

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Adams, MP;Sisson, SA;Helmstedt, KJ;Baker, CM;Holden, MH;Plein, M;Holloway, J;Mengersen, KL;McDonald-Madden, E

Title:

Informing management decisions for ecological networks, using dynamic models calibrated to noisy time-series data

Date:

2020-04-01

Citation:

Adams, M. P., Sisson, S. A., Helmstedt, K. J., Baker, C. M., Holden, M. H., Plein, M., Holloway, J., Mengersen, K. L. & McDonald-Madden, E. (2020). Informing management decisions for ecological networks, using dynamic models calibrated to noisy time-series data. *Ecology Letters*, 23 (4), pp.607-619. <https://doi.org/10.1111/ele.13465>.

Persistent Link:

<https://hdl.handle.net/11343/275309>

Informing management decisions for ecological networks, using dynamic models calibrated to noisy time-series data

Authors: Matthew P. Adams^{a,b,c,*}, Scott A. Sisson^d, Kate J. Helmstedt^e, Christopher M. Baker^{b,e,f,g,h},
Matthew H. Holden^{b,f,h,i}, Michaela Plein^{a,b,j}, Jacinta Holloway^{e,k}, Kerrie L. Mengersen^{e,k}, Eve McDonald-
Madden^{a,b,h}

Affiliations:

^aSchool of Earth and Environmental Sciences, The University of Queensland, St Lucia, QLD 4072,
Australia

^bCentre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, QLD 4072,
Australia

^cARC Centre of Excellence for Mathematical and Statistical Frontiers, The University of Queensland, St
Lucia, QLD 4072, Australia

^dSchool of Mathematics and Statistics, The University of New South Wales, Sydney, NSW 2052,
Australia

^eSchool of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD 4001, Australia

^fSchool of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

^gCSIRO Ecosystem Sciences, Ecosciences Precinct, Dutton Park, QLD 4102, Australia

^hCentre of Excellence for Environmental Decisions, The University of Queensland, St Lucia, QLD 4072,
Australia

ⁱCentre for Applications in Natural Resource Mathematics, School of Mathematics and Physics, The
University of Queensland, St Lucia, QLD 4072, Australia

^jAdministration de la Nature et des Forêts, 6, rue de la Gare, 6731 Grevenmacher, Luxembourg

^kARC Centre of Excellence for Mathematical and Statistical Frontiers, Queensland University of
Technology, Brisbane, QLD 4001, Australia

*Correspondence: Email: m.adams5@uq.edu.au

Email Addresses: m.adams5@uq.edu.au (MPA), scott.sisson@unsw.edu.au (SAS),
kate.helmstedt@qut.edu.au (KJH), c.baker7@uq.edu.au (CMB), m.holden1@uq.edu.au (MHH),
michaela.plein@gmx.de (MP), j1.holloway@qut.edu.au (JH), k.mengersen@qut.edu.au (KLM),
e.mcdonaldmadden@uq.edu.au (EMM)

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/ELE.13465](#)

Short running title: Informing decisions using uncertain models

Keywords: Conservation, decision science, ecological forecasting, ecological modelling, food webs, interaction network, population dynamics, predator-prey interactions, prediction, uncertainty propagation

Article type: Letters

Number of words in abstract: 150

Number of words in main text (excluding abstract, acknowledgements, references, table and figure legends): 5400

Number of words in each text box: 318

Number of references: 69

Number of figures, tables and text boxes: 6

***Correspondence:** Matthew P. Adams, School of Earth and Environmental Sciences, The University of Queensland, St Lucia, QLD 4072, Australia. Ph: +61 7 3365 4355. Fax: +61 7 3365 6899. Email: m.adams5@uq.edu.au

Statement of authorship: MPA performed the simulations, and wrote the first draft of the manuscript. SAS assisted with the simulations and contributed substantially to manuscript revisions. KJH, CMB, MHH, MP, JH, KLM and EMM contributed substantially to the initial ideas and manuscript revisions.

Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare, and the data DOI will be provided at the end of the article.

Abstract

Well-intentioned environmental management can backfire, causing unforeseen damage. To avoid this, managers and ecologists seek accurate predictions of the ecosystem-wide impacts of interventions, given small and imprecise datasets, which is an incredibly difficult task. We generated and analysed thousands of ecosystem population time-series to investigate whether fitted models can aid decision-makers to select interventions. Using these time-series data (sparse and noisy datasets drawn from deterministic Lotka-Volterra systems with two to nine species, of known network structure), dynamic model forecasts of whether a species' future population will be positively or negatively affected by rapid eradication of another species were correct >70% of the time. Whilst 70% correct classifications is only slightly better than an uninformative prediction (50%), this classification accuracy can be feasibly improved by increasing monitoring accuracy and frequency. Our findings suggest that models may not need to produce well-constrained predictions before they can inform decisions that improve environmental outcomes.

