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BRITISH ECOLOGICAL SOCIETY Methods in Ecology and Evolution

APPLICATION

EEMtoolbox: A user-friendly R package for flexible ensemble ecosystem modelling

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Abstract

1. Forecasting ecosystem changes due to disturbances or conservation interventions is essential to improve ecosystem management and anticipate unintended consequences of conservation decisions. Mathematical models allow practitioners to understand the potential effects and unintended consequences via simulation. However, calibrating these models is often challenging due to a paucity of appropriate ecological data.
2. Ensemble ecosystem modelling (EEM) is a quantitative method used to parameterize models from theoretical ecosystem features rather than data. Two approaches have been considered to find parameter values satisfying those features: a standard accept–reject algorithm, appropriate for small ecosystem networks, and a sequential Monte Carlo (SMC) algorithm that is more computationally efficient for larger ecosystem networks. In practice, using SMC for EEM generation requires advanced statistical and mathematical knowledge, as well as strong programming skills, which might limit its uptake. In addition, current EEM approaches have been developed for only one model structure (generalised Lotka–Volterra).
3. To facilitate the usage of EEM methods, we introduce EEMtoolbox, an R package for calibrating quantitative ecosystem models. Our package allows the generation of parameter sets satisfying ecosystem features by using either the standard accept–reject algorithm or the novel SMC procedure. Our package extends the existing EEM methodology, originally developed for the generalised Lotka–Volterra model, to two additional model structures (the multispecies Gompertz and the Bimler–Baker model) and additionally allows users to define their own model structures.

4. We demonstrate the usage of EEMtoolbox by simulating changes in species abundance immediately after the release of the sihek (*Todiramphus cinnamominus*, extinct-in-the-wild species) on Palmyra Atoll in the Pacific Ocean. With its simple interface, our package facilitates straightforward generation of EEM parameter sets, thus unlocking advanced statistical methods supporting conservation decisions using ecosystem network models.

KEYWORDS
approximate Bayesian computation, ensemble ecosystem modelling, population dynamics, R package, sequential Monte Carlo

1 | INTRODUCTION

The current biodiversity crisis requires urgent interventions to preserve ecosystems (Barnosky et al., 2011; Bergstrom et al., 2021). However, conservation decisions are risky, as they can lead to unexpected negative outcomes (Bergstrom et al., 2009; Buckley & Han, 2014; Roemer et al., 2002). Our ability to anticipate the consequences of interventions on ecosystems is critical to making informed decisions. Quantitative models can assist in making conservation decisions by simulating the effects of interventions (or disturbances) on ecosystem networks and predicting ecosystem changes (Adams et al., 2020). In practice, using these quantitative models requires large datasets to estimate driving parameters, such as species growth rates (Adams et al., 2020; Botelho et al., 2025), a difficult task in data-poor contexts such as biodiversity conservation, which limits quantitative model applications (Christie et al., 2021; Cook et al., 2013; McDonald-Madden et al., 2010).

When historical data are unavailable, ensemble ecosystem modelling (EEM, Baker et al., 2017) is a quantitative method for parameterising population models that uses theoretical ecosystem features rather than data. EEM can therefore be applied to any ecosystem for which a network structure (e.g. food web) has been proposed. Applications of EEM include risk analysis for the reintroduction of species (Baker et al., 2017; Peterson et al., 2021) and the management of invasive species (Rendall et al., 2021). To date, two algorithms are designed for EEM generation: an accept–reject algorithm in Baker et al. (2017) and an adaptation of the sequential Monte Carlo approximate Bayesian computation (SMC-ABC) algorithm of Drovandi and Pettitt (2011) in Vollert et al. (2024). While the accept–reject algorithm from Baker et al. (2017) is relatively straightforward to implement, this algorithm suffers from computational limitations for moderate to large ecosystems (Peterson & Bode, 2021), limiting its application to small ecosystem networks only. In contrast, the SMC-ABC algorithm of Vollert et al. (2024) can generate parameter sets (a sample of size N of parameter values) matching the desired features orders of magnitude faster for larger and more complex ecosystem networks but requires advanced statistical theory, mathematical knowledge and programming skills to implement.

