development Act (WRDA) authorizes the US Army Corps of Engineers (USACE) to modify existing projects for environmental restoration and to construct new projects to restore degraded areas. Project construction is approved after a comprehensive investigation demonstrates technical feasibility, environmental acceptability, and environmental benefits that are cost effective. In 2012, the SMART (Specific, Measurable, Attainable, Risk Informed, Timely) Planning process was introduced to enhance feasibility studies by reducing costs and completion times. Under SMART Planning, studies must conclude within three years, cost under \$3 million, and engage three levels (i.e., district, division, and headquarters) of USACE review. USACE restoration projects affect numerous ecosystem attributes, necessitating evaluation by multiple disciplines within time and budget constraints (McKay et al. 2019). These features and constraints of the project planning processes have heavily influenced the form of ecological modeling that has arisen within USACE and other organizations tasked with ecosystem restoration.

Ecologists use a wide array of models to understand ecosystem structure and function and to generate predictions about how ecosystems are likely to respond to management interventions or environmental perturbations (Swannack et al. 2012). During feasibility studies, ecological models are used to assess the likely ecosystem effects and benefits of projects, identify problem areas, and select among multiple alternative management scenarios. They are also used in the monitoring and evaluation phases of adaptive management before and after project implementation (Fischenich et al. 2019). Historically, organizations have used index-based habitat models (e.g., habitat suitability index [HSI] models and hydrogeomorphic approach models [HGMs]) to evaluate ecological outcomes (Brooks 1997; Roloff and Kernohan 1999). These models generally combine the size or quantity of an ecosystem (i.e., its length, area, or volume) with an assessment of the quality of that patch (i.e., a 0 to 1 index, where 1 indicates ideal ecological conditions for the target ecosystem or species).

While habitat models have remained a popular ecological modeling approach, ecological modeling has evolved in profound ways in the last 20 years, driven by several co-occurring factors. These factors include the

rise of large datasets, the development of novel analytical methods, the increase in computing power, and the advent of free software and training in complex analyses (Gimenez et al. 2014). Additionally, the fields of ecology and ecosystem restoration have matured significantly since their establishment in the 1950s and 1980s, respectively. The use of modern models has enabled progress in diverse areas of ecology, such as in forecasting harmful algal blooms (Manning et al. 2019) and predicting near-term distributions of commercial fish species (Eveson et al. 2021). The rapid growth of ecological modeling methods has the potential to enhance project execution, from feasibility to operations and maintenance. In particular, some nonhabitat modeling approaches may more directly measure project objectives, improve understanding of restoration benefits, and reduce uncertainty.

1.2 Objectives

The objectives of this technical report are to provide ecosystem restoration practitioners with an overview of modern ecological modeling families and approaches and to outline ways in which contemporary ecological modeling methods might be incorporated into project planning practices.

1.3 Approach

The information and ideas in this report are a result of a literature review on ecological modeling practices; communication with USACE districts and ecological modeling researchers; and discussions during a workshop, held 12–13 September 2023, on current ecological modeling approaches. Researchers and practitioners from the Environmental Laboratory (EL) at the US Army Engineer Research and Development Center (ERDC), the USACE Ecosystem Restoration Planning Center of Expertise (ECO-PCX), multiple USACE districts (e.g., Albuquerque, Sacramento, New York, Rock Island, and Baltimore), the Southern California Coastal Water Research Project, and the Pacific Northwest National Laboratory evaluated innovative methods for modeling habitat suitability, identified USACE's requirements for contemporary ecological models, and discussed opportunities and challenges in applying these models within USACE.

In Section 2, we discuss the strengths and limitations of habitat models. In Section 3, we present an overview of contemporary ecological model families, highlight the strengths and challenges of different modeling types, and identify how different models might best be incorporated into projects. Finally, in Section 4, we detail specific steps that might be taken to

promote the use of both advanced ecological models and good modeling practices within projects. Although our results are tailored to address the USACE planning process, they are applicable to any organizations' restoration planning process.

1.4 Scope

This report presents a possible future trajectory for ecological modeling within USACE and charts diverse ways that modern ecological modeling might be incorporated into USACE research and practice. We considered organizational constraints, such as short project planning timeliness, limited resources, and technical learning curves, in our analysis. While the examples presented on applying advanced ecological modeling within USACE practices have not been tested, research is underway to develop case study demonstrations using these methods. The outcomes of these demonstrations will be documented in future publications.

2 The Current State of Practice in Ecological Modeling for Restoration Project Planning

2.1 The Use of Habitat Models

Habitat models quantify the suitability or quality of habitats using indexes that range from 0 to 1 to indicate unfavorable or favorable habitat conditions. Inhaber (1976, as cited in FWS 1981) defined an index as the ratio of a focal value divided by a standard of comparison. In this approach, the focal value is an estimate or measure of habitat condition, and the standard of comparison is the ideal habitat condition. These models have been referred to by multiple terms, such as *habitat suitability models* (FWS 1981), *index-based models* (Swannack et al. 2012), and *functional assessments*, and have applications at population, community, and ecosystem scales. However, we use the more colloquial term *habitat models* to refer to this family of models.

Entities like USACE commonly use habitat models like HGM and HSI for ecosystem planning (Cole 2006; Tirpak et al. 2009). HGM models are used to assess wetland functions in the context of regulatory, planning, or management actions, and they consider the physical, chemical, and biological characteristics of wetlands. They use indexes from 0 to 1 to estimate the capacity of a wetland to perform various important ecosystem functions (e.g., cycling nutrients and provisioning habitat) relative to a reference wetland in a comparable geographic region that exhibits the highest sustainable level of function (Smith et al. 1995). In this report, however, our discussion of habitat models primarily focuses on HSI models due to their greater frequency of use within USACE restoration planning.

HSI models are used to assess the quality of a habitat based on its ability to meet the life requirements of a species. These models were established in 1974 by the US Fish and Wildlife Service (FWS) with the development of Habitat Evaluation Procedures (HEP) for project planning and environmental impact assessments (FWS 1980). The outcomes of HSI models are numerical indexes that indicate the capacity of a habitat to support a given fish or wildlife species (FWS 1981) and range from 0 to 1, where 0 indicates *least suitable* and 1 indicates *most suitable*.

HSI models allow scientists and engineers to link physical habitat changes to ecological effects on focal taxa. Model developers primarily use expert opinion to formulate simple mathematical formulas that relate physical habitat attributes to the species' life requirements. The simple and comprehensible nature of these models allows for collaborative and transparent model development processes, while meeting the strict time and budgetary constraints that typify project planning. Consequently, USACE commonly uses HSI models to estimate the amount of suitable habitat gained or lost as a proxy for a project's overall ecological effect.

2.2 The Limitations of Using Habitat Suitability Index (HSI) Models

While valuable in planning scenarios with constrained timelines and budgets, HSI models have a variety of shortcomings. Some overarching limitations of HSI models are their static nature, inadequate representation of input data variability, use of simplistic equations to represent complex species–habitat dynamics (Roloff and Kernohan 1999), and biases toward frequently utilized species or environmental variables for which data exist as opposed to the variables most important for a species. In many cases, HSI models also fail to incorporate ecologically appropriate spatial scales. Here, we discuss some of these limitations in greater depth.

HSI models were designed to index habitat potential, not variation in the dynamics of populations or habitats (Roloff and Kernohan 1999). Consequently, models assume that relationships between species and environmental variables remain constant over time and space. In reality, however, the forces that govern both populations and habitats are temporally dynamic, and the scales at which environmental variables affect species can also vary over geographic space. HSI models can also neglect considerations of ecological processes that occur across varying levels of biological organization (Yackulic and Ginsberg 2016).

HSI analyses often rely on overlain spatial datasets to characterize habitat quality, and ample hydrologic and environmental datasets are now available for most HSI models. However, spatial inaccuracy and uncertainty due to temporal variability can greatly bias habitat quality estimates. While variance associated with input data in HSI models can be accounted for using randomized procedures (Bender et al. 1996), in practice, overall uncertainty is rarely quantified; instead, HSIs are typically calculated deterministically (Zajac et al. 2015). Other features of the data

(e.g., its resolution, method of collection, and processing) can also affect computational results. Ideally, environmental datasets should be closely inspected for quality control via comparison with independent datasets (e.g., satellite imagery or georeferenced field measurements), but this is not always possible.

The manner in which overall HSI scores are calculated from the scores for each environmental variable can also generate improper conclusions. Suitability indexes for individual environmental variables are calculated using different mathematical functions (i.e., linear, logistic, and categorical) to generate suitability index curves or bars (if categorical) that represent species–habitat relationships for individual habitat components (e.g., vegetation density and tree canopy height). These indexes have breakpoint values, representing species-response thresholds. Indexes can be combined using a host of different functions (e.g., minimum values, products, and means) to produce a final composite HSI score (Carrillo et al. 2022). However, the choice of aggregation function may greatly influence model outputs and therefore potential management decisions. Additionally, combining suitability index curves may amplify any errors in suitability index graphs or their underlying assumptions and can also obscure any distinct qualitative differences between the environmental components (Van Horne and Wiens 1991).

When HSI models are used to select among project alternatives, a single species or a handful of species are often used to represent the overall effects on the ecosystem. Therefore, the modeled species may not represent effects on other species or the overall ecosystem condition. Furthermore, the selection of environmental variables to include in a model inevitably affects the model’s conclusions, but variables may be selected because they are easy to measure or already available rather than because they are essential to the life requirements of a species. In addition, variables that capture ecosystem processes such as nutrient and carbon cycling may affect ecological outcomes, but compared to structural dimensions of habitat (e.g., nutrient concentration, depth, and velocity), they are rarely included in HSI models. Choosing the appropriate number of environmental variables to include in models is also crucial because doing so balances trade-offs between model generality, tractability, and interpretability (Levins 1966; Larsen et al. 2016). However, while rigorous procedures exist for determining appropriate model complexity, these are often not carried out when applying HSI models.

Finally, in many environmental planning or restoration scenarios, models that explicitly target the population, species, or community level of ecological organization may more closely align with project objectives than models that analyze habitat. For example, if the goal of a restoration project is to provide explicit benefits to an endangered fish, modeling the population response of the species to restoration scenarios could provide relevant information on the benefits or costs of different alternatives, such as whether the extinction probability of a species changes (Bakker and Doak 2009).

3 The State of the Science for Ecological Modeling

3.1 Families of Ecological Models

A diverse array of ecological models beyond habitat models have the potential to improve planning processes carried out by USACE and other agencies conducting ecosystem restoration. For the sake of clarity, we define ecological models as mathematical or numerical representations of ecological systems in which outcomes of interest (e.g., the abundance of populations of imperiled species) are linked to environmental attributes or other factors amenable to intervention by managers (Glaser and Bridges 2007). To have utility in project planning, an ecological model should be able to

- distinguish between proposed project alternatives,
- include input from multiple sources once a conceptual model or model framework has been developed,
- apply to problems at different scales,
- be relevant to different levels of biological organization (e.g., species, community, and ecosystems), and
- communicate the benefits of a recommended restoration plan (Herman et al. 2018, 2019).

In this section, we discuss ecological model types that can meet these criteria or offer promise when assessing project scenarios or project alternatives. We define project scenarios as different types of planning projects and project alternatives as alternative options for a restoration project that are compared using benefits and costs. Our discussion focuses on the elements of ecological models that can help users decide whether a model is adequate for a given project scenario or for assessing planning alternatives. Considering model adequacy requires accounting for the time, expertise, and data available for a given modeling task (Harris et al. 2023) and the level of accuracy and sophistication that will be required based on the decisions that will be guided by the modeling effort (Getz et al. 2018). Identifying adequate ecological models also requires considering some model elements, such as data quality, model validation, and uncertainty, that this report does not dwell on in depth. For guidance on these subjects and other general ecological modeling topics, we direct readers to

Swannack et al.'s (2012) *Ecological Modeling Guide for Ecosystem Restoration and Management*.

Categorizing ecological models into model families can help potential model users understand the diversity of ecological modeling approaches available for different tasks and identify appropriate models for specific applications. One approach to categorizing ecological models is to do so based on their methodological or philosophical similarity. Swannack et al. (2012) employed this method in their guide on using ecological models for planning ecosystem restoration and management activities, and they described six classes of models: analytical, conceptual, index, simulation, statistical, and spatial. This categorization scheme acknowledges that two features of a project scenario—the amount of data available and the degree to which a system is understood mechanistically—may collectively point to the type of ecological model that might be best employed (Schuwirth et al. 2019).

