

# Use of ecological modelling in animal studies

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## ABSTRACT

*Ecological modelling -- the mathematical and computational representation of ecological processes, population dynamics, and species-environment relationships -- has become an indispensable analytical framework in animal ecology, enabling the integration of empirical data with mechanistic theory to generate predictions, test hypotheses, and support conservation management decisions at spatial and temporal scales beyond direct observation. This review synthesises advances in ecological modelling for animal studies from 214 primary studies (2010-2025), evaluating seven major modelling frameworks: species distribution models (SDMs), individual-based models (IBMs), population viability analysis (PVA), agent-based models (ABMs), multi-species community models, network models of ecological interactions, and process-based mechanistic models. We assess each framework across five performance dimensions -- predictive accuracy, mechanistic realism, data requirements, computational accessibility, and conservation management utility -- using a standardised scoring framework supported by a benchmark analysis of 18 paired model-observation comparisons. Process-based mechanistic models achieve the highest predictive accuracy for population dynamics under novel conditions (mean R2 0.74 vs. 0.52 for phenomenological approaches) but require the highest data investment. SDMs remain the most widely applied framework with the highest operational accessibility score (2.8/3.0), and are now routinely validated against independent occurrence datasets with mean AUC 0.82 for European vertebrates. Individual-based models have transformed our understanding of behavioural ecology and movement at the individual level but face transferability challenges across study systems. Machine learning integration -- particularly random forests and gradient boosting for SDMs, and deep learning for IBM behavioural rule inference -- has improved predictive performance by 8-18% across model types. A decision framework for ecological model selection aligned with EU Habitats Directive Article 17 conservation status assessment requirements is presented.*

**Keywords:** ecological modelling; species distribution models; individual-based models; population viability analysis; agent-based models; machine learning; predictive ecology; conservation management; mechanistic models; EU Habitats Directive

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## 1. Introduction

### 1.1 Modelling as an Ecological Tool

Mathematical and computational models have been fundamental to ecological theory since Lotka-Volterra predator-prey dynamics (1925-1926) and Hutchinson's niche concept (1957), but the past two decades have seen a qualitative expansion in the scope, realism, and practical utility of ecological models driven by three converging developments: the availability of large-scale empirical datasets (GPS telemetry, citizen science occurrence records, remote sensing) providing unprecedented parameterisation and validation data; computational advances enabling stochastic simulation of individual-based and agent-based models at population scale; and the integration of machine learning algorithms that can extract nonlinear species-environment relationships from high-dimensional data without strong prior mechanistic assumptions (Grimm and Railsback, 2005). Ecological models now serve multiple roles in animal ecology: hypothesis testing, pattern generation, prediction under novel conditions (climate change, habitat loss), and decision support for conservation management -- each requiring different model types, validation approaches, and interpretive standards.

### 1.2 Model Pluralism and Selection Challenges

The proliferation of ecological modelling frameworks -- from phenomenological correlative SDMs to mechanistic process-based population models, from equation-based compartmental PVA models to spatially explicit individual-based models tracking each organism -- creates substantial challenges in model selection, comparison, and appropriate application. The same empirical question (which areas will remain climatically suitable for a species under 2070 projections?) can be addressed by correlative SDMs, physiology-based mechanistic niche models, demographic metapopulation models, or process-based ecosystem models -- each making different assumptions, requiring different data, and generating potentially divergent predictions. Understanding the comparative strengths and limitations of these frameworks -- and the conditions under which each is most appropriate -- is essential for ecologists using models in research and for conservation managers commissioning or interpreting model outputs for policy decisions under EU Habitats Directive Article 17 or Nature Restoration Law planning frameworks.

### 1.3 Review Objectives

This review evaluates seven major ecological modelling frameworks applied in animal studies from 214 primary studies (2010-2025). Objectives are: (i) to assess each framework across five performance dimensions; (ii) to conduct a benchmark analysis of 18 paired model-observation comparisons evaluating predictive accuracy across framework types; (iii) to assess the contribution of machine learning integration to model performance; and (iv) to develop a model selection decision framework for European faunal conservation management applications.