EEM was initially designed for the generalised Lotka–Volterra model, a well-studied deterministic framework with convenient equilibrium properties for EEM (Baker et al., 2017). However, ecosystem population modelling literature considers many other structures. For example, the multispecies Gompertz model has been broadly used by the ecology community (Cooper et al., 2015; Hampton et al., 2013) because it is the time-continuous and deterministic equivalent of the first-order multivariate autoregressive model used elsewhere to simulate multispecies time series (Ives et al., 2003). While the generalised Lotka–Volterra model describes ecosystem dynamics based on logistic growth, this model uses a Gompertz growth, which models slower population growth due to interactions at high densities. A second alternative model is the Bimler–Baker model (Bimler et al., 2024), which can describe beneficial and harmful interactions between the same two species separately in a manner that makes these interactions structurally identifiable in the model. Generalising EEM to other models, such as the multispecies Gompertz and Bimler–Baker model, yields modelling flexibility that benefits the broader ecology community.

In this manuscript, we present a new R package, EEMtoolbox. Our package facilitates the usage of the recent statistical advances introduced in Vollert et al. (2024), offers a range of user-friendly functions allowing the parameter generation for three different ecosystem network model structures and can accommodate user-defined models. The package generates an ensemble of ecosystem models using a network and can also be used to forecast temporal changes in species abundances. As a case study, we demonstrate the usage of EEMtoolbox by simulating changes in species abundances immediately after the release of a small population of the avian top predator sihek (*Todiramphus cinnamominus*, extinct-in-the-wild species) on Palmyra Atoll, a United States minor outlying Island in the Pacific Ocean. EEMtoolbox is publicly available on GitHub at https://zenodo.org/records/14880924.

2 | METHODS

2.1 | Modelling dynamics of ecosystem networks

Ecosystems of interacting species are commonly represented as an ecosystem network (Cohen et al., 2012; Pimm et al., 1991): a graphical representation of how populations of species or groups of species (nodes) interact (edges) with other populations. Ecosystem networks can represent predator–prey (Post et al., 2000), competitive or mutualist (Waser & Ollerton, 2006) relationships between species.

Quantitative species models use this ecosystem network structure to forecast trajectories of species abundances (Adams et al., 2020; Baker et al., 2017; Ives et al., 2003; Murray, 2002). Our package EEMtoolbox can apply EEM (see Section 2.2) to three ordinary differential equation models of ecosystem networks (summarised in Table 1 and detailed on a simple predator–prey example in Appendix B, Data S1) and can also accommodate user-customised models (see Appendix C, Data S1).

2.2 | Ensemble ecosystem modelling

EEM generates parameter sets using theoretical ecosystem features: feasibility (species coexistence) and stability (recovery of equilibrium populations following disturbances) (Baker et al., 2017). Mathematically, feasibility implies that a steady state of the model exists in which all species' abundances are positive, and stability implies that the steady state is Lyapunov stable (see Appendix A, Data S1). Our package EEMtoolbox can apply EEM to other ecosystem models than the generalised Lotka–Volterra model using two sampling algorithms: an accept–reject approach developed by Baker et al. (2017) and an SMC-ABC (Drovandi and Pettitt (2011)) developed by Vollert et al. (2024). Our package extends these two sampling approaches that were originally designed for the Lotka–Volterra model to other ecosystem models (see Table 1).

The EEM algorithm from Baker et al. (2017) samples parameter values of the generalised Lotka–Volterra equations and uses an accept–reject procedure to select parameter sets that yield feasible and stable ecosystems. The process (hereafter called standard-EEM) continues until the desired number of parameter sets is generated. However, the probability of randomly generating parameter sets that meet the feasibility and stability criteria decreases dramatically as the size and complexity of the ecosystem increase (Allesina & Tang, 2015; May, 1972). Thus, the usage of standard-EEM becomes practically impossible for large ecosystem networks.

The SMC-ABC algorithm from Vollert et al. (2024) (hereafter called SMC-EEM) can generate feasible and stable parameter ensembles for larger ecosystem networks than the standard-EEM approach. SMC-EEM learns from the trialled parameter sets how to better suggest parameter sets more likely to satisfy the conditions of feasibility and stability. Essentially, this approach samples parameter values, measures how poorly the sampled parameters satisfy the feasibility and stability constraints (this is called the discrepancy) and resamples and perturbs parameters to sequentially minimise the discrepancy. The target distributions of standard-EEM and SMC-EEM are theoretically identical. Thus, for a large number of samples, the empirical distributions of the parameter sets produced by standard-EEM and SMC-EEM are equivalent (Vollert et al., 2024) (see Appendix B.5, Data S1). Figure 1 illustrates the difference between these approaches.