In this report, however, we pursue a different approach: We primarily categorize models based on the level of ecological hierarchy a model addresses (Figure 1). We chose this classification scheme because planning projects frequently target specific attributes of an ecosystem (i.e., objectives surrounding a focal taxon or an ecosystem process), and it is consistent to consider ecological models through the same lens. Therefore, we discuss in detail four classes of models that target different levels of the ecological hierarchy: individuals, populations (i.e., multiple individuals of the same species), communities (i.e., sets of co-occurring species), and landscapes (with a focus on models that assess hydrologic connectivity at the riverscape or river network scale). While the current suite of ecological models used in many planning projects predicts the amount of habitat expected to be created or lost under project alternatives, the levels of ecological organization assessed by the models that we highlight may frequently align better with project goals. In addition to considering models that target these levels of ecological organization, we also discuss another class of models with high relevance for restoration projects: machine learning (ML) approaches, which are not limited to any level of biological organization. Figure 1 and Table 1 provide an overview of these model families. Figure 1 indicates both that the modeling families in this report vary based on the level of ecological hierarchy that they typically address and the general amount of effort inherent in using each approach. Table 1 highlights some

of the strengths and challenges associated with using the different families of models.

Figure 1. The ecological model families plotted according to their typical level of effort and the level of ecological hierarchy they most commonly assess. The diffuse boundaries indicate that models within each class can vary widely in terms of effort and target level of ecological organization. Models in a given family may exist outside of the boundaries, which are drawn not to encompass every model that exists in that family but, rather, to emphasize the most frequent attributes of each model class. *Level of effort* refers to the investment in time, money, and expertise required to utilize models within that family. *Italicized phrases* indicate common features that may limit the use of these models.

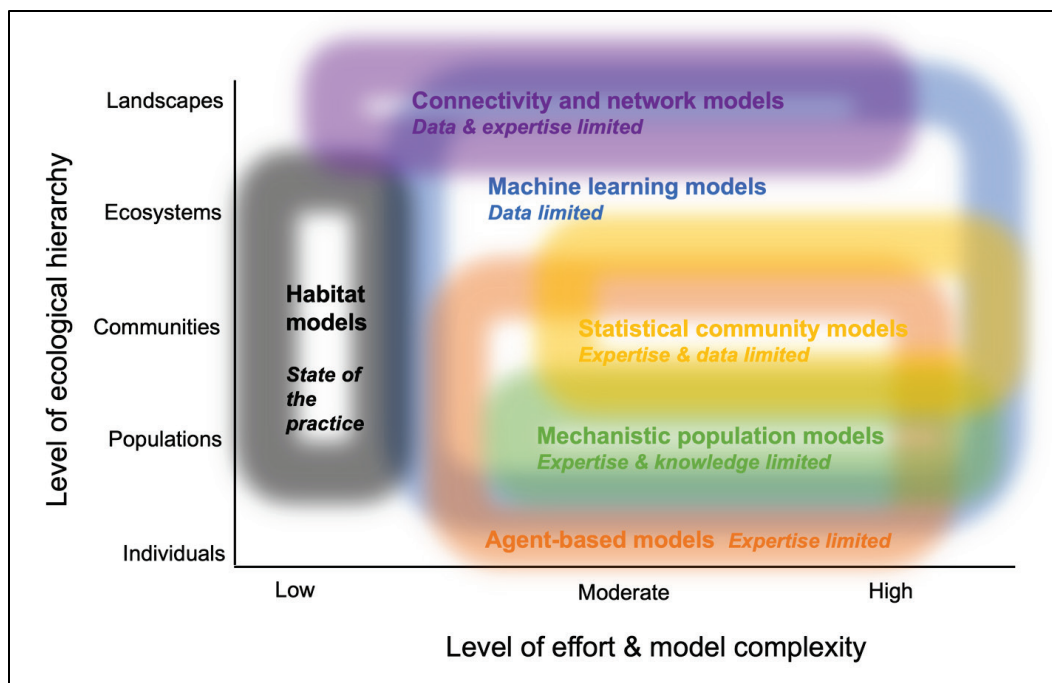


Table 1. An overview of the model families in this report and some advantages and challenges associated with them. Italicized models have been used within US Army Corps of Engineers (USACE) projects or were developed by USACE personnel.

Model Family	Advantages	Disadvantages	Representative Analytical Models	Example Management Question
Habitat models	• High familiarity in planning context • Easy to interpret • Relatively fast to implement • Can integrate a range of factors relevant to engineering design criteria • Hundreds of USACE-certified models	• Static in time and space • Largely overlook ecological interactions • Rarely incorporate uncertainty • Habitat is usually not the ultimate goal but a proxy for an outcome of greater interest	• <i>HSI</i> • <i>HGM</i> • <i>HEP</i>	How will the amount of habitat for a species of interest be altered under different restoration scenarios?
Agent-based models (ABMs)	• Incorporate individual heterogeneity • High flexibility but can be rule based • Capture spatiotemporal dynamics • Strong applicability to animal-movement-related analyses • Higher-level properties emerge from individual interactions • Visualizations make powerful communication tools	• Some level of coding is required • Model mechanics can be difficult to understand • Difficult to validate and evaluate using traditional methods • Sensitive to parameter values • Can be computationally demanding • Limited generalizability	• <i>Fish Habitat Assessment and Simulation Tool (FHAST)</i> • <i>Eulerian-Lagrangian-agent method (ELAM)</i> • <i>Dune Ecogeomorphic Vegetation Community Photosynthesis-Driven Spatial (DOONIES) model</i>	What proportion of salmon will successfully navigate a fish ladder, given the projected hydraulic environment, salmon swimming performance, and individual behavior?
Population models	• Direct connection to management objectives related to individual species • Can be simple or complex • Highly established methods that accommodate uncertainty • Strong linkage with conceptual models and ecological theory	• Often require significant data • Missing data can pose challenges • Many are highly technical • Time required for model development/computation can be large • In mechanistic versions, parameter values can be hard to obtain and subject to bias	• Occupancy models • Mark-recapture models • Matrix population models • Metapopulation models • Stochastic simulation models	Which management alternative will cause the greatest increases in abundance, recruitment, and survival for a target species?

Table 1 (cont.). An overview of the model families in this report and some advantages and challenges associated with them. Italicized models have been used within US Army Corps of Engineers (USACE) projects or were developed by USACE personnel.

Model Family	Advantages	Disadvantages	Representative Analytical Models	Example Management Question
Community models	- Align well with biodiversity-focused objectives - Frequently easy to interpret - Can integrate many features of the ecosystem and provide a nuanced understanding of the effects of management decisions	- Selecting an appropriate community metric can be difficult - Incorporating community interactions results in complex models - Often difficult to link to conceptual models - Can require complex statistical methods and expertise	- Ordination approaches (e.g., principal components analysis) - Biodiversity index assessments (richness and evenness)	How will different restoration scenarios affect lentic fish species richness?
Connectivity and network analytic techniques	- Large variety of tools, including easy-to-implement USACE-certified models - Many can be customized to the species of interest or to project specifications (e.g., passage at specific dam) - Some can incorporate spatial river network information; also environmental/ecological variables - Useful for prioritization/optimization	- Most metrics focus on structural elements (e.g., river lengths or interpatch distances), but these can be a poor proxy for movement or other ecological outcomes - Difficult to determine the most applicable measure of connectivity in many scenarios - Inaccurate species data can bias estimation of connectivity or passage - Incorporating network information may require technical expertise	- Dendritic connectivity index (DCI) <i>Fish passage connectivity index (FPCI)</i> <i>Watershed Upstream Connectivity Tool (WUCT)</i> - Spatial stream network model	Which fish passage alternative will increase upstream habitat the most for migratory fish? Which are the most cost-effective dams to remove in a basin to increase overall connectivity?
ML methods	- Data-driven/inductive - High predictive accuracy - Complex pattern recognition - Extreme flexibility (different data types and structures) - Standard sets of procedures - Support ensemble modeling - Rapid innovation in algorithms	- Little-to-no connection to conceptual models - Large data requirements - Susceptible to overfit models that do not transfer well - Model mechanics can be difficult to understand - Some expertise required, but lots of training available	- Random forest - Boosted regression trees - Support vector machines - Neural networks (convolutional, recurrent, and artificial) - Deep learning	How will the distribution of individual species and groups of species change following management alternatives?

The subsequent sections of this report provide a narrative discussion of each modeling family. For each model family, we also provide a box that highlights a compelling case study analysis in which that model type was used in a restoration or resource management context. For additional information about different ecological models, see Appendix A for a table of 15 different ecological models and the relevant management questions that they can assess. Appendix B includes a select bibliography of publications that provide guidance on ecological modeling in general and on specific classes of ecological models.

We believe that our model categorization approach will be helpful to project managers and biologists implementing ecosystem restoration projects, but there are some shortcomings to our method of classification. First, some categories, such as population models, contain approaches with a diverse range of methodological underpinnings (e.g., theoretical predator–prey models versus hierarchical occupancy models), and grouping these models together risks glossing over these distinctions. Relatedly, the potential breadth of methodological approaches that compose some of our categories limits the extent to which we can provide detailed descriptions of each distinct model within a class. Finally, there are some useful ecological models that do not fit easily into any of our categories. For example, structural equation models and other integrated ecosystem models can quantify the relationships among different elements or compartments (e.g., primary productivity, consumers, or predators) that compose ecosystems. We do not discuss this class of models in depth because the large data requirements at several levels of ecological organization and the computational requirements of many ecosystem models currently limit their potential utility within most planning projects.

3.2 Detailed Discourse on the Most Relevant Ecological Models: Attributes, Constraints, and Applications

3.2.1 Agent-Based Models (ABMs)

3.2.1.1 Model Description and Benefits

Agent-based models (ABMs) are designed to simulate system-scale properties that emerge from the behavior of individuals interacting with each other and the environment (Grimm and Railsback 2013). Although the individual is the focal unit of these models, ABMs distinguish themselves with their unique spatial capabilities, which enable ecologists to assess

how variability in the behavior of individuals leads to emergent properties, such as changes in abundance, distribution, or habitat uses, at the population and community levels—both of which are of greater interest to practitioners than the behavior of any one individual. ABMs have grown significantly in the past two decades, marked by the development of numerous modeling platforms (e.g., NetLogo) and substantial guidance on model development and usage (DeAngelis and Diaz 2019). ABMs allow for the explicit incorporation of decision-making by individual agents or organisms, which can be important in some management contexts, especially those seeking to influence the spatial distributions and movement patterns within a population.

3.2.1.2 Model Constraints

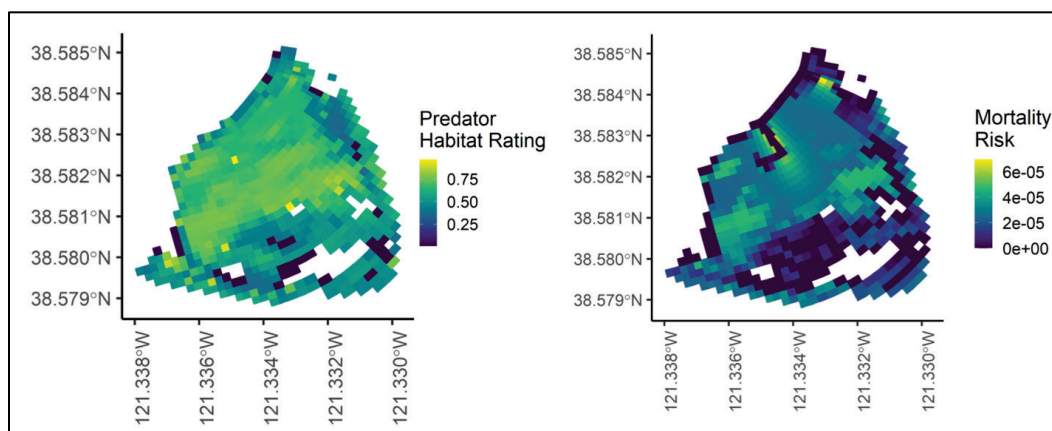
Several of the challenges in using ABMs are typical of complex modeling approaches: They require computational expertise, can be time-intensive to set up and run, and may be difficult to interpret and transfer to other locations or systems. Evaluating and validating ABMs can also present unique challenges (Augusiak et al. 2014; Grimm et al. 2020). The evaluation process in ABMs often revolves around comparing emergent patterns within the model to those observed in nature (e.g., pattern-oriented modeling; Grimm et al. 2005). Models that exhibit patterns closely resembling true observations are typically deemed more realistic. However, there is a risk that models may be able to generate emergent patterns that correspond well with empirical observations despite underlying misspecifications of the model (Augusiak et al. 2014), which could compromise the model's utility in novel scenarios. Additionally, independent empirical data for evaluation purposes may be scarce or nonexistent in some cases.

3.2.1.3 Model Application in Project Planning

ABMs have considerable utility in planning projects that feature complex systems in which individual variation, interactions among organisms, or behavior is important. ABMs have been used in multiple systems, including assessing fish responses to dam removal or passage measures (Goodwin et al. 2014), assessing oyster management scenarios in Chesapeake Bay (Kjelland et al. 2015), invasive mussel dispersal throughout Texas (Robertson et al. 2020) and the Western US (Carrillo et al. 2023), and dune development through plant and sediment interactions (Charbonneau et al. 2022).