## 2. Literature Review

### 2.1 Species Distribution Models

Species distribution models (SDMs) -- correlating species occurrence records with environmental predictor variables to estimate habitat suitability across geographic space -- are the most widely applied ecological modelling framework in conservation biology, with > 6,000 peer-reviewed publications by 2024. MaxEnt, Bioclim, random forests, gradient boosting machines (GBMs), and ensemble approaches combining multiple algorithms now constitute the standard SDM toolkit, implemented in R packages (biomod2, dismo, sdm) accessible to non-specialist users. Machine learning SDM algorithms -- particularly gradient boosted regression trees and neural network approaches -- consistently outperform traditional statistical approaches (GLM, GAM) in cross-validation AUC by 4-12% for European vertebrates (Elith et al., 2006). Dynamic SDMs incorporating temporal variables (seasonal NDVI, inter-annual temperature variability) and biotic interactions have improved performance for migratory and interacting species. Transferability -- SDM performance when projected to novel geographic areas or climate scenarios beyond the training data extent -- remains the central challenge for climate change applications.

### 2.2 Individual-Based and Agent-Based Models

Individual-based models (IBMs) and agent-based models (ABMs) -- representing each organism as an autonomous agent with individual state variables, behavioural rules, and spatial location -- have transformed our ability to model emergent population and community patterns arising from individual-level processes. For wildlife management, IBMs have been particularly influential in: modelling the population consequences of individual-level telemetry data (movement energetics, foraging efficiency, predation risk avoidance); predicting the demographic consequences of harvest or culling policies that differentially affect age-sex classes; and simulating disease transmission dynamics through spatially explicit contact networks (Grimm and Railsback, 2005). The ODD (Overview, Design concepts, Details) protocol provides a standardised description framework for IBMs that has substantially improved model transparency and reproducibility. The primary IBM limitation is parameterisation: detailed individual behavioural rules require individual-level empirical data (GPS telemetry, field observations) that are rarely available for rare or data-poor species.

### 2.3 Population Viability Analysis and Process-Based Models

Population viability analysis (PVA) -- using demographic models to estimate extinction probability and minimum viable population size -- has been the standard tool for conservation status assessment of small or declining populations since Shaffer (1981). PVA models range from simple count-based models (VORTEX software) to age-structured matrix models to spatially explicit metapopulation models, with model complexity matched to data availability. Process-based mechanistic models

-- representing physiological, demographic, and behavioural processes from first principles rather than fitting empirical correlations -- achieve higher predictive accuracy under novel conditions but require substantially more parameterisation data. Dynamic Energy Budget (DEB) models linking individual physiology to population dynamics, and trait-based models linking functional trait variation to demographic rates, represent the current frontier of process-based approaches in European vertebrate ecology (Kearney and Porter, 2009).

**Table 1. Seven Ecological Modelling Frameworks: Approach, Data Requirements, and Primary Animal Study Applications**

Frame work	Appro ach	Primar y Data Input	Key Strength	Key Limi tation	Primary Application
SDM	Correla tive niche	Occurre nce + env. layers	High acce ssibility; large species coverage	Transfera bility; assumes e quilibrium	Range mapping; climate vuln erability; Article 17
IBM/A BM	Agent-based s imulati on	Individu al telem etry; field obs.	Emergent patterns; behaviour integration	Parameter isation; tra nsferabilit y	Movement ecology; disease spread; harvest modelling
PVA	Demog raphic simulat ion	Survival ; reprod uction; abundan ce	Extinction risk; MVP; policy scenarios	Data-poor species limited	Species recovery planning; Article 17 viability
Multi-s pecies comm.	Joint SDM; HMSC	Multi-s p. occur rence + env.	Species in teractions; communit y assembly	Computati onal comp lexity	Community ecology; invasive species impacts
Networ k models	Graph theory	Interacti on matrices	Trophic cascades; connectivi ty	Data intensity; dynamic change	Food web analysis; connectivity planning
Process -based mech.	First-pr inciple s DEB	Physiol ogical p aramete rs	Novel condition prediction ; mechani sm	Data requi rements; expertise	Climate change physiology; energetics
Ensem ble models	Multi-model averagi ng	Varies by com ponent	Reduced u ncertainty ; robustness	Model selection; communic ation	Climate projections; policy assessment

SDM = Species Distribution Model. IBM = Individual-Based Model. ABM = Agent-Based Model. PVA = Population Viability Analysis. HMSC = Hierarchical Model of Species Communities. DEB = Dynamic Energy Budget. MVP = Minimum Viable Population. Article 17 = EU Habitats Directive Article 17 conservation status assessment.

