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# A protocol for the biodiversity model intercomparison project: BMIP 1.0

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**Abstract**. Model intercomparisons are emerging as a powerful approach to improve our understanding of biodiversity and ecosystem responses to global changes, thereby supporting policy design and decision-making. However, efforts to date have focused on climate change impacts on species richness at a global scale, while regional impacts remain comparatively understudied. To address this gap, we propose a protocol for a biodiversity model intercomparison project focused on regional-to-continental scale patterns of species abundance and occurrence across space and time. This protocol covers a continuum of modeling approaches, ranging from correlative to process-explicit models. We detail the standardized input data used for model calibration –climate, land-use, and biodiversity data– and outline a common framework for model validation and performance assessment. Our protocol is structured in two phases. The first phase involves model specification, calibration, and validation using historical data, together with counterfactual experiments designed to attribute observed changes in population abundance and occurrence to different environmental drivers. In the second phase, model projections are compared under future climate and land-use scenarios. This two-phase approach enables direct comparison of model predictive performance on common benchmark data, providing an empirical basis for assessing confidence in future projections. By combining regional-scale biodiversity time series, common calibration and out-of-sample validation, and explicit representation of ecological processes, this protocol advances regional biodiversity model intercomparisons and sets the stage to reveal fundamental insights into which models, processes, and drivers determine historical and future biodiversity dynamics.

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## 1 Introduction

Global biodiversity is changing rapidly due to accelerating anthropogenic drivers, such as land-use and climate change (Isbell et al., 2023; Newbold et al., 2015; Pecl et al., 2017), which cause widespread ecosystem degradation (Díaz et al., 2019; Trisurat et al., 2022). Land-use change is one of the primary drivers of past and current habitat degradation, and has led to changes to and loss of biodiversity (Jaureguiberry et al., 2022). In response to human-driven climate change, species have shifted their spatial distributions, abundance patterns, and interactions (Carter et al., 2018; Fadrique et al., 2026; Tylianakis et al., 2008), sometimes declining to extinction (Maclean and Wilson, 2011; Urban, 2015). These biodiversity changes also affect multiple ecosystem services and undermine nature's contribution to people (Díaz et al., 2018).

Addressing the global biodiversity crisis requires coordinated efforts across scales, from local conservation to international policy and action (McElwee et al., 2025). Accurate projection models are critical for underpinning and informing these actions (Houlahan et al., 2017; Mouquet et al., 2015; Purvis, 2025; Yates et al., 2018). For example, the Kunming-Montreal Global Biodiversity Framework (KM-GBF) targets (CBD, 2022) require robust projections to evaluate the potential consequences of implemented or planned interventions (Ferrier, 2026; Neugarten et al., 2025). However, biodiversity models can diverge widely in their predictions, differing in the magnitude and sometimes even the direction of biodiversity change (Johnson et al., 2024).

Accurate projection models can attribute changes in biodiversity to specific drivers and use these relationships to project the impacts of future scenarios and potential mitigation actions (Dietze et al., 2024). Hundreds of biodiversity modeling approaches have been developed, ranging from simple correlative models to complex process-explicit models that capture various ecological processes (Cabral et al., 2017; Dormann et al., 2012; Urban et al., 2022; Zurell et al., 2026). Although biodiversity projection models are commonly evaluated for their ability to describe the datasets on which they were trained, or more rarely, using independent data (Coppée et al., 2022; Lee-Yaw et al., 2021), systematic intercomparisons across modeling approaches and taxonomic groups remain limited (Zurell et al., 2026).

Model intercomparisons are coordinated scientific efforts that use a common, standardized experimental setup to compare multiple models and evaluate their agreement by harmonizing their outputs (Zurell et al., 2026). Climate model intercomparison projects have proven key to refining modeling frameworks, understanding the drivers of historical changes, quantifying uncertainty in predicted futures, and improving the credibility and interpretability

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of model-based insights (Durack et al., 2025; Touzé-Peiffer et al., 2020). To date, few model intercomparison projects have been proposed in biodiversity science, focusing on global terrestrial biodiversity and ecosystem services and on marine ecosystems and fisheries (e.g., Eddy et al., 2025; Kim et al., 2018; Pereira et al., 2024; Tittensor et al., 2018, 2021). These intercomparison projects have primarily focused on models of overall diversity or ecosystem properties rather than the spatiotemporal trajectories of individual species, reflecting the challenges inherent to global analyses.

The Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP 1.0) has led the way in including both correlative and process-explicit approaches across global and regional marine systems (Tittensor et al., 2018), while model intercomparisons in the terrestrial realm still lack the same level of process-based sophistication. In the first phase of the terrestrial-focused Biodiversity and Ecosystem Services Scenario-based Intercomparison of Models (BES-SIM 1.0), the included biodiversity projection models were mostly correlative species distribution models, whereas dynamic global vegetation models were used to project ecosystem services (Kim et al., 2018). BES-SIM 1.0 is restricted to terrestrial ecosystems on a global scale and focuses primarily on changes in species richness (Pereira et al., 2024). However, species richness can obscure species-specific changes relevant to species conservation and ecosystem functioning (Fletcher et al., 2025), while a focus on correlative models risks missing important mechanisms that mediate species responses to global change (Briscoe et al., 2019; Urban et al., 2016) and time lags (Essl et al., 2024; Zurell et al., 2025). Species-specific changes are key drivers of mass effects on ecosystem functioning and are directly embedded in conservation policies. In both BES-SIM 1.0 and Fish-MIP 1.0, the constituent models were fitted using disparate datasets, taxonomic groups, and spatial extents, complicating direct comparisons of predictive accuracy and constraining formal attribution of observed past biodiversity changes to specific drivers. While recent developments in Fish-MIP 2.0 have proposed attribution frameworks (Blanchard et al., 2024), equivalent protocols for terrestrial biodiversity models remain underdeveloped.