Spatially explicit ABMs provide multiple benefits to complex environmental projects by providing a spectrum of outputs, including habitat utilization, movement patterns, population distributions, interactive behaviors, and abundance metrics (McLane et al. 2011). Figure 2 and Box 1 demonstrate spatially explicit output from the Fish Habitat Assessment and Simulation Tool (FHAST), an ABM designed to assess the effect of management interventions on anadromous fish. Spatially explicit outputs not only broaden the range of information provided by the model but also extend the utility of ABMs beyond habitat models, allowing for a richer understanding of the system dynamics and providing a comprehensive assessment for decision-making processes. Because ABMs are inherently spatial, they can be used to generate either static or dynamic (i.e., movie-like) visualizations to display the breadth of potential outputs. This makes ABMs excellent communication tools because they can facilitate a deeper understanding of system dynamics, increase communication among partners, and promote coordination among different agencies (Le Page et al. 2013).

Figure 2. An example output from the Fish Habitat Assessment and Simulation Tool (FHAST), an agent-based model (ABM) that makes spatially explicit predictions relevant to anadromous fish.



Box 1. Example agent-based model (ABM).

The Fish Habitat Assessment and Simulation Tool (FHAST) is an agent-based model (ABM) for anadromous fish that produces habitat metrics, summaries, and indexes that can be used to make river management decisions. The US Army Corps of Engineers (USACE) Sacramento District funded the Southwest Fishery Science Center at the University of California, Santa Cruz, to develop FHAST. FHAST uses open-source software to compare habitat before and after management interventions within a river. The model focuses on the riverine life stages of anadromous fish, specifically Chinook, steelhead, and green sturgeon, in the mainstem and tributaries of the Sacramento River. Each fish life stage is modeled independently for analysis. The model framework is robust for cross-walking to other river systems with suitable hydraulic models (e.g., Hydrologic Engineering Center's River Analysis System [HEC-RAS]) and to additional fish species with sufficient physiological data. FHAST includes components for modeling bank vegetation growth, shade, food production, daily fish movement, stranding, metabolism, thermal risk, feeding, adult migration, and piscivore predation. FHAST can generate a large number of spatially explicit outputs. Here we show two example FHAST outputs for Chinook salmon in the American River in Sacramento, California: a measure of habitat suitability for predators (Figure 2a) and the probability of mortality across space (Figure 2b). Spatially explicit outputs can be summarized to produce metrics that can be used by decision-makers to select among project alternatives.

3.2.2 Population Models**3.2.2.1 Model Description and Benefits**

Population models are a diverse set of techniques used to quantify how animal or plant populations change in abundance and distribution through time and space, often in response to changing environmental conditions or other predictors. They can be linked to dynamic representations of habitat ranging from suitability indexes to explicit modeling of habitat quantity. They can also incorporate spatial structure (e.g., for patchy habitat or metapopulations; Robles and Ciudad 2012), but movement is typically a function of population characteristics or habitat conditions, not individual decisions as in ABMs.

Most population models can be classified as empirical, mechanistic, or a hybrid of the two (Kendall et al. 1999). Empirical population models (e.g., capture-mark-recapture analyses; Letcher et al. 2015) often use field monitoring data to estimate population attributes like survival, fecundity, or growth rate. They can be specified to the level of process detail for which data are available, or to the level that is critical for management decisions, while reducing complexity elsewhere. Empirical models are best implemented after a time series of monitoring data has been established. Management scenarios can also be modeled empirically if they have been implemented and monitored or, in future scenarios, by adjusting empirical relationships with hypothesized effects. Mechanistic models use mathematical functions to represent population processes, based on ecological theory or qualitative observations of life history, to simulate population dynamics. Mechanistic models can be specified to the level of detail needed for modeling management scenarios, including the effects of one or multiple management actions on specific life stages. Mechanistic models can be parameterized with monitoring data but may also use parameters estimated from other studies and systems to fill data gaps. By doing so, they can be implemented where no long-term monitoring data exist. It is possible to combine both empirical and mechanistic approaches in a single model, depending on the level of theoretical understanding, qualitative versus quantitative observational information available, and management needs.

A key reason to use population models is that they focus on the level of biological organization—the population—that is the target of many restoration or management measures. This is especially true for species that are imperiled, commercially important, or non-native. In contrast to most stand-alone habitat models, a benefit of population models is that they can be constructed to directly reflect how attributes of the environment—including ones that management measures can alter—govern vital demographic processes such as growth, survival, and reproduction. Consequently, they can model outcomes of interest to managers, such as population growth or decline, distribution among patches, or the risk of extirpation. Population models have been used and developed for decades, longer than other types of ecological models, and consequently, they are likely to feature the most established methodologies, published case studies, and number of variants among ecological models.

A strength of population models is their capacity to incorporate and account for multiple types of uncertainty, though this is not solely a feature of population models. All empirical models, population or otherwise, statistically estimate the value of model parameters (e.g., survival rate) along with estimates of uncertainty, such as 95% confidence intervals. Parameter uncertainty can be built into model-derived predictions to indicate the potential range of ecological responses to management actions. In mechanistic simulations and empirical–mechanistic hybrid models, uncertainty is incorporated by running many simulations while altering certain aspects of the model, especially parameter values, structural elements of the model (e.g., which environmental predictors are included), or the functional form of the relationships (e.g., linear versus nonlinear). The success with which surveys of animal populations detect individuals usually varies by site, season, or other factor, and population models can account for uncertainty related to the detection process in several ways (Dénes et al. 2015). Variability in environmental conditions that affect population parameters can also be included. By including uncertainty, population models express both the limitations of the data used and the variability inherent in many environments that may not be reducible. They can be used to assess the value of additional data collection and to identify which research areas would most improve the confidence intervals for management scenarios and, thus, confidence in decision-making.

3.2.2.2 Model Constraints

Population models require either fairly large amounts of monitoring data, ideally collected over time, from which to construct empirical models or adequate parameter estimates derived from other research that indicate how populations are likely to respond to environmental changes or management actions, which can then be used for running simulations. When such parameter estimates exist, it is important to consider whether the circumstances (e.g., location or season) in which they were derived are similar enough to the desired application to warrant their use. If neither monitoring data nor reliable parameter estimates are available, it may be necessary to collect additional data or consider other types of models to use. Prototype models constructed with limited data and expert opinion can be developed to help identify information needs. These can be useful for adaptive management in low-information situations: Models can inform monitoring and research and incorporate new information over time until they are mature enough to guide management decisions.

As with ABMs, population models, particularly complex ones, can require technical expertise to build and longer time frames to implement than simpler habitat models, and some planning projects may not be able to accommodate them under typical project timelines. However, the extent to which population model methodologies are well-developed—especially in the case of empirical models—means that if data exist in the right form, relatively complex population models can be built quickly using code developed for other projects and shared via books (e.g., Kéry and Schaub’s [2011] Bayesian population analysis text), in the supplemental material of papers, or in code repositories (e.g., GitHub).

3.2.2.3 Model Application in Project Planning

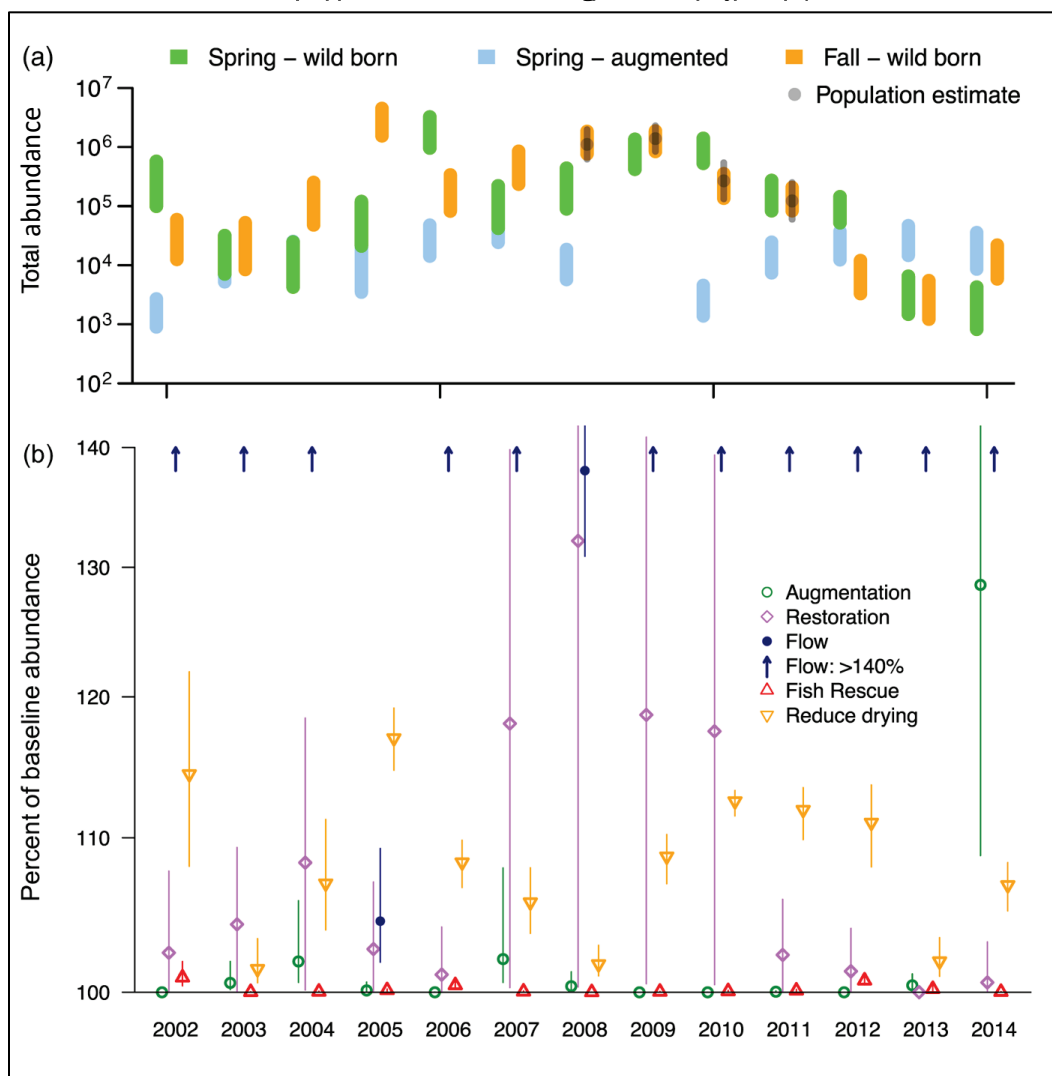
There are several restoration project scenarios in which population models might be particularly valuable, for reasons related to both project goals and logistics. If the objectives of a project target the recovery of a specific organism, then population models are a natural choice. This may be especially true if multiple projects within a district target the same species, which can help offset the initial investment in time and expertise required to build the population model. Population models are also a good fit for cases in which adaptive management is used because they can incorporate the effect of management activities on population parameters (directly or via habitat change) and can be updated following management intervention and new data collection to inform future decision-making (Buenau et al. 2014).

From a logistical standpoint, population models might be considered in systems with large amounts of environmental and population data or where detailed knowledge of the system exists that would enable the construction of mechanistic population models, although such features could also support the use of an agent-based or ML approach. Population models may already exist in some form for a focal species (e.g., a population viability analysis previously developed for a species recovery planning process that can be adjusted to meet project needs).

Outputs from population models can inform decision-making processes in multiple ways. Population models can estimate, with uncertainty, the expected abundance, density, or persistence of a species that a specific project might generate, and decision-makers could use this value to select among project alternatives instead of, or in addition to, using the amount of habitat created. They can also be used to assess the effectiveness of

different management strategies, including habitat restoration (Yackulic et al. 2022; Figure 3; Box 2). Some population models are spatially explicit and could be used to estimate metrics even more analogous to the output of a habitat model if desired. Spatially explicit occupancy models (e.g., Olea and Mateo-Tomás 2011) that incorporate the habitat metrics being manipulated via restoration could be used to predict the area of habitat that would likely be occupied by a given species following management actions. Such an approach would have the added benefit of producing maps that clearly communicate areas of the restoration project with the highest likelihood of future occupancy by the species of interest.

Figure 3. Sample results from a population model for the Rio Grande silvery minnow (RGSM). (Image adapted from Yackulic et al. 2022, Figures 4 and 8. CC BY 4.0, <https://creativecommons.org/licenses/by/4.0/>.)



Box 2. Example population model.