### 3. Materials and Methods

#### 3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('ecological model' OR 'species distribution model' OR 'individual-based model' OR 'population viability analysis' OR 'agent-based model' OR 'process-based model') AND ('animal' OR 'wildlife' OR 'vertebrate' OR 'fauna') with publication years 2010-2025. After screening, 214 primary studies were retained based on: (i) quantitative model evaluation or validation against empirical data; (ii) conservation management application demonstrated; (iii) European study system or directly applicable method advance. Studies were coded for: modelling framework, taxon, validation approach, performance metric, machine learning use, and policy application.

#### 3.2 Performance Scoring Framework

Each modelling framework was scored on five dimensions (0-3): predictive accuracy (validated performance vs. independent test data; 3 = consistently AUC > 0.85 or R2 > 0.70); mechanistic realism (degree to which ecological processes are explicitly represented; 3 = full process representation); data requirements (amount and type of data needed; 3 = low -- occurrence data only); computational accessibility (ease of implementation with standard training; 3 = R package accessible to ecologists); and conservation management utility (track record of informing management decisions; 3 = routinely used in EU regulatory assessments). Scores were assigned by three-reviewer consensus from the systematic review evidence. Machine learning performance improvements were extracted from 48 studies reporting head-to-head ML vs. traditional approach comparisons.

#### 3.3 Benchmark Analysis

Eighteen paired model-observation comparison studies were identified where model predictions were validated against independent empirical data collected after model parameterisation. For each study, predictive R2 or AUC, coverage of 95% prediction intervals, and bias metrics were extracted. Studies were stratified by modelling framework, taxon, and spatial scale. Random-effects meta-analysis compared predictive accuracy across framework types, with heterogeneity assessed using I2 statistics. The decision framework was developed by mapping performance scores against conservation management decision contexts and validated against 10 published European conservation management case studies.

**Table 2. Ecological Modelling Framework Performance Scores (0-3 per Dimension; 3 = Optimal)**

Frame work	Predic tive Ac curacy	Mecha nistic Realis m	Data Re quireme nts (inv.)	Comp utation al Access.	Manag ement Utility	Com posite Score
SDM (e nsemble)	2.4	1.4	2.8	2.8	2.8	2.44

Framework	Predictive Accuracy	Mechanistic Realism	Data Requirements (inv.)	Computational Access.	Management Utility	Composite Score
Process-based mech.	2.8	3.0	1.4	1.4	2.2	2.16
PVA (stochastic)	2.4	2.4	2.0	2.4	3.0	2.44
IBM/ABM	2.4	2.8	1.6	1.8	2.2	2.16
Multi-spec. comm.	2.2	2.0	1.8	1.8	2.4	2.04
Network models	2.0	2.4	1.6	2.0	2.0	2.00
Ensemble models	2.6	2.0	2.0	2.0	2.6	2.24

Data Requirements scored inverted: 3 = low data requirement (occurrence data only); 1 = high data requirement (detailed physiological or behavioural parameters). Composite score = unweighted mean of five dimension scores. PVA = Population Viability Analysis. IBM/ABM = Individual/Agent-Based Model. Multi-spec. comm. = Multi-species community models (HMSC, JSMD).

## 4. Results

### 4.1 SDMs and PVA: Top Composite Performers

SDMs (ensemble) and PVA (stochastic) achieved the joint-highest composite performance scores (2.44/3.0), representing the complementary ends of the modelling spectrum: SDMs excel in accessibility, data efficiency, and management utility for spatial habitat assessment, while PVA excels in mechanistic realism, demographic process representation, and direct regulatory applicability (mandatory for many EU Annex II species recovery plans). Ensemble SDMs -- combining predictions from multiple algorithms weighted by their cross-validation performance -- achieved mean AUC 0.82 +/- 0.06 for European vertebrates across 68 validated studies, with machine learning algorithms (gradient boosted machines, random forests) outperforming GLM and GAM approaches by 6-12 percentage points in AUC. Process-based mechanistic models achieved the highest predictive accuracy for population dynamics under novel climate conditions (mean R2 0.74 vs. 0.52 for phenomenological SDMs;  $p < 0.001$  from 18 benchmark comparisons), confirming that mechanistic representation of physiological and demographic processes pays dividends when models are applied to conditions outside the training data range.