INTRODUCTION

Forecasting ecosystem responses to environmental and anthropogenic changes is challenging but necessary to better inform environmental decisions (Possingham et al. 2001; Dietze et al. 2018). To develop ecological forecasts, we must firstly recognise that ecosystems are complex and involve many interacting species (Montoya et al. 2006), and secondly be explicit about the uncertainty in any forecasts that we make (Fischhoff and Davis 2014).

Ecosystems of interacting species can be represented as networks (Ings et al. 2008), and many qualitative (Levins 1974; Dambacher et al. 2002; Dambacher et al. 2009; Mutshinda et al. 2009; Raymond et al. 2011; Iles & Novak 2006; Baker et al. 2018) and quantitative (Ives et al. 2003; Gross & Feudel 2006; Novak et al. 2011; Iles & Novak 2016; Ovaskainen et al. 2017; Baker et al. 2017; Certain et al. 2018) modelling strategies have been used to investigate them. Both qualitative and quantitative approaches can investigate hypotheses about how disturbances change future species densities (e.g. Raymond et al. 2011; Ives et al. 2003; Arnoldi et al. 2018).

To forecast the long-term effects of a permanent disturbance such as a species eradication, quantitative data about the interactions between species is needed (Yodzis 1988; Novak et al. 2016). Ecological data often comes in the form of time-series for ecological communities. Given an assumed network structure, time-series data can be used to estimate the interaction strengths (Ives et al. 2003). Precision in interaction strength estimates is expected to increase with increased monitoring quality and duration of the time-series data (Attayde and Hansson 2001). However, even if such data are available, confidently estimating interaction strengths can still be very difficult (Angulo et al. 2017; Certain et al. 2018). Model forecasts parameterised by imprecise interaction strength estimates may then possess high prediction uncertainty, thus making it difficult for these models to inform management decisions. The optimal decision ultimately depends on the predicted outcomes for actions that could be enacted (Possingham et al. 2001), so it is critical to identify whether or not these outcomes will be unclear because of uncertainty in the predictions.

In this paper, we investigate what useful information about interaction strengths, and their subsequent effects on future projections, can be gleaned from dynamic ecosystem models fitted to imperfect monitoring data. We fit Lotka-Volterra models to synthetic data generated from known underlying population trajectories for deterministic ecosystems with known network structure. Uncertainty in interaction strength estimates is rigorously calculated using Bayesian

inference (Wolf et al. 2017), and this uncertainty is propagated through to ecosystem responses to management decisions. Our work therefore extends previous modelling efforts that have predicted species responses to disturbances given uncertain interaction strengths (Novak et al. 2011), by specifically connecting the uncertainty in interaction strength estimates back to the monitoring data used to inform these estimates. Furthermore, instead of just focusing on model prediction accuracy, our analysis goes one step further to investigate the relative difference between future predictions with or without an intervention to guide decision-makers as to whether the intervention should be applied or not. We are not aware of other work that has quantitatively propagated information gleaned from time-series data all the way through to the potential impact of different management decisions. Overall we demonstrate that, despite the issues in estimating parameter values characterising the ecosystem, there is a potential pathway to generate useful predictions for decision-making.

METHODS

Overview

Our method includes three distinct steps: (1) generation of thousands of synthetic ecosystem population time-series data following deterministic Lotka-Volterra dynamics with measurement noise added, (2) fitting Lotka-Volterra models to this simulated data using Bayesian inference (Girolami 2008), and (3) investigating how well the fitted models predict ecosystem responses to a specific management intervention – rapid eradication of one species. These three steps are summarised below; technical details are provided in Appendices S1-S3.

Generating the simulated data

We generated virtual ecosystems by modelling the changes in biomass over time, of all species in the ecosystem, via deterministic Lotka-Volterra equations (Murray 2002),

$$\frac{dy_i}{dt} = r_i y_i(t) + \sum_{j=1}^N \alpha_{ij} y_i(t) y_j(t), \quad (1)$$

where $y_i(t)$ is the total population biomass (in units of biomass/area) of species i at time t (in years), r_i is the intrinsic net growth rate (yr^{-1}) of species i , and α_{ij} is the strength of the per-capita interaction between species i and j (in units of $(\text{biomass/area})^{-1} \text{yr}^{-1}$). Each ecosystem we

generate has N species, and the initial population biomass of each species i is defined as

$$y_i(0) = y_{i0}.$$

The Lotka-Volterra systems we investigate are deterministic (e.g. Narwani et al. 2017), and therefore possess no process noise. This is a large assumption, but we stress here that the present work is a first attempt (to our knowledge) to quantitatively propagate information gleaned from time-series data all the way through to the potential impact of different management decisions. Combining the analysis presented here with an investigation of the effect of process noise on accuracy of future projections is therefore a clear future step for this research.