Yackulic et al. (2022) developed a population model that quantifies the effects of river discharge on the abundance of endangered Rio Grande silvery minnow (RGSM). Several agencies, including USACE, engage in extensive activities to aid this species, and this model provides insight into how effective different management strategies are at boosting RGSM populations. The top panel in Figure 3 shows estimates of the abundance (along with confidence intervals) of different RGSM life stages through time. Supplemental RGSM field monitoring from 2008 to 2010 enabled full estimates of the population in these years (gray points and lines in the figure's top panel), and the population model developed by Yackulic et al. (2022) leveraged these estimates to predict the abundance of different fish life stages in all years from 2002 through 2018 (years following 2014 are not depicted here). The bottom figure panel exhibits the efficacy of different management activities by indicating the percent increase in RGSM populations in different years that would have been caused by the management strategies featured in the legend, which include (1) augmenting wild RGSM populations with hatchery-reared fish, (2) restoring floodplain habitat to improve RGSM spawning, (3) releasing additional water from dams during spring to facilitate spawning, (4) rescuing fish from isolated pools during summer dry periods, and (5) decreasing the extent to which portions of the river become completely dry in summer. In all but one year, increasing spring flows via dam releases would have had the greatest effect on minnow abundance and was predicted to increase overall RGSM abundance by more than 140% in most years (i.e., the years with the blue arrows). Habitat restoration may have had a strong effect in a subset of years (e.g., 2007–2010), but these predictions were more uncertain than most management options based on large confidence intervals (i.e., the vertical lines associated with each point). Rescuing fish (red triangles) or augmenting populations with stocked individuals (green circles) would have had little influence on abundance in most years. Population analyses such as this one can help increase the efficacy of endangered species management.

3.2.3 Community Models

3.2.3.1 Model Description and Benefits

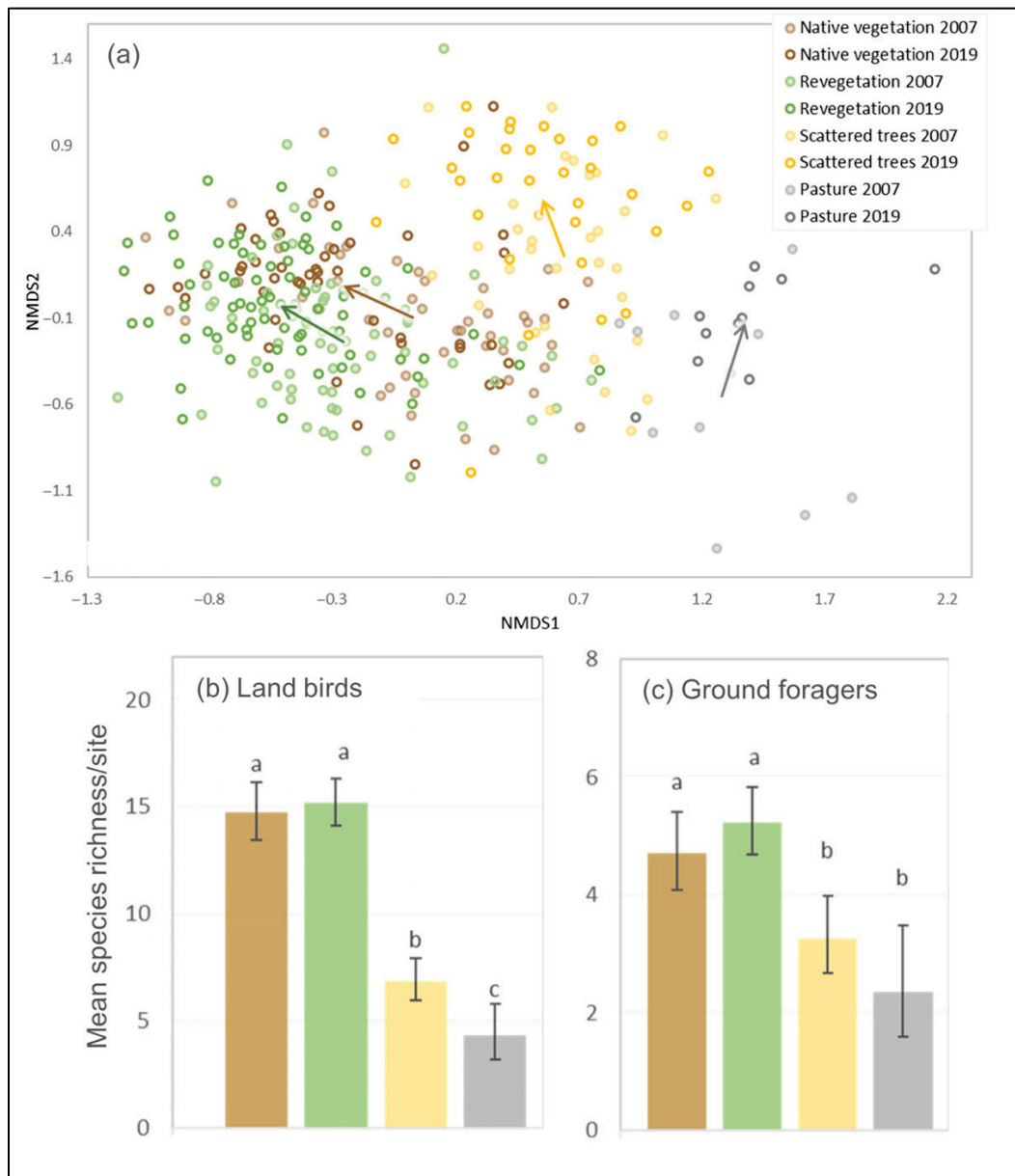
Community models are ecological models that consider more than a single species. These models often evaluate all species within a taxonomic group (e.g., all fish species at a site); a specific subset of a taxonomic group, such as the macroinvertebrate species that are deemed sensitive; or species at multiple trophic levels (e.g., producers, consumers, and predators). Societal objectives for restoration or mitigation projects often include goals related to protecting or augmenting biodiversity, and community models may align more closely to these types of objectives than to single-species ecological models.

Community models have diverse methodological underpinnings, but there are some key features that distinguish community model types. One is whether models explicitly incorporate interactions among species, such as competition and predation; including interactions typically results in models being substantially more complex. A second key feature is whether each species in a guild of interest (e.g., fish) is represented explicitly within the model or if multiple species are aggregated at the outset of modeling into a biodiversity metric (e.g., the number of lentic fish species present), and the model then evaluates how the chosen metric varies based on environmental predictors. Again, models considering the fate of multiple individual species, such as in the case of joint species distribution models or joint abundance models (Warton et al. 2015), tend to require more data and be more computationally challenging than those that evaluate biodiversity metrics. Consequently, it is common to see community models that constrain complexity by using multivariate methods (i.e., ordination approaches like principal component analysis) that reduce the dimensionality of the problem (Figure 4, top panel; Box 3) or by aggregating species into guilds or categories (Figure 4, bottom panel; Box 3). The choice by managers and modelers to use simpler models relying on biodiversity metrics like species richness—as opposed to multispecies models—is governed by how well the different metrics can capture the needs of a given project and what data and modeling expertise can be used.

In cases in which the community is represented by a biodiversity metric, the most appropriate metric should be selected carefully (Roswell et al. 2021) to ensure that the metric aligns with project goals. For example, if the objective of a restoration project is to increase fish biodiversity at a

site, models that predict changes in species richness (i.e., the number of species at the site before and after restoration) might be used. However, species richness is a simplistic measure that does not account for differences in the abundance of each species. Numerous alternative biodiversity metrics exist, theoretically enabling ecological modelers to select metrics that best fit their needs (Moreno et al. 2017).

Figure 4. Example results from a study assessing how farmland restoration affects bird communities. (Image adapted from Haslem et al. 2024, Figures 2, 4, and 5. CC BY-NC 4.0, <https://creativecommons.org/licenses/by-nc/4.0/#ref-commercial-purposes>.)



Box 3. Example community model.

Haslem et al. (2024) developed models to examine how farmland restoration strategies affected different aspects of bird communities in Australia through time. Their analysis used both ordination techniques and models that assessed biodiversity metrics, including the richness of different bird guilds, to examine differences in bird communities among sites with divergent land-use histories, including farmed pasture, revegetated former farmland, and forested reference sites. The top panel in Figure 4 is a plot depicting the results of a type of ordination called non-metric multidimensional scaling (NMDS) in which the differences in diversity and abundance of species at different sites is collapsed into two dimensions to more easily visualize the complex species–abundance data. Each point represents the bird community at a site, and points that are closer to each other have more similar bird communities, with axes representing unitless distances in ordination space. The ordination analysis indicates that the bird communities at sites restored via revegetation (green points) are similar to reference sites (brown sites), which suggests a measure of restoration success, especially as time-since-restoration increases (i.e., in 2019 versus 2007). The lower panels show a sample of their results that used biodiversity metrics, specifically the species richness (i.e., the number of different species present) in 2007 at sites featuring different land-use conditions (with colors corresponding to the legend in the top panel). For two bird guilds of interest, land birds (left panel) and ground foragers (right panel), sites restored via revegetation (green bars) had similar levels of species richness as the reference sites (brown bars), compared to sites with other land uses that had lower species richness. These two distinct types of community analysis methods provide complementary information, although metrics like species richness may be simpler to operationalize in management decision-making than results from ordination analyses.

3.2.3.2 Model Constraints

A downside of models seeking to evaluate or predict biodiversity responses is the lack of clear, mechanistic conceptual frameworks that link biodiversity metrics to environmental conditions or other underlying drivers. Many widely used tools for linking biodiversity metrics to environmental conditions, such as multispecies distribution models, often suffer from inconsistent reliability and quality and do not integrate fundamental

processes that shape community structure (Thuiller et al. 2013). Even the most fundamental conceptual theories about the drivers of biodiversity, such as the hypothesis that greater habitat heterogeneity leads to higher species richness, are frequently contradicted by empirical results (Tews et al. 2004). While it may be relatively straightforward to hypothesize environmental factors that govern the status and dynamics of a single population, it is frequently difficult to do so for many co-occurring taxa.

Selecting appropriate metrics to represent biological diversity may also be a challenge when using community models because numerous metrics exist, many vary in subtle ways, and selecting the wrong metric might lead to spurious management decisions (Jost 2009). For example, a management alternative that increases the overall number of species but also promotes the numerical dominance of a single species may be undesirable to managers. However, it might be unwisely deemed the optimal management scenario if species richness is the metric used to select among project alternatives.

Adequately quantifying the complex set of interactions that can occur among community members can be a substantial challenge, one that may require more data or technical expertise than are available. For example, in marine ecosystems, highly complex models (termed *end-to-end* models) have been developed to link baseline ecosystem productivity to fluctuations in the abundance of intermediate fish species and ultimately top predators. However, such models require high volumes of data (i.e., decades of time series data collected across large areas) and years of effort to develop (Geary et al. 2020). Therefore, very few USACE projects will likely have the data or time available to build complex community models featuring multiple interactions.

3.2.3.3 *Model Application in Project Planning*

Ecosystem restoration projects with goals related to biodiversity or multiple species should consider the use of community models. In many current scenarios, individual species are used as a surrogate for broader guilds of species (e.g., bluegill used to represent lentic fish in Upper Mississippi habitat restoration projects); in these cases, it may be especially worth considering community models instead of single-species habitat or population models if community-level data are available. Restoration- or management-relevant community analyses include studies of how fish communities and guilds differ below dams with differing operation practices

(Freeman et al. 2023) and how the abundance and diversity of fish as a whole and sensitive species change in the years following compensatory stream restoration (Stowe et al. 2023). In such cases, a comprehensive assessment of the entire community of species, as well as targeted subsets, can provide a nuanced understanding of how resource management affects ecosystems, likely beyond what single-species models could achieve.

In general, community models that incorporate interactions or the specific fates of multiple taxa may be outside the scope of planning projects. An exception, however, may be cases where species interactions are fundamental to the desired project outcomes. For example, where managers seek to control invasive species to protect imperiled native taxa, explicitly modeling the interaction of native and non-native species in a community model might be warranted.

Outputs from models that predict changes in biodiversity may be well suited to decision-making processes. For example, if models are built to predict the total number or the change in the number of fish species following restoration, this variable might easily substitute for model outputs that are currently used (e.g., habitat units). Conversely, outputs from commonly used ordination approaches, such as the one depicted in Box 3 and Figure 4, might present challenges to decision-makers because they typically represent community shifts using unitless metrics without any inherent biological meaning and feature techniques that can also be difficult for nontechnical audiences to grasp.