Process-explicit models are essential for capturing non-equilibrium dynamics and transient biodiversity responses to global change and for understanding how ecological and evolutionary processes shape these responses (Briscoe et al., 2019; Cabral et al., 2017; Urban et al., 2016, 2022). Careful consideration of key processes relevant for species response to global change, such as dispersal, demography and physiology, has been shown to improve model predictive accuracy (Zurell et al., 2016). To achieve the KM-GBF targets (Hughes, 2023), particularly those focused on population-level conservation (e.g., Target 4 – Halt

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Species Extinction, Protect Genetic Diversity, and Manage Human–Wildlife Conflicts), projecting biodiversity outcomes at the population level and including genetic diversity will require models that capture species-specific responses and explicitly represent biological processes. This level of detail can be realistically accomplished from regional (e.g., national or sub-continental) to continental scales using process-explicit modeling approaches. Model intercomparison projects spanning from correlative to process-explicit models could help address critical questions, e.g., by identifying the appropriate balance of complexity needed to accurately project biodiversity at different spatial and temporal scales (Zurell et al., 2026). Comparing models across diverse ecosystems and spatial scales will reveal general principles regarding the degree to which representing ecological processes within models leads to meaningfully better predictions (Eddy et al., 2025), thereby helping to balance predictive performance with forecasting efficiency (Zurell et al., 2016). Such intercomparisons can also provide fundamental insights and aid process understanding; for instance, inconsistencies between models may highlight limitations in process-explicit representations and point to missing or misspecified processes or time-lagged responses (Cheaib et al., 2012). Moreover, explicitly assessing the relevance and importance of different mechanisms across systems will not only improve confidence in future projections but also deepen our understanding of how different drivers contribute to biodiversity change.

Here, we detail version 1.0 of the Biodiversity Model Intercomparison Project protocol (BMIP 1.0), which provides a standardized framework for input data, methodology, and output metrics for species-level model intercomparisons at regional scales. BMIP 1.0 was designed to assess the impact of historical and future global changes on biodiversity. It focuses on terrestrial and freshwater species and quantifies spatiotemporal variations in abundance and occurrence in response to land-use and climate drivers. The protocol incorporates a spectrum of correlative and process-explicit modeling approaches to achieve three primary objectives: i) **assessment of model-driven performance and structural uncertainty:** to evaluate how the selection of model types and the inclusion of specific ecological processes influence the capacity to predict species distributions and abundances under historical conditions. ii) **driver attribution:** to isolate and quantify the relative contributions of individual environmental and anthropogenic drivers to observed biodiversity changes. iii) **future projections:** to generate and compare standardized projections of biodiversity change under diverse climate and land-use scenarios selected for their policy relevance. By establishing these standardized procedures, BMIP 1.0 facilitates a rigorous

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evaluation of model adequacy and enhances the transparency of biodiversity forecasting across various modeling frameworks.

## 2 Protocol overview

The initial phase of BMIP 1.0 incorporates 13 distinct modeling approaches, ranging from correlative frameworks to complex process-explicit systems (Table 1; Section S1 in the supplement). To ensure a comprehensive evaluation of model performance, these approaches were categorized based on their underlying concepts and the ecological processes they explicitly capture. In this version, we included correlative approaches and process-explicit models that explicitly account for processes such as metabolism, dispersal, population dynamics, and life-history traits (Table 1). Furthermore, process-explicit modeling approaches can adopt a hybrid structure that couples correlative projections with mechanistic processes. For instance, correlative suitability or ecophysiological predictions are used in process-explicit simulations of demography and movement (Backus et al., 2025; Buckley et al., 2023; de la Fuente et al., 2025). A detailed technical description of each modeling approach, including specific parameterization requirements and process representations, is provided in Section S1 (list of acronyms is in Appendices - Table A1).

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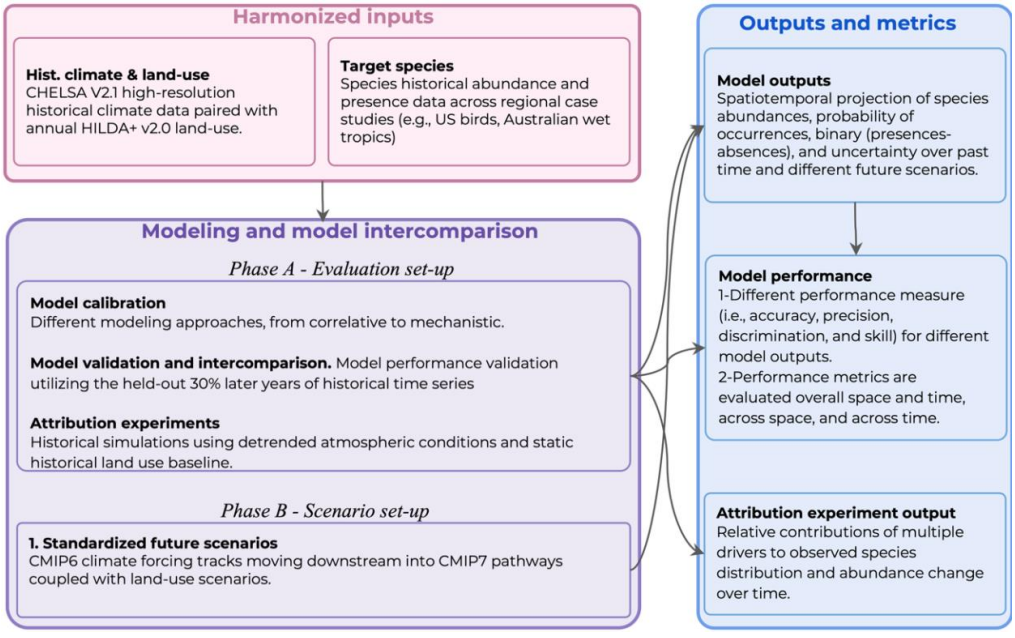