3 | DEMONSTRATING THE FUNCTIONALITY OF THE EEMtoolbox R PACKAGE

3.1 | Sihek case study

Sihek, a charismatic bird species endemic to Guam in the northwestern Pacific, went extinct in the wild following the accidental introduction of the invasive brown tree snake (*Boiga*

TABLE 1 Mathematical models of ecosystem networks supported by our EEMtoolbox R package.

Model	Parameters description
Generalised Lotka–Volterra (Murray, 2002): $\frac{dn_i}{dt} = \left[r_i + \sum_{j=1}^{N} \beta_{i,j} n_j(t)\right] n_i(t), \quad \forall i \in [1, \ldots, N]$	r_i: intrinsic growth rate of the ith species $\left(\text{time}^{-1}\right)$ $\beta_{i,j}$:per-capita interaction strength of jth species on the ith species abundance $\left(\text{area. biomass}^{-1}\text{time}^{-1}\right)$
Multispecies Gompertz (Gomatam, 1974; Ives et al., 2003): $\frac{dn_i}{dt} = \left[r_i + \sum_{j=1}^{N} \beta_{i,j} \log\left(n_j(t)\right)\right] n_i(t), \quad \forall i \in [1, \ldots, N]$	r_i: intrinsic growth rate of the ith species $\left(\text{time}^{-1}\right)$ $\beta_{i,j}$: per-capita interaction strength of jth species on the ith species abundance $\left(\text{time}^{-1}\right)$
Bimler–Baker (Bimler et al., 2024): $\frac{dn_i}{dt} = r_i n_i(t) \left[1 - \exp\left(-\alpha_{i,i} - \sum_{\substack{j=1 \\ j \neq i}}^{N} \alpha_{i,j} n_j(t)\right)\right] + \sum_{j=1}^{N} \beta_{i,j} n_j(t) n_i(t), \quad \forall i \in [1, \ldots, N]$	r_i: maximum intrinsic growth rate of the ith species $\left(\text{time}^{-1}\right)$ $\alpha_{i,i}$ and $\alpha_{i,j}$: per-capita beneficial interactions with conspecific and heterospecific populations, respectively ($\alpha_{i,i}$ are unitless and $\alpha_{i,j}$ in units of $\text{area. biomass}^{-1}$) $\beta_{i,j}$: per-capita interaction strength of jth species on the ith species abundance $\left(\text{area. biomass}^{-1}\text{time}^{-1}\right)$

Note: For all models, $n_i(t)$ represents abundance of the ith species at time t and N is the total number of species. The generalised Lotka–Volterra model represents ecosystem dynamics based on the principle of logistic growth. The multispecies Gompertz represents ecosystem dynamics using Gompertz growth. The Bimler–Baker model is able to separate beneficial and harmful interactions between all pairs of species.