3.2.4 Connectivity and Network Analytic Models

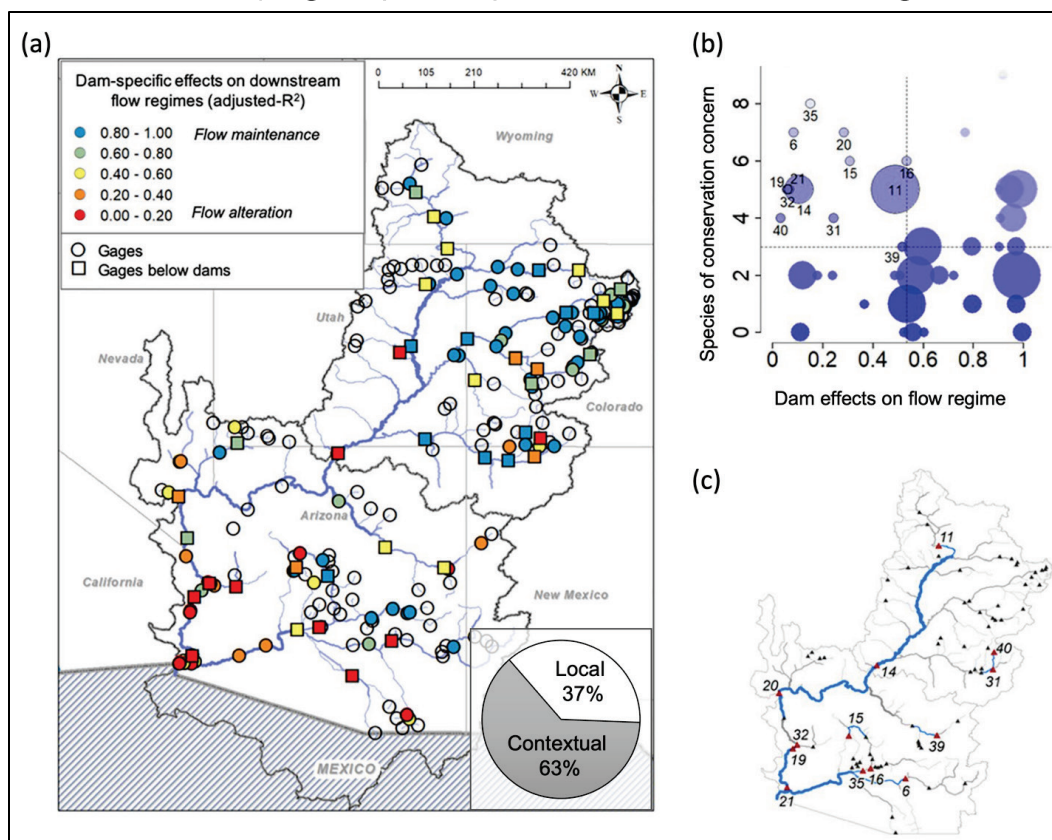
3.2.4.1 Model Description and Benefits

Connectivity models and network analytic models can be used to assess how management actions or other environmental changes alter hydrologic connectivity. Assessing hydrologic connectivity is crucial because it profoundly influences several aspects of river ecosystem integrity, including water quality, the flow regime, the propagation of threats, and biotic assemblages. Models assessing river connectivity are numerous and of varying complexity; Jumani et al. (2020) identified 29 different metrics and models that can be used to measure river connectivity given different objectives and data availability. These metrics can be classified as structural, potential, or actual (Calabrese and Fagan 2004). Structural connectivity metrics are concerned with physical attributes of the riverscape (e.g., the

ratio of total river length to the number of barriers), potential connectivity metrics integrate ecosystem or species-specific processes with riverscape features (e.g., the proportion of river accessible to migratory fish based on species-specific characteristics), and actual connectivity metrics are based on actual measurements of animal movements or ecosystem processes (e.g., telemetry data documenting the passage of individual fish).

Some assessments of hydrologic connectivity incorporate aspects of network analysis. Network analytic models study the behavior of systems composed of many interacting units and are often represented by a set of nodes and the links among them. In ecology, they have been used to analyze food webs, the spread of contaminants, groundwater–surface water interactions, and habitat connectivity. Network models are well-suited to studying riverine processes because they can explicitly incorporate information about the branching, flow-mediated structure of watersheds. For example, barrier removal studies can incorporate information on all of the dams in a watershed and the lengths of river between dams and prioritize the reoperation of those dams that have the most profound effects on connectivity or the flow regime (McKay et al. 2013; Ruhi et al. 2022; Figure 5; Box 4). Barrier-removal applications of network analysis have been modified to support many needs, including integrating protected-area planning into dam removal analyses to maximize overall conservation benefits (Erős et al. 2018). Network analysis has relevance in river systems beyond making decisions on dam removal. It can also be incorporated into studies that analyze fish metapopulations at multiple sites while incorporating riverine distances, flow direction, barrier removals (González-Ferreras et al. 2019), and assessments across watersheds to understand fine- versus broad-scale controls on stream water chemistry (McGuire et al. 2014), including how roads and mines influence stream conductivity (McManus et al. 2020).

Figure 5. Results from a network analysis that examined how dams affect hydrology in the Colorado River Basin. (Image adapted with permission from Ruhi et al. 2022, Figures 4 and 6.)



Box 4. Example network model.

Ruhi et al. (2022) used a spatial network model to study the individual and cumulative contributions of dams to hydrologic alteration throughout the Colorado River Basin. They found that the extent to which dams altered the flow regime varied considerably across the basin, with the greatest hydrologic alteration associated with downstream and main-stem dams (red and orange icons in Figure 5a). The effects of dams were explained more by dam network attributes (63%), like their network position, than by local dam attributes (37%), such as dam storage capacity (Figure 5a, inset pie chart). The authors also identified locations where changing dam operations might benefit native fish the most by plotting the negative effects of each dam on flows and the number of species of conservation concern present at each dam location (Figure 5b). In the figure, dams in the upper left quadrant should be prioritized for reoperation because they possess the highest number of species of concern and have the greatest detrimental effect on the flow regime. The numbers within Figure 5b indicate specific dams, the size of points indicates their distance from the next downstream dam, and the dashed lines indicate median values. The location of the priority dams identified in Figure 5b are shown in the map in Figure 5c (i.e., the numbered dams), and the downstream reaches that would be affected by reoperation efforts are shown in blue. Analyzing all Colorado River Basin dams in the network framework presented here enabled the researchers to compare, contextualize, and prioritize changes in dams arrayed across a vast area.

3.2.4.2 Model Constraints

A drawback of most connectivity indexes is the lack of empirical validation. Increases in connectivity are assumed to result in improved ecological outcomes, but the importance of connectivity in determining ecological outcomes can vary by species or time period. For example, while connectivity is frequently the most important factor for determining the occurrence of Chinook salmon nests, habitat size is more important than connectivity when population densities are low (Isaak et al. 2007). In some cases, increased connectivity may even have detrimental ecosystem effects, especially where non-native species (Fausch et al. 2009) or the propagation of pollution and contaminated sediments is a concern (Shuman 1995). Therefore, in some cases, models that incorporate both

positive and negative aspects of connectivity could be considered (Cooper et al. 2021).

Selecting connectivity metrics that capture the scale of interest is also challenging: Riverine ecosystem processes operate at various spatiotemporal scales, and values from some connectivity models may not accurately reflect the in-stream processes that govern connectivity. Moreover, connectivity is meaningful at different scales for different organisms or processes, and a connectivity metric that is suitable for one organism may be inappropriate for other outcomes of interest (e.g., a community or ecosystem process).

The lack of appropriate data can also limit the utility of some connectivity or network models. For example, many connectivity studies assess fish passage probabilities using swimming performance data from fish trials. However, these data do not exist for many species, and they may be a poor indicator of passage success, given the dynamic hydraulic environments involved and the potential declines in performance from passing multiple barriers.

3.2.4.3 *Model Application in Project Planning*

An increasing number of restoration projects, from dam removal and culvert replacement to dam reoperation, alter aquatic ecosystem connectivity. Network and connectivity models can play a large role in assessing the effects of such projects. Ecological models currently used for these purposes in many restoration or dam-related projects generate outputs similar to HSI models, such as estimates of how management actions will alter the amount of available river habitat for given species. An example of this type of approach is the fish passage connectivity index (FPCI), which was developed to calculate, based on fish swimming speeds and different dam passage designs, the habitat units associated with different dam passage alternatives for migratory species within the Alabama River.

At least one network analytic model has also been approved for use in USACE projects. The Watershed Upstream Connectivity Tool (WUCT) incorporates data on the shape and topology of watersheds to summarize cumulative connectivity throughout a watershed and how alteration or removal of different barriers affects connectivity throughout the basin (McKay et al. 2013). Output generated by these models (habitat area in the case of FPCI, and a 0–1 index in the case of WUCT) is typical of many

other connectivity models and may easily slot into planning projects as stand-ins for habitat model output. The WUCT tool can also incorporate uncertainty, so that if certain passage alternatives score similarly, the alternative with lower uncertainty might be selected. The availability of data for calculating actual connectivity metrics within some restoration projects may be more limited. However, in river basins where similar dam passage measures are installed sequentially and coupled with monitoring of actual passage rates, such data could then be applied to future projects to assess the likelihood of passage, which is a more direct measure than those based on swimming speed.

3.2.5 Machine Learning (ML) Models

3.2.5.1 Model Description and Benefits

ML models are a component of artificial intelligence (AI) consisting of statistical models and algorithms. ML models learn from data to perform tasks, recognize patterns, and generate predictions without programming specific instructions, as is required with traditional statistical approaches (Elith 2019). Thus, ML algorithms are inductive (i.e., the data determine model structure), which is a substantial philosophical difference from the deductive ecological model types discussed thus far. Deductive approaches have dominated statistics and ecological modeling: Models are constructed to reflect hypothesized relationships among predictors and responses, and then data are used to test these hypotheses. ML approaches typically make far fewer a priori predictions about how variables should relate to each other; instead, they rely on algorithms to uncover important relationships within the data. This approach, therefore, acknowledges that the world is complex, and the processes that generate data and observations are therefore unlikely to conform to simplistic conceptualizations.

ML models excel at pattern recognition and prediction. They are adept at sorting through multiple variables of interest to identify those that have important effects on outcomes of interest, which is extremely valuable for multiple stressor ecological analyses. Compared to traditional statistical models, they are also more proficient in situations featuring complex relationships, such as nonlinearities, among variables. These models are also versatile in handling different data types. For example, binary response variables, such as species presence or absence, can be modeled through classification techniques, and continuous data such as abundance can be modeled through regression techniques. In addition, categorical, contin-

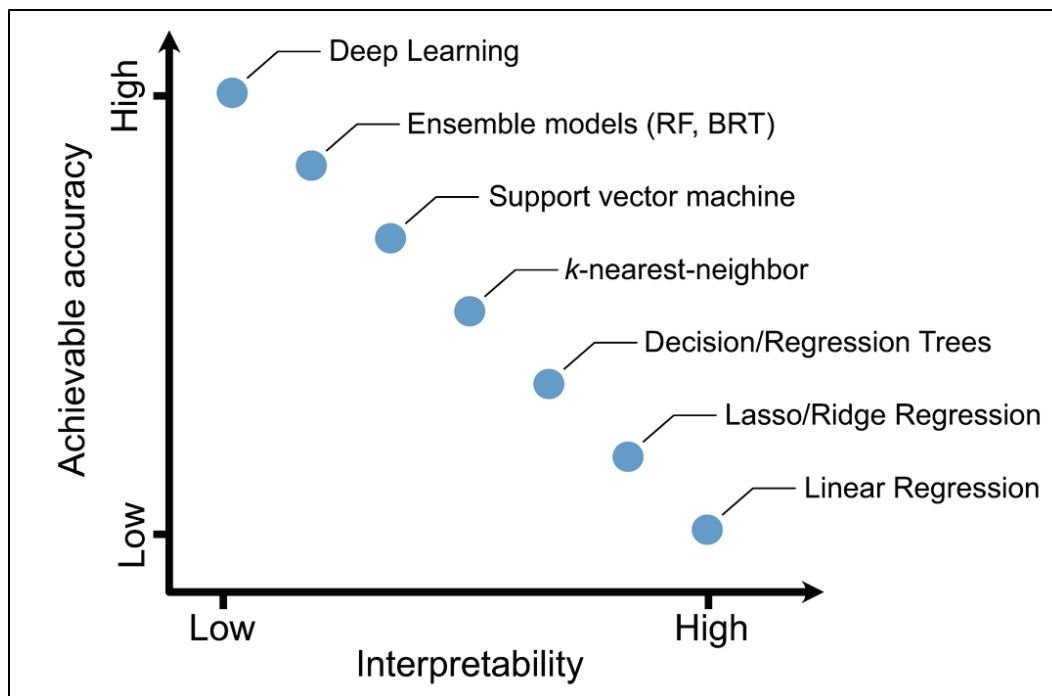
uous, and time-series data can be applied as both response and predictor variables, rendering ML appropriate for a wide range of applications.