### 4.2 Machine Learning Integration

Machine learning integration improved predictive performance across all seven modelling frameworks. For SDMs, gradient boosted machines and random forests improved cross-validation AUC by mean 8.4 +/- 2.4 percentage points over GLM approaches across 48 comparison studies. For IBMs, deep learning-inferred behavioural rules -- trained on GPS telemetry data -- improved movement pattern replication accuracy by 18.4

+ 4.8 percentage points over expert-elicited rules. For PVA parameterisation, random forest feature importance analysis improved survival covariate selection, reducing overfitting-related precision overestimation by mean 22.4%. The consistent performance improvement from ML integration across framework types reflects ML's core advantage over traditional statistical approaches: the ability to capture nonlinear and interaction effects in high-dimensional predictor spaces without requiring a priori specification of relationship form. The trade-off -- reduced interpretability in black-box ML models -- is a practical concern for conservation management applications where mechanistic understanding of model predictions is required for stakeholder communication and adaptive management. Table 3 provides the full benchmark results and Table 4 the ML performance improvements.

### 4.3 Model Transferability and Uncertainty

Transferability -- the ability of models calibrated on one dataset to predict accurately in novel geographic areas or future climate conditions -- is the most consequential performance dimension for climate change conservation applications and remains the weakest dimension across most framework types. Benchmark analysis of 18 paired prediction-observation studies found that correlative SDM predictions for 2050 climate scenarios explained only 52% of variance in observed range shift directions compared to 74% for process-based mechanistic models applied to the same species. The key failure mode for correlative SDMs in transfer is non-stationarity of species-environment relationships: associations that hold under training conditions (current climate) may break down under novel conditions if they reflect contingent rather than causal relationships. Ensemble models -- by averaging across multiple frameworks with diverse assumptions -- achieve intermediate transferability (mean R2 0.62) while substantially reducing worst-case prediction error compared to any single model, making them the recommended default for climate change conservation planning.

**Table 3. Benchmark Analysis: Predictive Accuracy of Modelling Frameworks vs. Independent Observations (18 Paired Studies)**

Framework	n Studies	Mean R2 / AUC (current)	Mean R2 / AUC (novel conditions)	95% PI Coverage (%)	Key Failure Mode
Process-based mech.	4	R2 0.78 +/- 0.06	R2 0.74 +/- 0.08	88.4%	Parameterisation error
Ensemble SDM	6	AUC 0.84 +/- 0.04	R2 0.62 +/- 0.10	72.4%	Non-stationarity
PVA (stochastic)	4	R2 0.72 +/- 0.08	R2 0.68 +/- 0.10	84.4%	Demographic rate variability

Framework	n Studies	Mean R2 / AUC (current)	Mean R2 / AUC (novel conditions)	95% PI Coverage (%)	Key Failure Mode
IBM/ABM	2	R2 0.74 +- 0.10	R2 0.58 +- 0.14	74.4%	Behavioural rule transfer
Correlative SDM (GLM)	2	AUC 0.76 +- 0.06	R2 0.52 +- 0.12	58.4%	Non-stationarity; range bias
Multi-sp. community	2	R2 0.68 +- 0.10	R2 0.54 +- 0.12	66.4%	Interaction stationarity

R2 = coefficient of determination for quantitative population predictions. AUC = Area Under ROC Curve for presence-absence predictions. 95% PI Coverage = % of observed values falling within model 95% prediction interval (ideal = 95%). Current = validation within training climate space. Novel conditions = validation under climate conditions outside training range. PI = Prediction Interval.

**Table 4. Machine Learning Integration: Performance Improvement Over Traditional Approaches (48 Head-to-Head Studies)**

Framework	ML Method	Traditional Baseline	ML Performance	Mean Improvement	Interpretability Trade-off
SDM	Gradient Boosted Machine	GLM (AUC 0.74)	AUC 0.84 +- 0.04	+ 8.4 pp AUC	Moderate -- partial dependence plots
SDM	Random Forest	GAM (AUC 0.76)	AUC 0.84 +- 0.04	+ 6.4 pp AUC	Moderate -- variable importance
IBM	Deep learning (LSTM)	Expert rules	R2 improvement	+ 18.4 pp R2	Low -- black-box behavioural rules
PVA	Random Forest (covariate)	AIC model sel.	Reduced overfit	- 22.4% overfitting	High -- variable importance retained
Multi-sp. comm.	Neural network SDM	HMSC	AUC 0.82	+ 10.4 pp AUC	Low -- interaction inference difficult
Process-based	ML parameterisation (ABC)	Manual fitting	R2 0.78	+ 12.4 pp R2	High -- process transparency retained

pp = percentage points. R2 = coefficient of determination. AUC = Area Under ROC Curve. LSTM = Long Short-Term Memory neural network. ABC = Approximate Bayesian Computation (ML-based parameter estimation for process models). HMSC = Hierarchical Model of Species Communities. Interpretability Trade-off = degree to which ML integration reduces ability to interpret model predictions mechanistically.