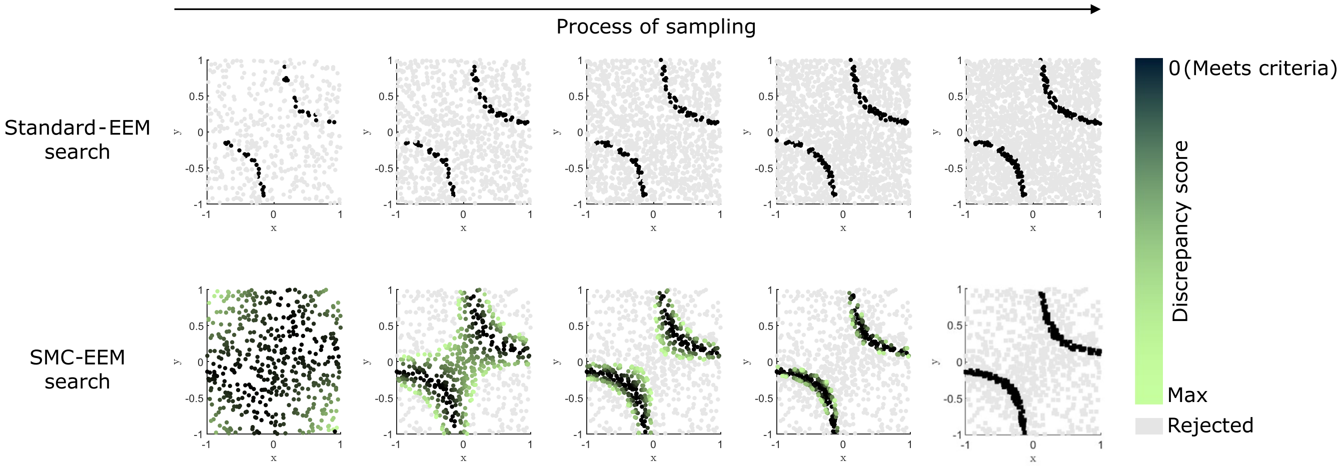

FIGURE 1 A conceptual diagram comparing the process of sampling using standard-EEM (top row) and SMC-EEM (bottom row) algorithms. The standard-EEM search method (top row) randomly samples parameter sets from a pre-specified region, rejecting parameter sets that do not meet the constraints (grey dots) and accepting those that do (black dots). The SMC-EEM search method (bottom row) creates a discrepancy score that measures how different the desired and sampled system properties are to sequentially adapt sampling towards the objective region. Parameter sets that meet the constraints are accepted (black dots), while parameter sets that do not meet the constraints are rejected depending on their discrepancy score (grey dots are rejected and light green dots will be resampled from and perturbed to sequentially minimise the discrepancy score). This two-dimensional illustration aims to obtain parameter sets where $0.1 \le xy \le 0.15$ (curves in top right and bottom left region of parameter space); however, for EEM, these algorithms aim to obtain regions of parameter space that yield feasible and stable ecosystem models. EEM, ensemble ecosystem modelling; SMC, sequential Monte Carlo.

irregularis) in its native range (Savidge, 1986; US Fish and Wildlife Service, 1990). Re-establishing a population of sihek in the wild is urgent due to the limited capacity of zoos and the increasing genetic concerns related to the species' small current population size (Trask et al., 2021). Since reintroducing sihek to their endemic range is not yet feasible, an experimental conservation introduction to Palmyra Atoll is being conducted in the meantime. Due to their ecology, Canessa et al. (2022) anticipate sihek replacing carnivorous crabs and cane spiders as top predators in Palmyra Atoll upon introduction.

We use EEM to explore the potential impacts of sihek introduction on the abundances of the resident species of Palmyra Atoll. Following Canessa et al. (2022), we simplify the system and assume that all species will coexist after the release of the sihek (including sihek) and the ecosystem will eventually reach a stable equilibrium. We aim to simulate how the resident species' abundances would change over time when the initial abundance of sihek is set to a small number. We use EEM to analyse changes in the abundance of all species predicted to interact directly with the sihek (nine species or groups of species; Figure 2) immediately after the sihek release up to 10 years post-introduction. We use the upper bounds for the species' growth rates and types of interaction derived by Canessa et al. (2022), summarised in Table S1 and Figure 2.

3.2 | Methods for generating ensembles of ecosystem models

EEM is the main function of the R package, and it can generate an ensemble of parameter sets that yield feasible and stable ecosystem networks (see Table 2 for relevant arguments of the function). Usage of the function for a two-species example is provided in Appendix B.2 (Data S1). A second, more illustrative example is provided by the following code, which generates 5000 parameter sets satisfying the feasibility and stability features of the whole ecosystem for the generalised Lotka–Volterra model of the sihek case study (see Table S1):

```
library(EEMtoolbox)
interaction_matrix = matrix(
        c(-1, 1, 1, 1, 1, 1, 1, 1, 1,
        -1, -1, 0, -1, 0, 0, 0, 0, 1,
        -1, 0, -1, -1, 0, 0, 0, 0, 1,
        -1, 1, 1, -1, 0, 0, 1, 1, 0,
        -1, 0, 0, 0, -1, 1, 1, 1, 0,
        -1, 0, 0, 0, -1, -1, 0, 1, 0,
        -1, 0, 0, -1, -1, 0, -1, 0, 1,
        -1, 0, 0, -1, -1, -1, 0, -1, 1,
        0, 1, -1, -1, 0, 0, 0, 1, -1),
        ncol=9, nrow=9, byrow=TRUE)
upper_bounds_growth_rate = c(1.1, 1.1, 1.5, 1.5, 0.39, 0.49, 3.0, 3.0,
3.0)
parameters_GLV = EEM(interaction_matrix,
        upper_bounds_growth_rate = upper_bounds_growth_rate,
        algorithm = "SMC-EEM")
```