ML models have a reputation for being technically challenging to implement, but many of the most popular ML algorithms, such as random forest (RF) and boosted regression trees (BRT), have a long history of use (Breiman 2001), ample guidance on implementation (e.g., Elith et al. 2008), and wide communities of users. These features may render some ML models easier to implement than their reputations suggest. Advances in ML are also moving at a pace unmatched by progress in other modeling disciplines, and consequently, newer ML procedures capable of even higher predictive accuracy (e.g., deep learning) will likely play an increasingly important role in ecological modeling in the future (Pichler and Hartig 2023).

3.2.5.2 *Model Constraints*

With ML models, there is often a trade-off between predictive accuracy and interpretability: The models with the highest predictive capacity tend to be the most difficult to interpret (Pichler and Hartig 2023; Figure 6). For example, ML approaches do not allow for inference on the causal relationships among variables (Arif and MacNeil 2022), while mechanistic models can be built to test specific ecological hypotheses (Baker et al. 2018). Low interpretability can mean that models may be transferred and used to make predictions in inappropriate scenarios or novel habitats where observational data are scarce. Furthermore, the lack of interpretability can limit overall transparency, which has been identified as an important element for engaging diverse partners in USACE ecological modeling practices (Herman et al. 2019). Unlike many statistical or index models, ML models are difficult to break down into more digestible pieces, such as simple linear equations or suitability diagrams. Where a mechanistic understanding of the ecological processes or higher transparency is prioritized, other model types might be more appropriate. However, ML models can be used in an iterative fashion and combined with mechanistic models to leverage the divergent strengths of the two approaches (Baker et al. 2018) or with other models that incorporate population dynamics (Barber-O'Malley et al. 2022). Furthermore, some advances have recently been made to render the overall AI process more explainable (Ryo et al. 2021), and approaches for using ML to understand causal mechanisms are also progressing (Wager and Athey 2018; Wesselkamp et al. 2022).

Figure 6. Different machine learning (ML) approaches, arranged according to their achievable accuracy and interpretability. RF and BRT refer to *random forest* and *boosted regression trees*, respectively. (Image reproduced from Pichler and Hartig 2023, Figure 4. CC BY 4.0, <https://creativecommons.org/licenses/by/4.0/>.)



While many statistical models can require large amounts of high-quality data, this is especially true of ML models; deep learning, the ML technique requiring the highest amount of data, is not feasible for most ecological studies (Pichler and Hartig 2023). Therefore, ML models may have limited utility outside of data-rich scenarios. Other technical considerations can also limit the utility of ML models. Some ML approaches, especially newer deep-learning algorithms, may be technically difficult for most practitioners to implement. Substantial computing power and long run times may be required for some larger analyses. As with statistical models, ML models may also be prone to overfitting, where models learn training data too well and consequently perform poorly in new scenarios or locations. However, approaches like cross-validation and regularization can mitigate overfitting.

3.2.5.3 Model Application in Project Planning

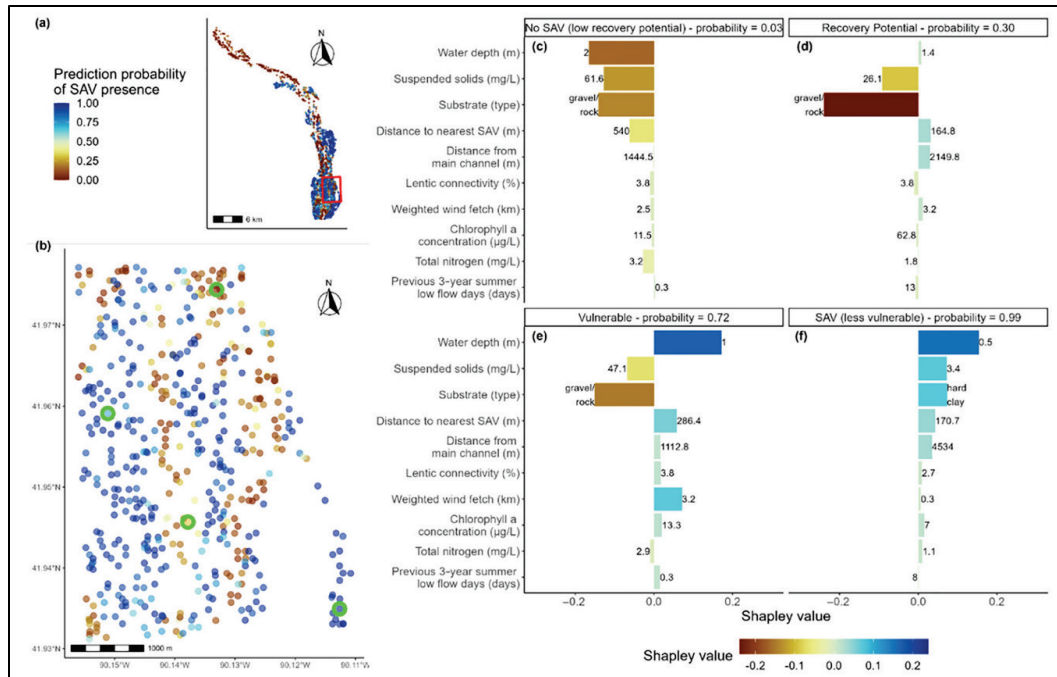
If adequate data exist, ML models should have high utility in many planning scenarios that currently employ habitat models to determine the features of the environment that are most correlated with organism characteristics and then predict how changes in habitat will influence

organism presence or abundance. Similar analyses are well-documented in scientific literature. For example, BRT was used to identify landscape determinants of bald eagle presence and then predict where the species would occur under future restoration scenarios (Percy et al. 2023). ML can also be applied to simulate changes in physical factors under different management actions—for example, predicting changes to stream flow under various scenarios and then applying the modeled data to predict changes in the distribution of species to assess vulnerability (Taniguchi-Quan et al. 2023).

Furthermore, ML models are not limited by the response variable of interest, so restoration projects targeting the recovery of species, communities, or other attributes of ecosystems might all consider the use of ML models. Of course, for many restoration projects, there may not be suitable data for using these models. Therefore, these models may have the most relevance within large restoration programs with long histories of data collection, such as the Upper Mississippi River (Figure 7; Box 5), with the caveat that state, regional, or national datasets that might be leveraged for modeling purposes are increasingly becoming available.

ML model outputs that could be used for decision-making could take a variety of forms given the diversity of ML algorithms. Because ML models are widely used for spatial applications like species distribution modeling (Beery et al. 2021), ML models could be used to predict distributions of organisms pre- and postrestoration, with the results used to both visualize likely outcomes of restoration and also provide quantitative estimates of how much habitat might be occupied by a target organism following restoration, analogous to the output of many habitat models. However, ML models could also be used to predict quantitative estimates akin to the output for population or community models (e.g., abundance or species richness of desired taxa). Furthermore, by predicting outcomes under a variety of scenarios, ML can be versatile in management scenario development, which can inform decision-making through trade-off analysis and highlight potential mitigation approaches through the identification of influential stressors.

Figure 7. Example ML model results assessing submersed aquatic vegetation in the Upper Mississippi River. (Image adapted from Delaney and Larson 2023, Figure 5. CC BY 4.0, <https://creativecommons.org/licenses/by/4.0/>.)



Box 5. Example machine learning (ML) model.

Delaney and Larson (2023) used random forest (RF), a supervised machine learning (ML) algorithm, to predict the presence of submersed aquatic vegetation (SAV) at sites in the Upper Mississippi River and identify sites of SAV management interest, including promising locations for SAV and sites vulnerable to potential SAV loss. Work was carried out in four navigation pools, including Pool 13. Figure 7a and b indicate the probability of SAV presence at sites throughout Pool 13, demonstrating SAV probabilities that range from very high (blue points) to low (red points). Because predictions from machine learning models are often accurate but difficult to interpret, Delaney and Larson used an explainable ML method called *Shapley values* to identify the environmental variables most responsible for SAV predictions at every site. The panels on the right (Figure 7c–f) depict Shapley values for the environmental variables that the model identified as being primary factors in determining the presence or absence of SAV at the four green highlighted sites in Figure 7b. Blue bars in these panels indicate predictor values in ranges that promote the presence of SAV, while red colors indicate predictors with values that inhibit SAV. The top panels on the right show two sites with no SAV: One (c) has low recovery potential (probability of SAV = 0.03) and is constrained by water depth, suspended solids, and substrate type, based on negative Shapley values; the other (d) has a higher probability of occurrence (0.30) and is mostly constrained by substrate type, which might be manipulated via restoration. The lower panels on the right show two sites containing SAV: One (e) is more vulnerable to SAV loss (0.73), while the other (f) has very low vulnerability to SAV loss (0.99). This analysis highlights the value of using ML algorithms to help make data-informed management decisions. The authors also designed a user dashboard to allow managers to explore the possibility of restoration or loss of SAV at nearly 7,500 sites. The ability to make predictions at so many sites is a function of the extensive monitoring data available in this area, which is possible because of the USACE-funded Long Term Resource Monitoring Program in the upper Mississippi River.

3.2.6 Guiding Questions for Selecting Modeling Approaches

USACE participants at our previously mentioned workshop on ecological modeling approaches indicated that an ecological model selection tool is

needed to guide restoration applications. We considered the possibility of designing such a tool, but in practice, ecosystem restoration modeling applications are highly constrained by project-specific particularities (e.g., location, project objective, data availability, timelines, and expertise), and thus a single tool is unlikely to meet all needs. Instead, we offer the guiding questions that follow to help users select applicable ecological models. Table 2 depicts several of these considerations.

Table 2. Important considerations for selecting appropriate ecological models for a given scenario. Each row indicates factors that may help guide the choice of modeling approach. The value of each criteria (i.e., row) for a given scenario can help determine an appropriate ecological model for that case. For example, if data availability is high, using an ML approach might be the most logical choice, but a population or community model might also be reasonable. The placement of a model at a given level indicates the best match between the guiding factor and model but should not be seen as prescriptive. For example, if a high level of technical expertise were available, agent-based, ML, or community models might also be excellent choices. We have not included the connectivity and network tools in this table because they apply most readily to a narrow set of scenarios (e.g., barrier removal and organism passage studies).

Factors Guiding Choice of Modeling Approach	Most Relevant Models Under Different Levels of Each Factor			
	Low	Medium Low	Medium High	High
Technical expertise required to apply models	Habitat	—	Agent-based, ML, Community	Population
Data availability	Habitat	Agent-based	Community	ML, Population
Existing theoretical knowledge of system	—	Habitat, ML	Community	Agent-based, Population
Predictive accuracy required	Habitat	Community, Agent-based	Population	ML
Frequency of model use	Habitat	ML, Agent-based	Community	Population

3.2.6.1 What Level of Ecological Hierarchy Will a Project Target?

Ecological modeling efforts should focus, to the maximum extent that the data and other project constraints allow, on the ecological attribute that a project will target. When this is not possible, modelers should use the closest possible surrogate or proxy (often a habitat model). Similarly, some ecological outcomes of a project may be goals specified by the team (e.g., restore riparian condition), whereas others may be constraints or

compliance requirements specified by another entity (e.g., avoid effects to imperiled bats). These outcomes may align at different levels of ecological hierarchy and ultimately affect the choice of one or more models to address different outcomes.

3.2.6.2 Is There a Conceptual Understanding of the System?

A strong conceptual understanding of the ecological system is a good reason to consider models that are more mechanistic, such as population or ABMs. However, if a system is poorly understood from a conceptual standpoint, an ML approach should be considered if the data allow.

3.2.6.3 How Much Data Are Available?

Where data are scarce, habitat models may be the best available option, but models that use parameter estimates from other studies (e.g., ABMs or simulation-based population models) could also be considered if parameter estimates are available and were derived within a similar location or context. If substantial data are available, ML or empirical population or community models should be considered.

3.2.6.4 Will the Model Be Used One Time or for Many Applications?

If the model is to be used multiple times, an additional upfront investment of time, expertise, and even data collection may be warranted to develop a sophisticated model (e.g., an agent-based, population, or ML model). If the model is to be applied in diverse scenarios or across spatial scales, mechanistic models like population models may be preferred because they may achieve higher transferability than ML approaches, which can have predictive accuracy that is constrained by context. In some cases, complex models could be paired with simple tools (e.g., graphical user interfaces) to enable a variety of users, including those with less technical acumen, to harness the models' capabilities through time.

3.2.6.5 What Level of Predictive Accuracy Does the Application Require?

If a high level of precision is required, an additional upfront investment of time, expertise, and data generation may be warranted to develop a sophisticated model. ML models should generally be considered in these cases given their potential to make accurate predictions.

3.2.6.6 How Comfortable is the Project Team with Indirect or Surrogate Measures?

If teams are not comfortable with indirect or surrogate approaches, it may be worth additional investments in time and resources to build models that directly assess the outcome of interest.