**Figure 1**. Methodological architecture and workflow of the Biodiversity Model Intercomparison Project protocol (BMIP 1.0).

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192 **Table 1.** Modeling approaches used in BMIP 1.0 and their characteristics.
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| Model category | Acronym (software)* | Type | Can be hybrid | Brief model description | Input data | Yearly output | Key references |
|---|---|---|---|---|---|---|---|
| Species distribution models | SDM (flexsdm) | Correlative | No | Correlates species occurrences (and absences or pseudo-absences) with environmental variables to predict species suitability and distribution throughout space and time. | Species presence. Environmental data over time.** | Continuous or binary suitability maps | (Elith and Leathwick, 2009; Franklin, 2010) |
| Abundance-based species distribution models | ASDM (adm) | Correlative | No | Correlates species abundance with environmental data to predict species abundance and distribution over space and time. | Species abundance. Environmental data over time. | Abundance maps | (Waldock et al., 2022) |
| Species exposure models | SEM (several R packages) | Correlative | No | Exposure forecasts seek to identify elevated risks when conditions require extrapolation beyond the limits of biological observations by focusing on realized niche. | Species presence. Environmental data over time.** | Continuous or binary suitability maps | (Serra-Diaz et al., 2026) |
| Dynamic occupancy models | DOM (Stan, Nimble, or JAGS) | Process-explicit | No | Characterizes explicit changes in site occupancy status over time, as a function of local extinction and colonization processes, and potentially accounts for imperfect detection. | Replicated species detection/non-detection. Environmental data over time.** | Occupancy, local colonization and local extinction maps | (MacKenzie et al., 2003; Royle and Kéry, 2007) |

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| Model category | Acronym (software)* | Type | Can be hybrid | Brief model description | Input data | Yearly output | Key references |
|---|---|---|---|---|---|---|---|
| Dispersal hybrid models | MigClim* | Process-explicit | Yes | SDM predictions are coupled with distance-dependent colonization probabilities and simulation. | Species suitability over time. Different species traits.** | Occupancy map | (Engler and Guisan, 2009) |
| Metabolically explicit metapopulation range model | metaRange* | Process-explicit | Yes | Spatially-explicit, niche-based metapopulation model with local population dynamics, with dispersal between populations and metabolically constrained demographic parameters | Environment and suitability over time. Different species traits. | Abundance maps | (Fallert et al., 2025) |
| Spatially and temporally explicit population simulations | STEPS* | Process-explicit | Yes | Simulates spatiotemporal population dynamics using stochastic matrix models driven by habitat suitability maps, carrying capacities, and empirically derived demographic and dispersal rates. | Species abundance. Suitability over time. Different species traits. | Abundance maps | (Visintin et al., 2020) |
| Individual-based model | RangeShiftR* | Process-explicit | Yes | Spatially explicit, individual-based model simulating local population dynamics and dispersal. | Suitability over time. Different species traits. | Abundance maps | (Bocedi et al., 2014; Bocedi et al. 2021; Malchow et al. 2021) |
| Age-structured dynamic range model | DRM (drmr) | Process-explicit | Yes | Bayesian approach models spatiotemporal population dynamics by linking demographic rates (e.g., recruitment | Species abundance. Environmental data over time. Age-specific mortality rates. | Abundance maps | (Da Cunha Godoy et al., 2026; Fredston et al., 2025) |

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| Model category | Acronym (software)* | Type | Can be hybrid | Brief model description | Input data | Yearly output | Key references |
|---|---|---|---|---|---|---|---|
| | | | | and survival) to environmental conditions. | Survey effort. | | |
| Ecophysiological models | NicheMapR and TrenchR * | Process-explicit | Yes | Process-explicit niche models based on the principles of biophysical ecology. | Daily or hourly environmental data. Morphological, physiological, and behavioral data. Different species traits. | Abundance or population growth; suitability | (Briscoe et al., 2022) |
| Mean simple model | MSM | Statistical | No | The mean of the last 10 years for all cells. | Abundance or occurrence data | Abundance maps | |
| Temporal Autocorrelation Model | TAM | Statistical | No | Extrapolates linear relationship at each cell. | Abundance or occurrence data | Abundance maps | |
| Spatial Autocorrelation Model | SAM | Statistical | No | Fits a local spatial autocorrelation function to data. | Abundance or occurrence data | Abundance maps | |

194 * Acronym and software name are the same
195 ** Model output could also be transformed into abundance