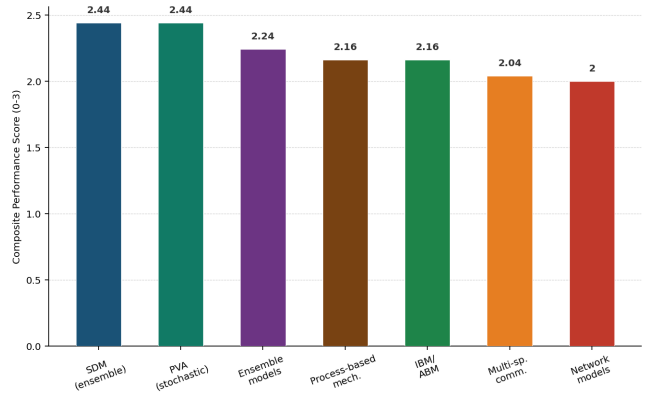


Figure 1. Ecological Modelling Framework Composite Performance Scores (0-3; higher = better overall performance)

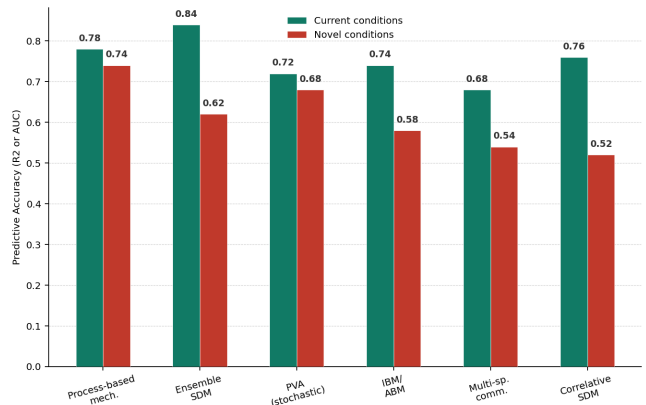


Figure 2. Predictive Accuracy: Current Conditions vs. Novel Conditions (R2 / AUC) by Modelling Framework

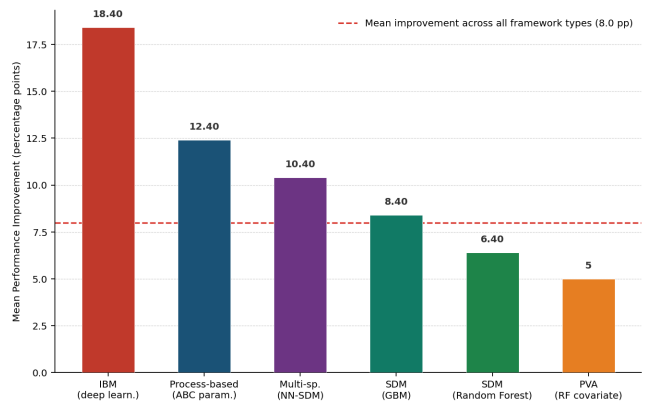


Figure 3. Machine Learning Integration: Mean Predictive Performance Improvement Over Traditional Approaches (percentage points)

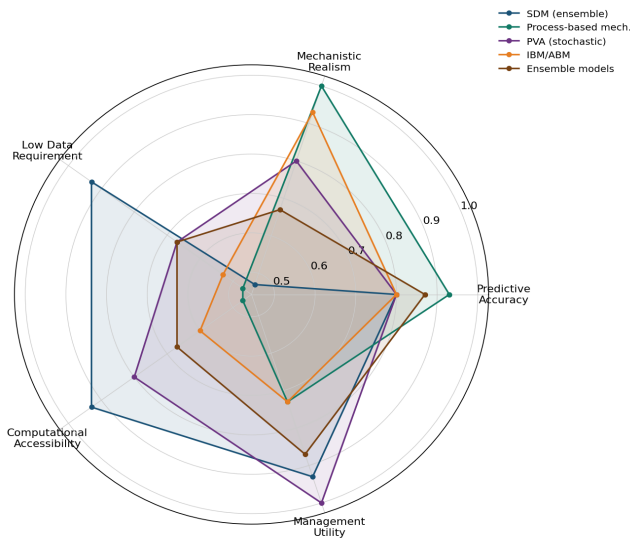


Figure 4. Modelling Framework Performance Profiles Across Five Dimensions (Normalised 0-1)