3.2.6.7 What Level of Technical Expertise Is Available?

If little technical expertise is available for model development, habitat models may be the best option, especially if they incorporate the best available information on the ecosystem elements to be modeled. However, if a model will be used repeatedly, additional measures should be incorporated to build models with higher achievable accuracy.

4 Recommendations for Advancing Ecological Modeling Practices in Project Planning

Using HSI or other habitat models for the ecological modeling aspects of restoration project planning is a long-established practice (Brooks 1997; Roloff and Kernohan 1999). Habitat models are a key part of project planning because of constraints typical of many projects, including strict timelines and budgets, practitioner expertise that is geared toward habitat models, and in the case of USACE specifically, the need for models that are certified (Section 4.4). Given that habitat models are the most common approach, strategic efforts in targeted focal areas will likely be required to facilitate the use of other ecological modeling approaches that can bring additional value to project planning. This section of the report highlights several approaches that we believe could foster increased adoption of contemporary ecological modeling techniques within project planning contexts.

4.1 Incorporating Data Science Best Practices into an Ecological Model

Ecological model development, integration, and application can be improved using data science best practices. Here we describe a few of the most compelling data science practices that can be incorporated into project planning; doing so may be an excellent first step in advancing ecological modeling in planning contexts because these approaches can improve modeling done both with habitat models and with other techniques.

First, additional testing and validation of models should lead to models with higher predictive accuracy. Independent data can be used to assess whether the current environmental variables included in models have the expected effect on outcomes of interest. In scenarios or locations where the same suite of ecological models is used repeatedly over years of restoration activities—which occurs in some large restoration programs—retrospective analyses can be conducted to test whether habitat models accurately predicted the effect of restoration activities (Thorson 2019). Similarly, adaptive management programs can be designed such that monitoring data are used to continuously improve the ecological models that are used and help steer management techniques (Johnson et al. 2015).

Using multiple models instead of single ecological models, often termed *ensemble modeling* (Araújo and New 2007), can also improve modeling outcomes. Ensemble modeling can lead to higher predictive accuracy and less bias compared to individual models (Marmion et al. 2009). Models from very different model families (e.g., regression, classification, ML) can be used in combination, with the potential to leverage the strengths of the different modeling approaches while minimizing the effect of anomalies produced by any given model. R packages like Biomod2 (Thuiller et al. 2009) and Tidymodels (Kuhn and Silge 2022) can ease the implementation of ensemble modeling, particularly for applications that develop species–habitat relationships that are relevant for project planning.

Next, incorporating reproducible research methods into modeling for project planning can improve the transparency and transferability of ecological models used in this context. The hallmark of reproducible research is the sharing of data and code used in an analysis (Peng 2011). Sharing code can enable practitioners to understand how a model works and to transfer new approaches directly to their own projects. Several USACE projects or tools (e.g., the WUCT model described in Section 3.2.4) employ reproducible research methods, such as sharing model code on GitHub, an online repository where users store, disseminate, and collaborate on code. There are many online repositories where data can also be shared (e.g., Zenodo and Figshare), which can also help others understand how analyses are conducted. Finally, dynamic documents created with programs like Rmarkdown, Bookdown, and Quarto can be used to knit together texts, figures, and code in an elegant format that can improve the overall communication of how an analysis was conducted and what the results were. For example, USACE planners and researchers are using Rmarkdown and Bookdown to describe and document the New York Bight Ecological Model (McKay et al. 2022), which is being developed to assess the potential effects of different coastal storm risk management measures on estuarine ecosystems near New York City. These tools enable documents to be hosted online and seamlessly updated when new data are collected.

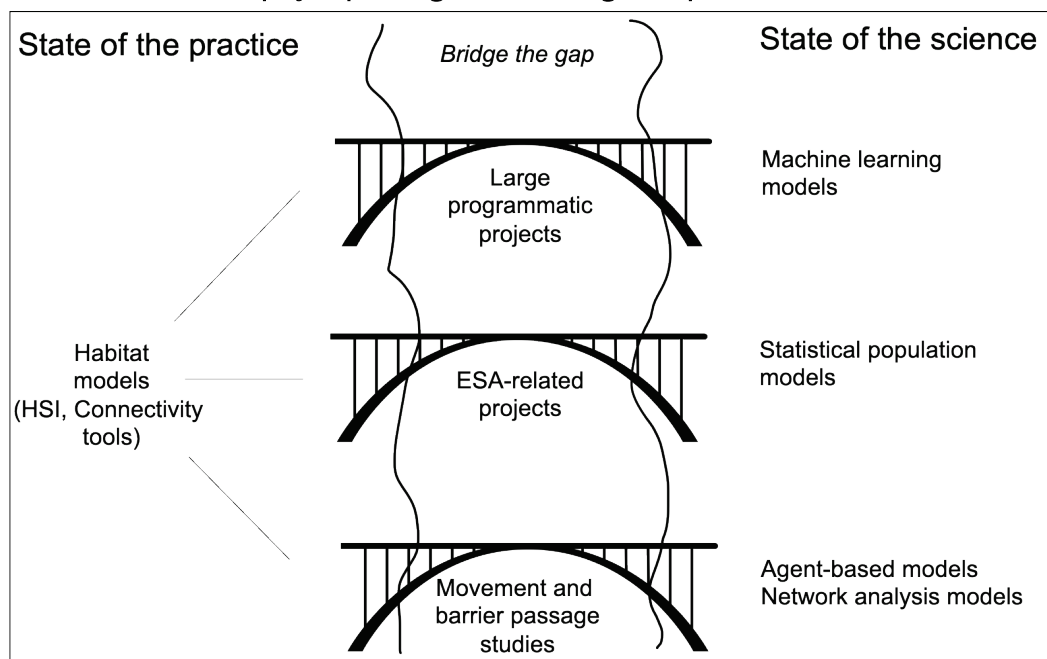
Finally, the development of custom tools can make novel modeling approaches easier for practitioners to employ. These tools include R packages that streamline analyses (e.g., the EcoREST R package for implementing HSI models for more than 300 species; McKay and Hernandez-Abrams 2020) or ArcGIS toolkits that simplify spatial analyses (e.g., Geospatial Suitability Indices Toolkit; Saltus et al. 2022). Where end users

lack training in using specialized software (e.g., ArcMap or R), web applications or dashboards (e.g., Shiny apps) can be developed. On these online graphical user interfaces, users upload or manually input data and then generate outputs like figures or summary data. Advanced ecological models built in R or other programming languages can operate behind the scenes, thus enabling powerful analyses without overwhelming code or technical details. Example web-based modeling applications include an online version of the EcoREST package (Shaw et al. 2022), the submersed aquatic vegetation (SAV) prediction tool described in Box 5 (Delaney and Larson 2023), and the Lahontan Cutthroat Trout Population Simulator (n.d.). The latter application estimates the viability of cutthroat trout populations under different climate and management scenarios (Leasure et al. 2019). These examples illustrate the importance not only of considering what ecological model to use for a given project, but also how to maximize the utility of whatever modeling approach is selected.

4.2 Demonstration Case Studies

Discussions with biologists and other personnel from USACE districts during our ecological modeling workshop indicated that an increase in the use of novel ecological modeling approaches in planning scenarios might be most likely to occur if the utility of new approaches—and perhaps even the superiority of such approaches over habitat models—was clearly demonstrated. As part of this conversation, one practitioner emphasized that HSI and other habitat models work well under typical project constraints, and so for him to consider the use of different models, their benefits must be proven within the context of planning projects. Consequently, we anticipate that case study applications may be a key mechanism for initiating the use of more advanced ecological modeling approaches in project planning, particularly if case studies represent planning scenarios that recur often, which we later outline in greater detail and depict graphically in Figure 8.

Figure 8. Conceptual diagram demonstrating potential case study projects and how they can help bridge the gap between the state of the practice and the state of the science within project planning. ESA = Endangered Species Act.



One case study with the potential to demonstrate the substantial benefits of novel ecological modeling practices is an ML analysis within a large restoration program (e.g., the Upper Mississippi River Restoration Program or Comprehensive Everglades Restoration Plan). Some of these programs feature decades of restoration activities along with systematic research and monitoring activities, which provide compelling opportunities to compare habitat model predictions with more advanced ecological models. For example, in the Upper Mississippi River, the benefits of backwater restoration to lentic fish are frequently predicted using an overwintering bluegill HSI model (Mooney et al. 2025). However, ML approaches are a natural fit for such scenarios because ML algorithms excel at leveraging large amounts of data and sorting through numerous potential environmental variables, including situations that can stymie traditional models (e.g., when there are interactions among predictors or nonlinear effects), to make accurate predictions. Consequently, restoration programs with substantial data represent great scenarios in which to explore ML approaches to predict how organisms will respond to restoration measures. When paired with output from a traditional HSI model, we believe that this will demonstrate the substantial additional benefits of using ML approaches.

Large-scale ecosystem restoration projects often involve collaborative efforts to aid in the recovery of imperiled taxa, especially federally protected species. Consequently, another valuable case study would entail using a population model to predict how the abundance or other population characteristic (e.g., survival or recruitment) of an imperiled species might be affected by restoration activities. Currently, such projects might rely on habitat models as a proxy for assessing the intended effects on imperiled organisms, but population modeling employed in these scenarios can provide more direct and proximate predictions of restoration benefits along with estimates of uncertainty. Work focused on the recovery of specific taxa is widespread in ecosystem restoration, including projects focused on imperiled migratory fish species such as coho salmon (Ramos and Ward 2023). One location where such a case study might prove particularly effective is the Middle Rio Grande, where considerable management efforts target populations of the endangered Rio Grande silvery minnow (RGSM) and where partnering agencies have collected extensive long-term fisheries and hydraulic data (Yackulic et al. 2022). Substantial floodplain restoration occurs in this system to benefit RGSM (Valdez et al. 2021). Consequently, an analysis that leverages and translates existing population models (e.g., Yackulic et al. 2022; Figure 3; Box 2) to estimate an explicit link between floodplain inundation and abundance levels of RGSM could be used in planning contexts to predict how populations of this endangered fish will respond to different floodplain restoration scenarios. This case study could showcase how working in partnership with other agencies to collect, share, manage, and analyze data using advanced models can result in more informed decision-making and aid in the conservation and restoration of endangered species.

In addition to potential case studies using ML and population modeling, results from additional ongoing USACE or USACE-affiliated projects using cutting-edge techniques could be highlighted beyond their project-specific audiences to demonstrate advanced ecological models that are already improving restoration project outcomes. Projects that fall into this category include ongoing work using population models and adaptive management to assess the effect of dam operation and emergent sandbar habitat creation on endangered piping plovers in the Missouri River system (Buenau et al. 2014) and research using ABMs to understand factors influencing tribally important anadromous alewife populations on Martha's Vineyard.

4.3 Training and Guidance on Ecological Modeling

The advancement of ecological modeling tools used for project planning will likely require continued focus on training and technology transfer to increase model developer and end user capabilities. Some efforts that have been undertaken by USACE personnel specifically highlight powerful approaches for training practitioners to develop planning models, especially the creation of interactive ecological modeling workshops. These workshops consist of a sequence of modules on key aspects of ecological modeling, include participants from various disciplines, and culminate in the real-time development of ecological models with planning applications (Herman et al. 2019). Other training courses have been developed in recent years that introduce restoration practitioners to advanced ecological modeling, such as a course on agent-based modeling designed for and offered to USACE districts and universities (Swannack 2022). Further training on using advanced ecological modeling in project planning is required to address the increasing need to predict how ecosystem management activities will affect complex socio-ecological systems. A variety of planning-oriented training approaches could be considered to facilitate greater uptake, including in-person workshops and asynchronous, prerecorded training modules and videos. Outside the project planning realm, various training modules in ecological modeling exist, so some effort could also be expended to identify or adapt the existing training materials that are most relevant to project planning and then disseminate these to practitioners. For example, the Ecological Forecasting Initiative created short courses on ecological forecasting for decision-making that feature modeling exercises posted on GitHub and instructional videos available on YouTube (Ecological Forecasting Initiative, n.d.).

In addition to expanding training opportunities in ecological modeling, workshop participants have recommended developing USACE-oriented guidance documents on a few key aspects of modeling. Guidance documents can help translate the substantial literature that exists on modeling material into a format that grounds these subjects in project planning processes, which can generate increased confidence in and familiarity with these topics by restoration practitioners. Table 3 contains the aspects of ecological modeling for which further exposition may be most beneficial.

Table 3. Ecological modeling topics identified by workshop participants as warranting further documentation for restoration planner practitioners.