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## 3 Input data

### *3.1 Species presence and abundance data*

BMIP1.0 requires observation data as spatial and temporal, species-specific abundance, or occurrence data for model calibration and evaluation. Here, we briefly describe the species data that constitute the common benchmarking datasets (Urban et al., in prep), while acknowledging that the BMIP1.0 protocol could also be utilized for other species, taxa, and regions. We harmonized input data for four datasets from different regions and taxonomic groups, providing abundance or occurrence data at high spatial and temporal resolutions. These datasets include monitoring data for North American breeding birds, Finnish vascular plants, European freshwater invertebrates, and Australian Wet Tropics vertebrates (birds, mammals, and reptiles) (Urban et al., in prep) and are supplemented with opportunistic occurrence data sourced from GBIF (https://www.gbif.org). In total, 72 species (18 per dataset) were selected for use as benchmark data (Urban et al., in prep). To represent the breadth of species range dynamics and range sizes, we selected 18 species, targeting two species for each combination of temporal trend (declining, stable, increasing) and range size category (small, medium, large). These trend and range size categories are defined by the quantiles in each dataset (i.e., the extent of each range size category varies among taxonomic groups).

### *3.2 Dispersal, demographic, and trait data*

Most process-explicit models require additional trait information related to aspects such as dispersal (e.g., dispersal probability and distance), demography (e.g., growth rate, fecundity, and survival), morphology (e.g., body mass), metabolism (e.g., metabolic rate, body mass, and body temperature), physiology (e.g., thermal limits and temperature dependence of biological rates), or behavior (e.g., thermoregulation). Such trait data can be extracted from existing trait databases (e.g., Salguero-Gómez et al., 2016; Tobias et al., 2022) or other publications and must be provided along with each model's code. Imputing traits based on related species to fill in missing values is a common approach (Fandos et al., 2026; Penone et al., 2014), and each modeling team decides whether or not to use raw traits or a trait data imputation approach.

### *3.3 Climate-related forcing*

Historical climate data are obtained from the CHELSA-daily data set, which provides climate variables at daily resolution and 30 arcseconds (~1 km) generated with the CHELSA

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V2.1 downscaling model (Karger et al., 2017) for the years 1941-2025. Data for mean, minimum, and maximum near-surface (2 m) air temperature (*tas*, *tasmax*, and *tasmin*), precipitation rate (*pr*), surface downwelling shortwave flux in air (*rsds*), and relative humidity (*hurs*) are extracted for the four study regions of the standardized benchmark datasets and reprojected to an equal-area projection (Europe and Finland: EPSG:3035, USA: ESRI:102003, Australia: EPSG:9473). Climate data are provided in two combinations of spatial and temporal resolution: 1) daily data at 10 km resolution and 2) monthly data at 1 km resolution. Additionally, 19 bioclimatic variables are calculated at 1 km and 10 km resolution from monthly precipitation, maximum temperature, and minimum temperature (Booth et al., 2014). Most biodiversity models are fitted with climatic data at a one-year resolution. However, ecophysiological models are fitted using daily air and surface temperatures, solar radiation, and precipitation data.

### *3.4 Land-use related forcing*

Historical land-use data are sourced from HILDA+ v.2.0 (Winkler et al., 2025). This database provides global annual data on land use/land cover between 1960 and 2020 at 1 km resolution through a data-driven reconstruction approach integrating multiple open data streams and using a base map from 2000 based on ESA World Cover (Zanaga et al., 2021). Each grid cell is classified into one of 13 classes: Urban areas, Annual crops, Tree crops, Agroforestry, Pasture/Rangeland, Evergreen Needle Leaf Forest, Evergreen Broad Leaf Forest, Deciduous Needle Leaf Forest, Deciduous Broad Leaf Forest, Mixed Forest, Unknown/Other Forest, Unmanaged Grass/Shrubland, and Sparse/No vegetation.

### *3.5 Additional environmental variables*

Although climate conditions are recognized as one of the primary determinants of species distribution (Gardner et al., 2019), other environmental variables can also influence species distribution and abundance (Velazco et al., 2017). Modeling teams may collectively decide to include additional species-specific predictors—such as edaphic properties for terrestrial plants, fire history for sensitive birds and mammals, or stream variables for aquatic organisms—provided these data are made available to all participants. To maintain comparability and accurately assess relative driver importance across models, any additional non-climate or non-land-use variable selected for a given species must be applied consistently by all modeling teams.

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## 4 BMIP phases

Similar to the Inter-Sectoral Impact Model Intercomparison Project - ISIMIP (Frieler et al., 2024), which provides a framework for consistent climate impact simulations across different sectors (Frieler et al., 2024), we differentiated two phases within BMIP: (i) the evaluation set-up, which includes model calibration and evaluation of model runs on observed historical data as well as attribution experiments, and (ii) the scenario set-up, which includes simulations for future scenarios of climate and land-use forcing.

### *4.1 Phase A - Evaluation set-up*

Model calibration and evaluation in Phase A are divided into three subphases: 1) model calibration, 2) comparative model validation, and 3) attribution experiments. For the first two subphases, we split the species data (i.e., presence and abundance data) into a training set comprising the first 70% of years of the total available time period, leaving the last 30% of years as out-of-sample data for model evaluation and comparison. Only the training set is provided to modelers. All models are evaluated against the held-out years to assess their predictive accuracy in space and time. For the third subphase, attribution experiments are used to quantify the impact of climate-related forcing and direct human forcing (e.g., land-use change) (Frieler et al., 2024) on observed biodiversity dynamics based on retrospective simulations using counterfactual scenarios with detrended or constant forcing data (Frieler et al., 2024; Thomas et al., 2026) (see details in Section *4.3 Attribution experiment*).