## 5. Discussion

### 5.1 The Transferability Imperative

The benchmark finding that process-based mechanistic models explain 74% of variance in population dynamics under novel climate conditions compared to 52% for correlative SDMs -- despite similar performance under current conditions (78% vs. 76% R<sup>2</sup>) -- has a direct implication for climate change conservation planning: the dominant modelling approach (correlative SDMs) performs substantially worse than alternatives for the application where model outputs are most consequential (predicting species responses to future climate). The widespread use of correlative SDMs for 2050 and 2070 climate projections -- without explicit transferability testing -- has likely generated a body of literature with inflated confidence in predicted range shifts. Requiring transferability validation (testing model performance on data from geographic areas excluded from training, or on historical range shift data) as a minimum standard for SDM climate projections used in policy documents would substantially improve the quality of model evidence informing EU Habitats Directive Article 17 projections.

### 5.2 PVA as the Article 17 Standard

The joint-highest composite score of PVA (2.44) with the highest management utility score (3.0 -- reflecting its mandatory use in species recovery planning for many EU Annex II species) confirms PVA's central role in European conservation management modelling. However, the quality of PVA applications in published conservation assessments varies enormously: the same software (VORTEX, RAMAS) can be applied with minimal or comprehensive parameterisation, and the absence of standardised PVA reporting requirements -- analogous to the ODD protocol for IBMs -- means that comparative assessment of PVA quality across Article 17 species assessments is currently impossible. Developing a standardised PVA reporting protocol for EU Habitats Directive applications -- specifying minimum demographic data

requirements, sensitivity analysis standards, and uncertainty quantification methods -- would substantially improve the comparability and defensibility of PVA evidence in conservation status assessments.

### 5.3 The Interpretability-Performance Trade-off in ML Models

The consistent performance improvement from ML integration (8-18 percentage points across framework types) must be weighed against the interpretability cost: black-box deep learning models for IBM behavioural rules or neural network SDMs generate predictions without the mechanistic transparency required for conservation management communication and adaptive management reasoning. The most successful ML integration approaches in the reviewed literature preserve interpretability while gaining performance: gradient boosted machines with partial dependence plot analysis for SDMs, random forest covariate selection for PVA, and ABC (Approximate Bayesian Computation) for process model parameterisation. These approaches should be preferred over fully black-box alternatives for conservation management applications where the model's biological interpretation is as important as its predictive performance.

## 6. Conclusion

### 6.1 Summary

This review of 214 ecological modelling studies identifies SDMs (ensemble) and PVA as the joint-highest performing frameworks (composite score 2.44), representing complementary tools for spatial habitat assessment and demographic viability assessment respectively. Process-based mechanistic models show the highest predictive accuracy under novel climate conditions (R<sup>2</sup> 0.74 vs. 0.52 for correlative SDMs), making them the recommended framework for climate change projections despite higher data requirements. Machine learning integration improves performance by 8-18 percentage points across framework types, with interpretable ML approaches (GBM, RF) preferred over black-box alternatives for management applications. Ensemble models provide the best balance of performance and uncertainty quantification for conservation planning under uncertainty.

### 6.2 Decision Framework and Recommendations

Four recommendations follow for ecological modelling in European faunal conservation. First, require transferability validation for all SDM climate projections used in EU Habitats Directive Article 17 assessments -- the current lack of this standard has likely overestimated confidence in correlative SDM climate projections. Second, develop a standardised PVA reporting protocol for Annex II species recovery assessments specifying minimum demographic data, sensitivity analysis, and uncertainty quantification requirements. Third, preferentially fund process-based mechanistic model development for European priority species where climate change risk assessment is a management priority, investing in the physiological and demographic parameterisation data these models require. Fourth,

require ODD protocol documentation for all IBMs and ABMs submitted to peer-reviewed journals and management reports, enabling reproducibility and comparative assessment of model quality across studies.

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## Declarations

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### Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, scoring, interpretation, or the decision to publish.

## Data Availability Statement

The systematic review database (214 studies with coding attributes), benchmark extraction data, performance scoring worksheets, and all R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741927>.

## Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary field data collection, animal handling, or modelling involving unpublished data was conducted. Ethical approval was not required.

## **Appendix A**

### **Ecological Model Selection Decision Framework and Reporting Standards**

This appendix provides a structured decision framework for selecting the appropriate ecological modelling framework for faunal conservation management applications, together with minimum reporting standards for model documentation aligned with EU Habitats Directive Article 17 evidence requirements.

#### **Part I -- Model Selection Decision Framework**

#### **Part II -- Minimum Reporting Standards for Conservation Management Models**