This code (using the SMC-EEM algorithm) allowed us to generate 5000 parameter sets in approximately 4 min (wall time) on a virtual machine (AMD EPYC 7702 64-Core Processor with 64 GB of RAM,

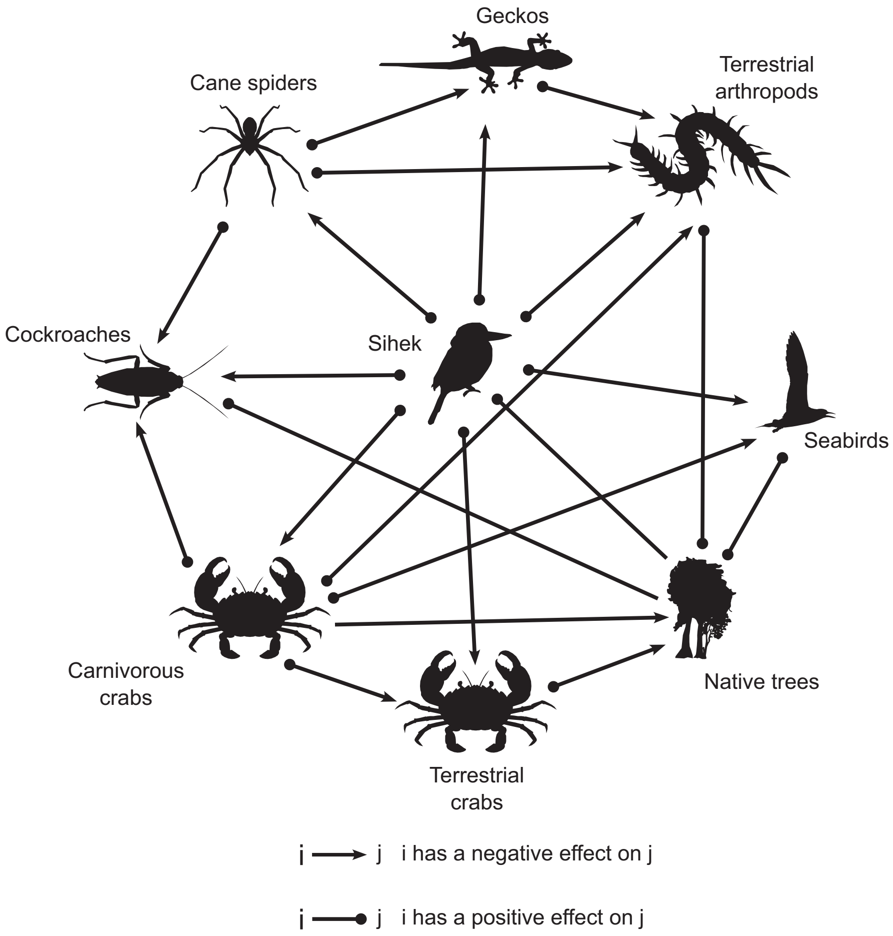

FIGURE 2 Species interactions network for the sihek case study. All species also possess a negative intraspecies interaction, as is commonly assumed in ecosystem network models (Adams et al., 2020; Baker et al., 2017).

TABLE 2 Summary of relevant arguments of the EEM function.

Argument name	Description	Default value
interaction_matrix	Bounds of interaction matrix for the ecosystem network	-
lower_bounds_growth_rate	Lower bounds for sampled growth rates (r_i)	0
upper_bounds_growth_rate	Upper bounds for sampled growth rates (r_i)	5
n_ensemble	Number of desired parameter sets	5000
model	Model representing species interactions	'GLV'
algorithm	Sampling algorithm	'standard-EEM'
n_cores	Number of cores used for sampling	1L

Note: For the model argument, 'GLV' stands for generalised Lotka–Volterra. The argument n_cores sets the number of clusters used for generating parameter sets. The default value 1L signifies that the sampling process is sequential. Setting n_cores to a value larger than 1L parallelises the sampling process on the number of desired clusters. We refer the reader to the documentation of the function for further details, including possible parameter values for each argument.