#### *4.1.1 Model calibration*

Teams may employ diverse methodologies for model optimization, including but not limited to fine-tuning, model selection, pattern-oriented modeling (e.g., via numerical optimization of summary metrics or Approximate Bayesian Computation), machine learning, or Bayesian inference (Malchow and Hartig, 2026). Models are fitted at 1 km or 10 km spatial resolution, with the specific resolution determined by both the dataset constraints and model-specific requirements. All teams must document data requirements by reporting the number of parameters needed and data completeness for model parameterization, i.e., proportion of available vs. required data for parameterization of specific ecological processes (e.g., dispersal rates and distances). Model characteristics and specific details of the calibration methodology are reported in Section S1.

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*4.1.2 Model validation and intercomparison*

Model performance is validated using the held out 30% of the historical time series of occurrence-abundance data. Modeling teams are required to provide predictions for the validation period. All predictions are provided at a 1 km resolution. For models calibrated at a 10 km resolution, downscaling to the 1 km grid is required based on a bilinear interpolation approach. Validations are restricted to a species-specific region defined by a 100 km buffer around available occurrence data to constrain the spatial domain and computational burden of model evaluation while capturing plausible range expansion. Only predictions within this buffered area are evaluated.

Several steps are taken to ensure that models produce standardized and harmonized outputs as a prerequisite for intercomparison(Zurell et al., 2026). Modeling teams must provide a suite of different spatiotemporal outputs for comparison, including predictions of abundance (if abundance was observed in the original data), continuous probability of occurrence, and presence/absence classifications based on a threshold. If observed abundances are available but a specific model only outputs suitability or presence/absence (Table 1), these outputs must be converted into abundance by the respective modeling team.

For models predicting habitat suitability, various empirical conversion approaches can be explored and tested against available abundance data to select the highest-performing relationship for a given species. Models producing abundance or continuous suitability are required to define a threshold to derive binary (presence/absence) predictions.

Furthermore, an estimate of uncertainty must be provided. The method to quantify uncertainty may be model-specific and, for instance, involve deriving standard deviations from MCMC posterior distributions, bootstrapping, or obtaining standard errors for maximum-likelihood estimates. If no uncertainty is provided, the predictions are assumed to have no associated uncertainty.

Different model predictions (i.e., abundance, presence probability, and binary) are compared based on performance metrics that capture measures of accuracy, discrimination, precision, and skill. Accuracy refers to the extent to which a model's predictions correspond to the observed data (Waldock et al., 2022). Precision measures a model’s capacity to predict values closer to the observed data variation (Waldock et al., 2022), assessing whether it is systematically biased and whether its uncertainty estimates are reliable. Discrimination describes how well a model distinguishes between low and high values (Norberg et al., 2019;

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Waldock et al., 2022), and therefore, it evaluates the rank correspondence with observations. Skill refers to each of these performance measures relative to a naive reference baseline (e.g., historical mean) (Murphy and Epstein, 1989). BMIP validation must be based on the integration of at least one performance metric for each performance measure (Table 2 and Section S2).

These components are compared in three ways: overall (performance across all sites and years), across space (averaged across years), and across time (averaged across all sites) (Briscoe et al., 2021; Malchow et al., 2023) (Table 1, Section S1). The overall mean by grid cell and time period are used as the reference across the validation period. Predictions for abundance, occurrence probability (or suitability), and binary predictions are compared based on multiple metrics, given various strengths and detriments, and their ability to detect various aspects of performance.

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344 **Table 2.** Performance measures and potential metrics used to evaluate different model output
345 types (abundance, probability of occurrence, and binary output). See Section S2 in
346 supplement for details about metric equations.

| Model output type | Performance measures | Metric | Description | Reference |
|---|---|---|---|---|
| Abundance; probability of occurrence | Accuracy | Mean Absolute Error (MAE) * | Mean Absolute Error (MAE) evaluates the average absolute difference between predictions and observations without exponential error weighting. | (Moriasi et al., 2015) |
| Abundance | Accuracy | Root Mean Square Error (RMSE) * | Root Mean Square Error (RMSE) quantifies the average magnitude of the coordinate distance between predictions and observations, penalizing larger outliers. | (Moriasi et al., 2015) |
| Abundance; probability of occurrence | Accuracy | $R^2$ and pseudo-$R^2$ | Coefficient of determination for abundance - proportion of variance in observed values explained by model predictions. Pseudo-$R^2$ for probability of occurrence predictions (i.e., binomial model). | (Moriasi et al., 2015) |
| Probability of occurrence | Accuracy | Brier score (BS) * | Brier score (BS), average squared error of the probability forecast, where the observation is either matched or not. | (Simonis et al., 2021) |
| Abundance | Precision | Slope and intercept | Slope and intercept derived via OLS regression of observations on predictions; perfect model prediction requires a slope of 1 and an intercept of 0. | (Waldock et al., 2022) |
| Abundance | Precision | Percent Bias *** | Percent Bias calculates the average systemic direction of errors, revealing long-term model tendencies toward overestimation or underestimation. | (Moriasi et al., 2015) |
| Abundance | Precision | Coverage probability | Proportion of observations falling within stated prediction/credible intervals; compares nominal to empirical coverage. | (Liu et al., 2011; Morris et al., 2019) |