Guidance Subject	Relevance for Project Planning	Document Focal Areas
Ensemble modeling: combining multiple distinct models to generate accurate predictions	• High relevance where empirical data are used to relate environmental variables to ecosystem attributes (e.g., species presence) • Can substantially increase predictive accuracy compared to single models	• Reasons to consider using ensemble models • Types of ensembles • Ensemble modeling tools and workflows • Relevant examples from literature • Problems and technical decisions when using ensemble modeling
Incorporating uncertainty into ecological models	• Quantify uncertainty to identify key knowledge/data gaps • Highlight model components in need of improvement • Provide decision-makers with key information on model precision	• Common sources of uncertainty and how to incorporate them in models • Benefits of including uncertainty • Key methods for quantifying uncertainty (e.g., simulation or sensitivity analyses)
Model integration: quantitatively linking ecological and physical models	• Valuable for projects with feedback loops between physical and ecological systems • Many restoration scenarios feature such physical–ecological feedbacks	• Types of model integration • Scenarios in which the added complexity of integrated models is worthwhile • Best practices for integrating models

4.4 Ecological Model Certification

A potential constraint to incorporating modern ecological models into USACE processes specifically is the requirement that models used for planning studies must go through an external peer review and be approved and certified by the USACE ECO-PCX. Model certification ensures that the model is scientifically defensible and reproducible and that its development was transparent. While the certification process is not onerous and can occur concurrently with other steps in the planning process, it does take time. Several actions may help further facilitate model certification. First, research projects undertaken by USACE that result in the development of ecological models may explicitly budget time and resources toward model certification, where relevant, to ensure that tools that are developed by research staff can subsequently be used by USACE districts

for planning purposes. ERDC and district staff might collaborate to identify priority models for certification so that investments in certification focus on models with the potential to be used for the greatest number of projects or the ones with the largest effects. Likewise, ERDC and district staff may need to collectively provide time and expertise to shepherd models through the certification process. Finally, providing additional avenues for model certification may ease this constraint. For example, the certification process now allows scientific journal article peer reviews to be used as part of the model certification process; if feedback on models received via other forums (e.g., workshops or webinars) can also be included in the certification process, that might also facilitate increases in efficiency in the model certification process.

5 Conclusions

Effective ecological modeling is a crucial component of ecosystem management and restoration. The ability to accurately predict how organisms, communities, and ecosystems will respond to management interventions like restoration can enable decision-makers to select the best project alternatives and increase the overall efficacy of restoration activities. Impediments to adopting more powerful ecological modeling practices within project planning are not trivial because current index-based modeling practices are widely integrated in planning processes (Brooks 1997; Roloff and Kernohan 1999). Consequently, this document does not advocate a prescriptive approach for integrating new modeling techniques into restoration project planning. Instead, incorporating newer modeling approaches will require efforts on multiple fronts simultaneously. These include educating current and would-be ecological modelers about the types of ecological models that exist and when they might be applied to maximum effect and demonstrating tangible benefits of ecological modeling approaches and novel data science practices. We therefore hope that this document provides a foothold into the world of contemporary ecological modeling and also highlights some of the best next steps for improving the uptake of nonhabitat models in restoration project scenarios.

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Appendix A: Ecological Model Examples and Management Application

Table A-1 contains information on commonly used ecological models.

Table A-1. Commonly used ecological models. Each model is categorized into an outcome-oriented model family and an analytical model family. For each model, a representative question answered by the model and an example paper or reference are provided. H = habitat, I = individual, P = population, and C = community. The outcome-oriented family for a given model is an indication of the outcomes more commonly assessed by each model; other outcomes may be possible but are less commonly observed.

Outcome-Oriented Family	Analytical Family	Model	Representative Question Answered	Example Paper or Reference
H	Index	Habitat suitability index (HSI)	How will the amount/quality of habitat for species/community of interest be altered given different management alternatives?	USACE (2018)
H	Index	Hydrogeomorphic approach model (HGM)	How will the amount/function of wetlands change given different management alternatives?	USACE Memphis District (2013)
H, P, C	Statistical/empirical	Linear models (generalized linear model [GLM], generalized additive model [GAM], and generalized linear mixed model [GLMM])	What is the statistical relationship between species abundance and habitat covariates, and if habitat changes in the future, how are future populations likely to change?	—
P, C	Statistical/empirical	Time-series models	What is the extinction risk of populations over the next 20 years based on time-varying future covariates?	Neville et al. (2019)
P	Statistical/empirical	Hierarchical models (state-space occupancy; <i>n</i> -mixture models)	How will the modeled presence/abundance of one or multiple species change following certain management interventions?	Sauer et al. (2013)
P	Statistical/empirical	Demographic/projection models (integral projection model and matrix projection model)	How will a population of interest respond to different management scenarios based on effects on different vital rates / life stages?	DuFour et al. (2021)
P	Statistical/empirical	Metapopulation model	How might metapopulation persistence or extinction risk change if management alternatives affect different habitats?	Drechsler et al. (2003)
H, P, C	Machine learning (ML)	Random forest (RF)	What degree of alteration in specific flow metrics will result in threshold shifts in populations or communities?	Bower et al. (2022)

Table A-1 (cont.). Commonly used ecological models. Each model is categorized into an outcome-oriented model family and an analytical model family. For each model, a representative question answered by the model and an example paper or reference are provided. H = habitat, I = individual, P = population, and C = community. The outcome-oriented family for a given model is an indication of the outcomes more commonly assessed by each model; other outcomes may be possible but are less commonly observed.

Outcome-Oriented Family	Analytical Family	Model	Representative Question Answered	Example Paper or Reference
H, P, C	ML	Boosted regression trees (BRT)	Which watersheds should flow restoration be prioritized in, based on the responses by multiple taxonomic groups? What will habitat suitability be for bald eagles in 20 years with and without implementation of a coastal restoration plan?	Irving et al. (2022) Percy et al. (2023)
H, P	Deep learning	Convolutional neural networks	How will species distributions change following management alternatives?	Deneu et al. (2021)
P	Deep learning	Recurrent neural networks	How will animal movement or demographic rates change following management intervention?	Joseph (2020) Rew et al. (2019)
I	Mathematical/simulation	Agent-based models (ABMs)	What are the environmental and commercial benefits of different oyster management strategies considering the complex life cycle of oysters?	Kjelland et al. (2015)
H	Mathematical/simulation	Network analysis	Which are the most cost-effective dams to remove to increase overall hydrologic connectivity?	Mckay et al. (2013)
P	Mathematical/simulation	Stochastic population simulation models	How do fluctuating habitat volumes brought about via management actions alter the demographic rates and population sizes of target species?	Buenau et al. (2013)
H, P, C	Mathematical/simulation	State-transition model	Which ecological states (e.g., vegetation community, fish population) will occur most frequently under different management or climate regimes (e.g., different frequencies of drought)?	Bond et al. (2022)

Appendix B: Relevant Publications on Selecting and Using Ecological Models

B.1 Ecological Modeling Overviews, Decisions, and Philosophy

- Baker, R. E., J. M. Pena, J. Jayamohan, and A. Jérusalem. 2018. “Mechanistic Models Versus Machine Learning, a Fight Worth Fighting for the Biological Community?” *Biology Letters* 14 (5): 20170660. <https://doi.org/10.1098/rsbl.2017.0660>.
- Bower, S. D., J. W. Brownscombe, K. Birnie-Gauvin, et al. 2018. “Making Tough Choices: Picking the Appropriate Conservation Decision-Making Tool.” *Conservation Letters* 11 (2): e12418. <https://doi.org/10.1111/conl.12418>.
- Getz, W. M., C. R. Marshall, C. J. Carlson, et al. 2018. “Making Ecological Models Adequate.” *Ecology Letters* 21 (2): 153–166. <https://doi.org/10.1111/ele.12893>.
- Schmolke, A., P. Thorbek, D. L. DeAngelis, and V. Grimm. 2010. “Ecological Models Supporting Environmental Decision Making: A Strategy for the Future.” *Trends in Ecology & Evolution* 25 (8): 479–86. <https://doi.org/10.1016/j.tree.2010.05.001>.
- Schuwirth, N., F. Borgwardt, S. Domisch, et al. 2019. “How to Make Ecological Models Useful for Environmental Management.” *Ecological Modelling* 411: 108784. <https://doi.org/10.1016/j.ecolmodel.2019.108784>.
- Zurell, D., C. König, A. K. Malchow, et al. 2022. “Spatially Explicit Models for Decision-Making in Animal Conservation and Restoration.” *Ecography* 2022 (4). <https://doi.org/10.1111/ecog.05787>.

B.2 Agent-Based Models (ABMs)

- Le Page, Christophe, Didier Bazile, Nicolas Becu, et al. 2013. “Agent-Based Modelling and Simulation Applied to Environmental Management.” In *Simulating Social Complexity: A Handbook*, edited by B. Edmonds and R. Meyer. Springer. https://doi.org/10.1007/978-3-540-93813-2_19.
- McLane, A. J., C. Semeniuk, G. J. McDermid, and D. J. Marceau. 2011. “The Role of Agent-Based Models in Wildlife Ecology and Management.” *Ecological Modelling* 222 (8): 1544–56. <https://doi.org/10.1016/j.ecolmodel.2011.01.020>.

B.3 Community and Ecosystem Models

- Geary, W. L., M. Bode, T. S. Doherty, et al. 2020. “A Guide to Ecosystem Models and Their Environmental Applications.” *Nature Ecology & Evolution* 4 (11): 1459–71. <https://doi.org/10.1038/s41559-020-01298-8>.

Moreno, C. E., J. Calderón-Patrón, V. Arroyo-Rodríguez, et al. 2017. “Measuring Biodiversity in the Anthropocene: A Simple Guide to Helpful Methods.” *Biodiversity and Conservation* 26: 2993–98. <https://doi.org/10.1007/s10531-017-1401-1>.

B.4 Connectivity and Network Models

Calabrese, J. M., and W. F. Fagan. 2004. “A Comparison-Shopper’s Guide to Connectivity Metrics.” *Frontiers in Ecology and the Environment* 2 (10): 529–36. [https://doi.org/10.1890/1540-9295\(2004\)002\[0529:ACGTCM\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002[0529:ACGTCM]2.0.CO;2).

Jumani, S., M. J. Deitch, D. Kaplan, et al. 2020. “River Fragmentation and Flow Alteration Metrics: A Review of Methods and Directions for Future Research.” *Environmental Research Letters* 15 (12): 123009. <https://doi.org/10.1088/1748-9326/abcb37>.

Peterson, E. E., J. M. Ver Hoef, D. J. Isaak, et al. 2013. “Modelling Dendritic Ecological Networks in Space: An Integrated Network Perspective.” *Ecology Letters* 16 (5): 707–19. <https://doi.org/10.1111/ele.12084>.

B.5 Machine Learning (ML)

Barnard, D. M., M. J. Germino, D. S. Pilliod, et al. 2019. “Cannot See the Random Forest for the Decision Trees: Selecting Predictive Models for Restoration Ecology.” *Restoration Ecology* 27 (5): 1053–63. <https://doi.org/10.1111/rec.12938>.

Christin, S., É. Hervet, and N. Lecomte. 2019. “Applications for Deep Learning in Ecology.” *Methods in Ecology and Evolution* 10 (10): 1632–44. <https://doi.org/10.1111/2041-210X.13256>.

Liu, Z., C. Peng, T. Work, J.-N. Candau, A. DesRochers, and D. Kneeshaw. 2018. “Application of Machine-Learning Methods in Forest Ecology: Recent Progress and Future Challenges.” *Environmental Reviews* 26 (4): 339–50. <https://doi.org/10.1139/er-2018-0034>.

Pichler, M., and F. Hartig. 2023. “Machine Learning and Deep Learning—A Review for Ecologists.” *Methods in Ecology and Evolution* 14 (4): 994–1016. <https://doi.org/10.1111/2041-210X.14061>.

Abbreviations

ABM	Agent-based model
AI	Artificial intelligence
BRT	Boosted regression trees
C	Community
DCI	Dendritic connectivity index
DOONIES	Dune Ecogeomorphic Vegetation Community Photosynthesis-Driven Spatial
ECO-PCX	Ecosystem Restoration Planning Center of Expertise
EL	Environmental Laboratory
ELAM	Eulerian–Lagrangian-agent method
ERDC	Engineer Research and Development Center
ESA	Endangered Species Act
FHAST	Fish Habitat Assessment and Simulation Tool
FPCI	Fish passage connectivity index
FWS	US Fish and Wildlife Service
GAM	Generalized additive model
GLM	Generalized linear model
GLMM	Generalized linear mixed model
H	Habitat
HEC-RAS	Hydrologic Engineering Center’s River Analysis System
HEP	Habitat Evaluation Procedures
HGM	Hydrogeomorphic approach model
HSI	Habitat suitability index
I	Individual

ML	Machine learning
NMDS	Nonmetric multidimensional scaling
P	Population
RF	Random forest
RGSM	Rio Grande silvery minnow
SAV	Submersed aquatic vegetation
SMART	Specific, Measurable, Attainable, Risk Informed, Timely
USACE	US Army Corps of Engineers
WRDA	Water Resources Development Act
WUCT	Watershed Upstream Connectivity Tool

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