16 virtual processors). In contrast, generating 5000 parameter sets using the standard-EEM algorithm was achieved in approximately 2 days and 7 h (wall time) on the same virtual machine. Both sampling processes were parallelised in the code using the optional argument n_cores (see Table 2).

Therefore, for this sihek case study (with nine interacting species), the SMC-EEM method was much faster, and it is impractical to use standard-EEM. However, when the number of interacting species is small—typically less than seven species (Vollert et al., 2024)—the standard-EEM approach is often faster. In Appendix B.5 (Data S1), we compare these sampling procedures for a two-species network. In this example, generating 20,000 parameter sets with the standard-EEM approach required 20 s (wall time), while the SMC-EEM approach required 35 s (wall time).

3.3 | Generating projections of future abundances

The function plot_projections uses the obtained parameter sets to forecast changes in species abundances by numerically solving ordinary differential equations (ODEs, see Algorithm S1). This function inputs parameter sets (e.g. generated by the EEM function), initial species abundances and a time window for the forecast. For each parameter set, plot_projections solves the corresponding ODE using the function ode from the R package deSolve (Soetaert et al., 2010). Finally, the function estimates the median abundance and 95% prediction intervals for each species, and then at each time step (i.e. the 2.5% and 97.5% quantiles of the projected abundances), plots the corresponding graph (see Figure 3). We summarise in Table 3 all relevant parameters of the function. The following code forecasts species abundances over 10 years, when the initial abundance of sihek is 0.1 (individuals per hectare) and those of the other species are 1 (individuals per hectare). For a more detailed demonstration of this function on a simple two-species example, see Appendix B.3 (Data S1), and for projections scaled to the steady state, see Appendix B.4 (Data S1).

```
plot_projections(parameters=parameters_GLV,
        initial_condition=c(0.1, 1, 1, 1, 1, 1, 1, 1, 1),
        t_window = c(0,10))
```

To generate projections as a data.frame and generate customised plots, the function calculate_projections included in our package can be used.

3.4 | Comparing projections from different sampling algorithms

To illustrate that the standard-EEM and SMC-EEM approaches give equivalent predictions, we generated 20,000 parameter sets with the standard-EEM and the SMC-EEM approaches for a two-species ecosystem network (fully described in Appendix B, Data S1) and compared the abundance predictions (Figure 4). We used a two-species ecosystem network instead of the sihek case study because obtaining equivalent predictions would require impractically long time frames using the standard-EEM method