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| Model output type | Performance measures | Metric | Description | Reference |
|---|---|---|---|---|
| Abundance | Precision | $P_{\text{dispersion}}$ ** | Assess variance matching based on the ratio between the standard deviation of prediction and the standard deviation of observed data. | (Waldock et al., 2022) |
| Abundance; probability of occurrence | Discrimination | Correlation | Non-parametric Spearman rank or parametric Pearson correlations between predictions and observations. | (Waldock et al., 2022) |
| Abundance | Discrimination | Continuous Ranked Probability Score (CRPS) * | CRPS evaluates the distance between full predictive cumulative distributions and observations. | (Brier, 1950; Simonis et al., 2021) |
| Probability of occurrence | Discrimination | Log-score * | Log-score or Negative log-likelihood measures the probability that the model successfully predicted the observed binary outcome (1 for presence, 0 for absence). | (Simonis et al., 2021) |
| Abundance; probability of occurrence | Discrimination | Harrell's Concordance Index (C-index) | Evaluates the probability of correct pairwise relative rank ordering across all observed combinations. | (Harrell, 1982) |
| Probability of occurrence | Discrimination | Area Under the Receiver Operating Characteristic Curve (AUC) | Computes binary rank discrimination across the entire spectrum of threshold cutoffs | (Fielding and Bell, 1997) |
| Probability of occurrence | Skill | Brier Skill Score (BSS) | Averages squared error of the probability forecast where the observation is either matched or not relative to a reference model baseline. | (Brier, 1950) |
| Abundance | Skill | CRPS skill score | Evaluates the distance between full predictive cumulative distributions and observations relative to a reference model baseline. | (Brier, 1950; Matheson and Winkler, 1976) |
| Abundance | Skill | Moving window forecast skill | Mean Squared Error performance improvements evaluated across a sequence of rolling temporal horizons | (Zivot and Wang, 2006) (Murphy and Epstein, 1989) |

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| Model output type | Performance measures | Metric | Description | Reference |
|---|---|---|---|---|
| | | | relative to a reference baseline. | |
| Binary presence-absence | Accuracy | Overall accuracy | Proportion of all predictions correctly classified. | (Fielding and Bell, 1997) |
| Binary presence-absence | Accuracy | Sensitivity (True Positive Rate) | Proportion of presence records correctly predicted as presence. | (Fielding and Bell, 1997) |
| Binary presence-absence | Accuracy | Specificity (True Negative Rate) | Proportion of absence records correctly predicted as absence. | (Fielding and Bell, 1997) |
| Binary presence-absence | Precision | Positive predictive value | Of all predicted presences, the proportion truly occupied. | (Lobo et al., 2008) |
| Binary presence-absence | Precision | Negative predictive value | Of all predicted absences, the proportion truly unoccupied. | (Lobo et al., 2008) |
| Binary presence-absence | Precision | F1 score (Sorensen) | Harmonic mean balancing sensitivity and positive predictive value to evaluate classification performance under high data imbalance. | (Leroy et al., 2018; Sørensen, 1948) |
| Binary presence-absence | Discrimination | Cohen's kappa | Chance-corrected agreement matrix measuring classification alignment with observations relative to purely random matching. | (Cohen, 1960) |
| Binary presence-absence | Discrimination | True Skill Statistic (TSS) | Standardizes validation performance by combining sensitivity and specificity metrics. | (Allouche et al., 2006) |

347 * A lower value indicates better model performance.
348 ** Values closer to one denote better model performance.
349 *** Values closer to zero denote better model performance.

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*4.1.3 Attribution experiment*

Attribution approaches are used to quantify and evaluate the relative contributions of multiple drivers to observed species abundance distribution change. This can be achieved by comparing observations to a baseline or reference that characterizes system behavior in the absence of external drivers (counterfactual state) (Gonzalez et al., 2023; Schrodt et al., 2025; Thomas et al., 2026).

To isolate the historical impacts of climate and land-use change, BMIP 1.0 implements a prediction-based attribution framework in which observed factual trends are compared with model simulations of counterfactual baselines under detrended climate and land-use (Malchow et al., 2023). This baseline should be employed to characterize system behavior in the absence of observed changes in external drivers (Mengel et al., 2021).

Climate data are detrended using the ATTRIbuting Climate Impacts (ATTRICI) approach (Mengel et al., 2021), combining ISIMIP detrending from 1901 onwards (Frieler et al., 2024) with study-specific counterfactuals, for which detrending is initiated from the start of each biodiversity time series, which varies by dataset. Land-use counterfactuals are constructed by keeping land-use variables at a constant level from the first year.

The relative impact of climate and land-use change is then defined as the difference in prediction errors between factual realizations (observations minus factual model predictions) and counterfactual baselines, effectively controlling for model-specific predictive uncertainty.

Following the conceptual framework adapted from Langhammer et al. (2024), this comparative analysis categorizes species-level responses over time into four distinct ecological trajectories based on the divergence between factual observations and counterfactual scenarios. **Absolute winners:** species exhibiting an overall positive trend over time alongside higher abundance or occupancy under factual conditions relative to counterfactual scenarios. **Relative winners:** species that maintain higher abundance or occupancy under factual drivers than under counterfactual scenarios, despite demonstrating an overall negative temporal trend. **Relative losers:** species experiencing an overall positive baseline trend over time yet displaying lower abundance or occupancy under factual data compared to counterfactual scenarios. **Absolute losers:** species characterized by an overall negative temporal trend paired with diminished abundance or occupancy under factual conditions relative to counterfactual scenarios (Langhammer et al., 2024). As our setup for Phase A provides training data that only include the onset of climate change, the

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counterfactual baselines mostly target land-use effects on biodiversity (i.e., the impacts of climate change are difficult to detect and attribute; Oliver and Morecroft, 2014; Stone et al., 2013). However, due to the differential set of species types and latitudinal variation chosen for the intercomparisons, we expect that climate change attribution may be possible for high-latitude species.