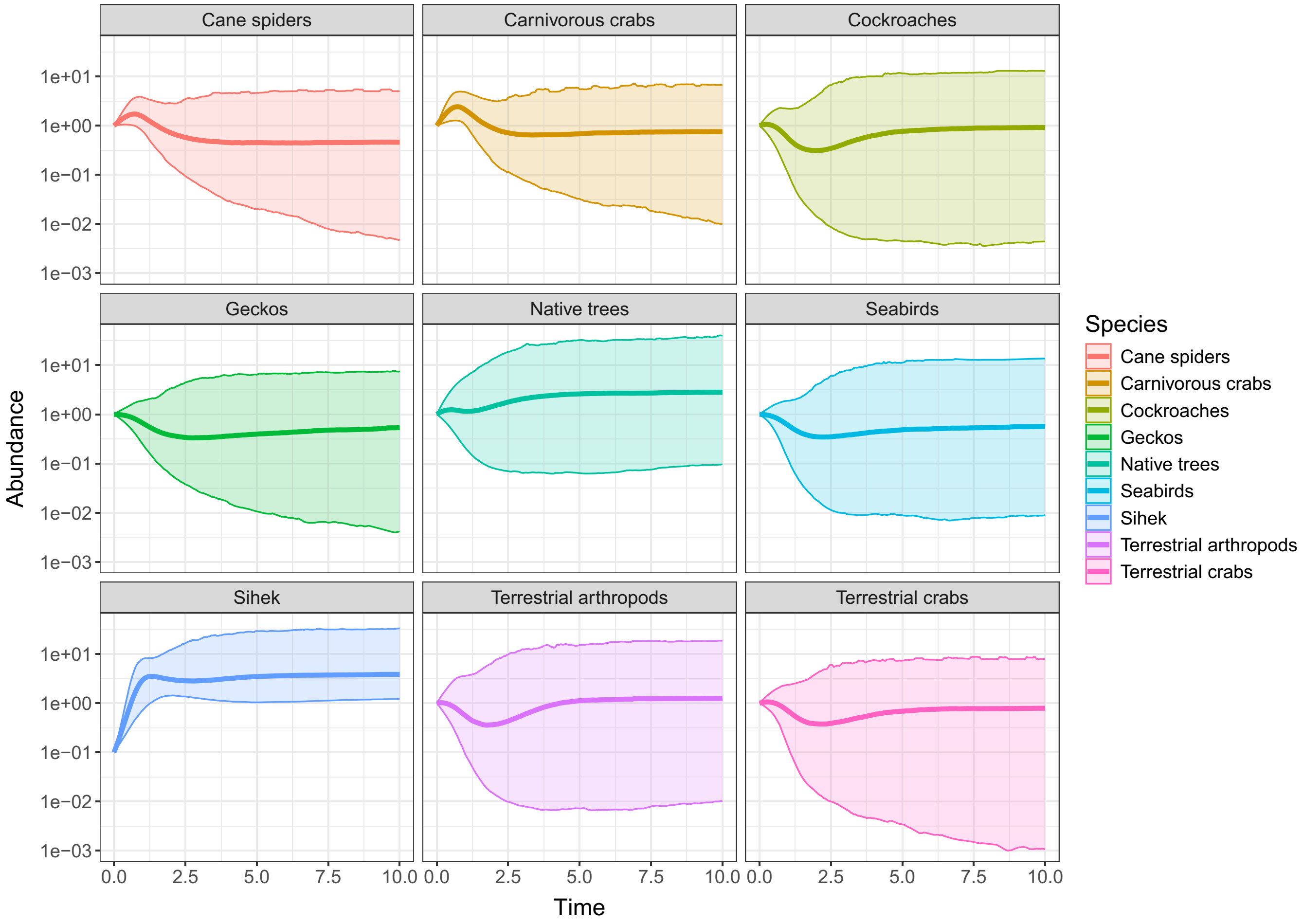

FIGURE 3 Forecasts of species abundances over 10 years for the sihek case study using the generalised Lotka–Volterra model. For illustrative purposes, we set the initial abundance of sihek to 0.1 (individuals per hectare) and the other species to 1 (individuals per hectare). Thicker lines represent the mean abundance and thin lines the 95% prediction interval (2.5% and 97.5% quantiles of the projected abundances). Forecasts for the multispecies Gompertz and the Bimler–Baker model are provided in Appendix E (Figures S5 and S6).

TABLE 3 Summary of parameters for the plot_projections function. All these parameters require user specifications.

Argument name	Description
parameters	List like object of ensemble of parameters (outputs of EEM)
model	Model representing species interactions (default 'GLV')
initial_condition	Initial species abundances
t_window	Time window for projections

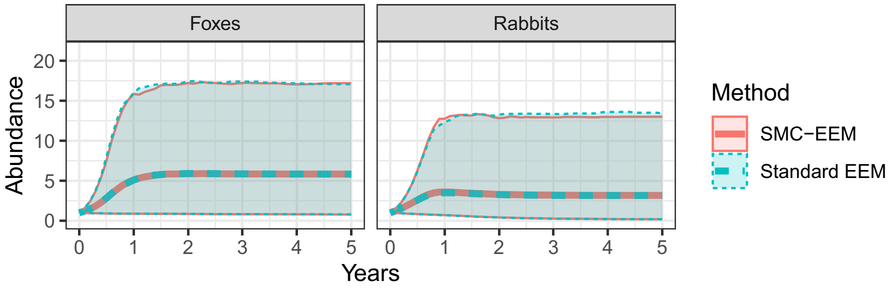

FIGURE 4 Example of abundances' predictions from parameter sets obtained with the standard-EEM approach and the SMC-EEM approach. Thick lines represent the median abundance and thin lines bound the 95% prediction intervals (2.5% and 97.5% quantiles of projected abundances). EEM, ensemble ecosystem modelling; SMC, sequential Monte Carlo.