To ensure the statistical robustness of these designations, attribution outputs are stratified by confidence tiers, explicitly distinguishing results derived from models that achieved high predictive accuracy during the historical validation phase. Given the structural variance across models, this categorization relies on strictly probabilistic evaluation metrics—such as the Continuous Ranked Probability Score (CRPS) or Harrell's Concordance Index (C-index)—to capture components of output discrimination skill.

The primary expected outcomes of this analytical framework include the systematic mapping of relative driver impacts across species, the formal quantification of model-based uncertainty during attribution tasks, and the identification of systematic structural biases inherent to different biodiversity modeling paradigms.

### *4.2 Phase B - Scenario set-up*

Regarding future projections, the BMIP 1.0 protocol is structured to accommodate evolving generations of global emission scenarios dynamically. While initial implementations rely on the established Coupled Model Intercomparison Project 6 (CMIP6) framework, which comprises Shared Socioeconomic Pathways (SSPs) paired with Representative Concentration Pathways (RCPs), BMIP 1.0 anticipates the integration of the emerging CMIP7 core emission pathways detailed by the ScenarioMIP framework (Van Vuuren et al., 2026). Consequently, as bias-adjusted and downscaled data from these new trajectories become operationally available, participating modeling teams are requested to transition to these updated forcings.

Regardless of whether CMIP6 or CMIP7 forcing architectures are deployed, the protocol mandates using the widest spectrum of scenarios to cover projection uncertainties and multiple plausible futures. To systematically isolate climate model structural uncertainty from scenario uncertainty, multi-model ensembles utilizing diverse Atmosphere-Ocean General Circulation Models (AOGCMs) and Earth System Models (ESMs) must be employed for each scenario. Because the predictive uncertainty of models increases as the time horizons move further away from the training data (Wesselkamp et al., 2025), the

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models are projected through the year 2100 within the CMIP6 framework, with extensions beyond the end of the century preferred where available in CMIP7.

Crucially, internal consistency should be considered between climate forcing and corresponding land-use change scenarios during future projections. Decoupling these drivers can introduce confounding errors, as climate and land-use pathways are fundamentally linked via shared socioeconomic assumptions, greenhouse gas mitigation strategies, or biophysical feedback (Hurtt et al., 2020; Popp et al., 2017). For instance, an emission pathway representing aggressive global climate mitigation cannot be realistically paired with a land-use scenario characterized by unrestricted agricultural expansion, as the underlying carbon cycle dynamics would be structurally incompatible (O'Neill et al., 2017). Therefore, to preserve the structural and ecological integrity of the BMIP 1.0, consistent narrative scenarios must govern both the atmospheric forcings and the landscape transitions used in the biodiversity models.

The primary outputs derived from these standardized future simulations encompass detailed spatiotemporal range and abundance dynamics across target species and regions. Specifically, the protocol requires the calculation of both absolute and relative changes in species abundance and occurrence probabilities between historical baselines and designated future periods, as previous studies have repeatedly indicated that relative abundance changes are often more reliable than absolute changes in abundance (Beissinger and Westphal, 1998; Zurell et al., 2016). Together, these model outputs allow for the systematic isolation of the relative effects of different scenarios, while simultaneously constraining the model-driven uncertainty embedded within climate and land-use change projections.

To maximize the robustness of these final projections, outputs from all participating modeling frameworks are generated, but their use is stratified based on validation performance. Projections originating from models that demonstrate higher confidence—established via predictive performance during the historical validation step—are explicitly differentiated from those with lower performance.

## 5 Discussion

BMIP 1.0 provides a modeling protocol for intercomparison of biodiversity projection models at the scale relevant for species, namely at the regional to continental scales. This represents a significant advancement in biodiversity modeling by incorporating several novel features that enhance both the ecological realism and predictive robustness of its outputs at

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the species level. By harmonizing input data spanning climate, land-use, and multi-taxa datasets, BMIP 1.0 enables a rigorous evaluation of how varying model architectures—from correlative species distribution models to complex process-explicit simulations—influence predictive performance over time and space, an assessment of model uncertainty, and the execution of attribution analyses.

Previous intercomparison projects, such as BES-SIM and FishMIP, have provided foundational insights into trends at the ecosystem level and global biodiversity (Kim et al., 2018; Pereira et al., 2024; Tittensor et al., 2018). However, they have been limited in validation; performance assessments have often been hampered by the use of different biodiversity and environmental calibration datasets, and have focused on aggregate metrics rather than individual species trajectories. BMIP 1.0 improves consistency of training data across models to enable more robust comparisons, integrates multiple process-explicit approaches, and shifts from an evaluation of overall diversity or ecosystem properties for large regions or at a global scale towards regional species abundance and occurrence, allowing it to capture ecological components (e.g., ranging from metabolic/ecophysiological to demographic and dispersal) through more process-explicit approaches. Model intercomparisons that include process-explicit approaches explore how a more explicit representation of biological processes might improve the reliability of model projections.