(2 days and 7 h for 5000 samples) and a large number of samples due to the size of the ecosystem network (Vollert et al., 2024). For all species, the abundances predicted by models sampled with both methods overlap almost identically. This result suggests that the SMC-EEM approach produces the same distribution of parameter sets as the standard-EEM approach, and substantial additional evidence for this point is detailed in Vollert et al. (2024). Any discrepancies are due to the stochasticity inherent in the random sampling processes used in both methods, due to the finite number of samples used in both methods, often referred to as Monte Carlo error.

4 | DISCUSSION

This paper showcases a new R package EEMtoolbox that quickly and easily generates parameter sets for ecosystem model ensembles, for up to three different model structures, as well as for user-defined models. The package can either sample parameter values using a standard accept–reject approach recommended for small networks as in Baker et al. (2017) or via an SMC-ABC algorithm recommended for larger networks (Drovandi & Pettitt, 2011; Vollert et al., 2024). By facilitating the usage of these advanced statistical methods within an R package, EEM can now be applied to parameterize models of a broad range of ecosystem network structures, yielding immediate utility for improving conservation decisions based on these models. Our package extends EEM to three model structures (generalised Lotka–Volterra, the multispecies Gompertz and the Bimler–Baker models) and can be applied to user-defined model structures (see Appendix C, Data S1), which allows the broader ecology community to benefit from greater flexibility of EEM methods.

We acknowledge other factors might hinder EEM applications. First, EEM assumes the studied ecosystem will reach a stable and feasible equilibrium, which is convenient for parameterization but not always appropriate (Cuddington, 2001; Francis et al., 2021; Vollert et al., 2025). Examples include ecosystems with species' extinctions or those that are strongly impacted by external influences. We refer the reader to Vollert et al. (2025) on the applicability of feasibility and stability in conservation modelling and alternative calibration approaches. Second, EEM requires defining a species interaction network, which remains a difficult task (see, e.g. Peterson et al., 2021). Uncertainties in the ecosystem network (such as existence or not of direct interactions between species, and misspecification of interaction) might result in misleading predictions of species abundances (Adams et al., 2020). Third, EEM can provide new information but not direct recommendations for ecosystem management (Baker et al., 2017). In our case study, the sihek recovery team used EEM as an additional source of insights about predation and competition, following a broad risk screening for sihek introduction to Palmyra Atoll (Vernet et al., 2024). EEM is therefore especially useful when rapid exploration of scenarios and frequent updating of projections and risk assessments are desired by decision-makers (Canessa et al., 2022).

AUTHOR CONTRIBUTIONS

Luz Valerie Pascal led the research, developed the R package and led the writing. Matthew P. Adams conceived the project and supervised the study. Sarah A. Vollert contributed to the idea and methodology design. Malyon D. Bimler and Christopher M. Baker designed and provided insights towards the model development. Maude Vernet and Stefano Canessa provided the case study. Malyon D. Bimler, Maude Vernet and Stefano Canessa tested the R package.

Christopher Drovandi revised the manuscript and provided insights on the statistical methods used. All authors edited the manuscript, contributed to interpretation of the results and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70032.

DATA AVAILABILITY STATEMENT

The R package is available on GitHub at https://github.com/luzvpascal/EEMtoolbox and archived on Zenodo at https://zenodo.org/records/14880924 (Pascal et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Ecosystem interaction network for the fox-rabbit example.

Figure S2. Example of abundances' predictions using the plot_projections function, for the three ecosystem models supported by the EEMtoolbox R-package.

Figure S3. Example of abundances' predictions scaled to the steady state using the plot_projections function, for the three ecosystem models supported by the EEMtoolbox R-package.

Figure S4. Forecasts of species abundances over 10 years for the sihek case study using the multi-species Gompertz model.

Figure S5. Forecasts of species abundances over 10 years for the sihek case study using the Bimler-Baker model.

Table S1. Summary of interactions between species for the ecosystem network of the sihek case study (interaction matrix) and maximum growth rate for each species.

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