In this BMIP, we explicitly evaluate model performance based on out-of-sample validation data not included in model calibration. Crucially, BMIP seeks to evaluate model performance across diverse contexts—including taxonomic groups, species traits (e.g., dispersal and range size), and population trends—rather than identifying a single "best" model. Another key strength lies in its explicit incorporation of uncertainties and an attribution framework to disentangle the impacts of land-use and climate change. By acknowledging variability in model design and parameterization, BMIP 1.0 enhances the credibility and robustness of its biodiversity forecasts, addressing a critical gap in prior modeling efforts that often overlook these uncertainties. The integration of the attribution framework further strengthens the BMIP's analytical capacity. This framework enables the disentanglement of the effects of land-use and climate change as global drivers of biodiversity change, allowing for more precise assessments of anthropogenic influences.

Despite these advances, BMIP faces several challenges. Process-explicit models inherently demand high computational resources, which constrain their scalability and accessibility, particularly for researchers with limited computational infrastructure (Briscoe et al., 2019). Moreover, even our broad range of models still excludes important biological

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processes, such as species interactions and evolutionary adaptation, which can be key to estimating species response to environmental changes (Bush et al., 2016; Staniczenko et al., 2017; Urban et al., 2016). The development of reproducible model calibration pipelines remains a formidable task, complicated by the scarcity of reliable trait data and mechanistic parameters necessary for accurate model calibration. Additionally, the precision and resolution of the environmental and driver datasets pose significant limitations. For example, climate data resolution and land-use classifications could fail to capture the fine-scale heterogeneity that is biotically meaningful, thereby reducing the fidelity of model outputs and potentially obscuring important ecological dynamics.

Currently, the requirement for validation data restricts analyses to a narrow subset of taxonomic groups and geographical regions. An area for future exploration is to understand the degree to which results of this study apply to other taxonomic groups or regions. Expanding the datasets taxonomically and geographically would be desirable in the future if high-quality datasets can be collected over sufficiently long time periods and spatial scales. Overcoming these data constraints is imperative to expand the applicability of the BMIP and similar frameworks, thereby supporting more comprehensive biodiversity assessments and conservation planning.

Overall, BMIP 1.0 addresses several crucial challenges to improve biodiversity projections, inform decision-making, and close an important gap in existing biodiversity model intercomparison projects (Zurell et al., 2026). We expect that this regional and process-explicit focus and standardized model calibration and evaluation will create a step change in understanding species-level responses to global change and the underlying mechanisms, and provide important insights regarding the level of model complexity needed to project this response accurately. Focusing on terrestrial and freshwater taxa, BMIP 1.0 complements existing efforts in the marine realm (Blanchard et al., 2024; Eddy et al., 2025). By projecting biodiversity outcomes at the population level, BMIP 1.0 moves beyond global species richness estimates (Fletcher et al., 2025) to provide national-to-regional metrics (Burgess et al., 2024) and inform population-level biodiversity targets (Hughes, 2023). Thus, BMIP 1.0 provides a foundation for developing a robust forecasting capacity to guide effective policymaking and conservation efforts in a rapidly changing world.

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## 6 Appendices

**Table A1:** List of acronyms

| Acronym | Meaning |
|---|---|
| AOGCM | Atmosphere-Ocean General Circulation Model |
| ASDM | Abundance-based Species Distribution Model |
| ATTRICI | ATTRIbuting Climate Impacts |
| BES-SIM | Biodiversity and Ecosystem Services Scenario-based Intercomparison of Models |
| BMIP | Biodiversity Model Intercomparison Project |
| CMIP | Coupled Model Intercomparison Project |
| DOM | Dynamic Occupancy Model |
| DRM | Age-structured Dynamic Range Model |
| ESM | Earth System Model |
| Fish-MIP | Fisheries and Marine Ecosystem Model Intercomparison Project |
| ISIMIP | Inter-Sectoral Impact Model Intercomparison Project |
| KM-GBF | Kunming-Montreal Global Biodiversity Framework |
| metaRange | Metabolically explicit metapopulation range model |
| MIP | Model Intercomparison Project |
| MSM | Mean Simple Model |
| NicheMapR | NicheMapR R package for biophysical microclimate and mechanistic niche modeling |
| RangeShiftR | RangeShiftR R package for individual-based spatiotemporal population dynamics |
| RCP | Representative Concentration Pathway |
| SAM | Spatial Autocorrelation Model |
| SDM | Species Distribution Model |
| SEM | Species Exposure Model |
| SSP | Shared Socioeconomic Pathway |
| STEPS | Spatially and Temporally Explicit Population Simulations |
| TAM | Temporal Autocorrelation Model |
| TrenchR | TrenchR R package for microclimate and biophysical trait modeling |

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## Code and data availability

This model inter-comparison protocol has no code associated with it. The historical climate data from CHELSA V2.1 l (Karger et al., 2017) is available at: https://www.chelsa-climate.org. The historical land-use data from HILDA+ v.2.0 (Winkler et al., 2025) is available at: https://doi.pangaea.de/10.1594/PANGAEA.921846?format=html#download.

## Author contributions

SJEV, DZ, GB and MCU conceived the idea. All authors contributed substantially to discussion of the content. SJEV led the writing. All authors reviewed and/or edited the manuscript before submission.

## Competing interests

The contact author has declared that neither they nor their co-authors have any competing interests.

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