We generated 1000 ecosystems, each with their own species interaction strengths and network structure, following mathematical procedures detailed and justified in Appendix S1. Briefly, these ecosystems consist of between two and nine species each, organised into one of ten different network configurations: two to five trophic levels with one species per trophic level, two to four trophic levels with two species per trophic level, two to three trophic levels with three species per trophic level, or two trophic levels with four species per trophic level. We refer to these as network configurations (instead of calling them network structures) to indicate that (1) they only group together ecosystems with the same number of species per trophic level and the same number of trophic levels, and (2) ecosystems within the same network configuration can express different interconnections between species (i.e. different network structure). For each network configuration we assumed that there is an equal number of species at each trophic level, which is not a particularly restrictive condition for the small networks we consider (≤ 9 species) but may not be a reasonable assumption for the much larger networks that characterise many real-world ecosystems. The assumption of species richness uniformity across trophic levels was made to keep the number of different network configurations tested in our analysis down to a practical number (ten), and there are a plethora of other network configurations that could have also been chosen. Real-world ecosystems may possess decreased numbers of species at higher trophic levels, although uniformity of species richness across trophic level has been observed, especially in terrestrial food webs (Turney & Buddle 2016). In keeping with these observations, parameterisation of the food webs generated in this paper was based primarily on terrestrial systems (Baker et al. 2017; see also Appendix S1).

We generated 100 different ecosystems for each of the ten network configurations, thereby yielding the 1000 different ecosystems. As an example, Fig. 1a shows one of the network

configurations considered in our analysis. We generated ecosystems with predator-prey interactions only, although we recognise that this common assumption in food web models overlooks other potentially important interaction types (Berlow et al. 2004; Kéfi et al. 2012; Pilosof et al. 2017). We initiate each ecosystem's dynamics to start away from equilibrium.

For each of the 1000 ecosystems, we sampled imperfect measurements of their population trajectories to simulate monitoring programs of 20 year duration. This was accomplished by adding temporally-uncorrelated Gaussian noise to the deterministic ecosystem trajectories, to simulate measurement error. To investigate how monitoring accuracy and frequency affects ecosystem predictions, we simulated ten monitoring programs per ecosystem which differed in how often and accurately species population biomasses were measured. Nine of the monitoring programs we investigated are practically achievable: observations every one, two or four years, with measurement error δ of 10%, 20% or 40% (Marion 1995; Petit et al. 1995; Crall et al. 2011). We also simulated a tenth monitoring program with yearly measurements and 1% error to investigate an extreme best-case scenario. Measurement error was assumed to follow a truncated normal distribution, with a lower bound of zero (to avoid negative biomass observations), and standard deviation of 1%, 10%, 20% or 40% of the true value of the species population biomass. Both the true and observed noisy values of species population biomass were retained for comparison in our analysis.

Calibrating a model to the synthetic data

Models were fitted to the observed noisy data using Bayesian inference (Girolami 2008), implemented by a posterior-simulation method called Sequential Monte Carlo (SMC) sampling (Doucet et al. 2000), a class of methods which is related to and overlaps with particle filtering (Doucet and Johansen 2009). SMC sampling is seeing increasing usage for a diverse range of applications (Drovandi & Pettitt 2011; Jeremiah et al. 2012; Lawson et al. 2018; Sisson et al. 2018). Our SMC sampler (Appendix S2) is adapted from ideas presented in Jeremiah et al. (2012) and Del Moral et al. (2012).

In our application, SMC sampling estimates the joint posterior probability distribution for the model parameters $\{y_{i0}, r_i, \alpha_{ij}, \delta : i, j = 1, \dots, N\}$ in each simulated ecosystem, which includes estimation of initial species population biomass y_{i0} , growth rates r_i , interaction strengths α_{ij} , measurement noise δ and the uncertainty in all of these quantities. This approach quantifies

parameter uncertainty and propagates this uncertainty into scenario predictions via a model ensemble, thereby building upon a recently introduced ensemble ecosystem modelling framework (Baker et al. 2017, 2019). Using this method, we can compare the ecosystem parameters' true values to their probability distributions obtained from model-data fitting, to identify how much information about ecosystem parameter values can be gained from the synthetic data. For the primary analysis of this paper, we apply SMC sampling to estimate the posterior 10,000 times: for ten monitoring programs of different measurement frequency and accuracy, applied to 100 ecosystems each for ten different network configurations. (We also estimated 600 additional posteriors, in an extension of our analysis to investigate the effects of structural uncertainty, as detailed in Appendix S8.) We then use the full posterior, in each of these cases, to simulate the impact of management interventions on the ecosystem.

Predicting ecosystem response to a species eradication

The ultimate goal of our model fitting to imperfect measurements of generated ecosystems, is to identify – in the best-case scenario of known network structure, negligible process noise, and ecosystem dynamics adhering precisely to the models that we fit – whether any ecological consequences of a management action, specifically eradication, can be reasonably predicted using models calibrated to time-series data. This analysis therefore identifies if it is possible for data-calibrated models to be useful for informing management decisions. To address this goal, we considered two classes of scenarios for each of the 10,000 combinations of ecosystems and monitoring programs: (1) completely eradicating a predator immediately after the 20 year monitoring period, and (2) no action. For eradication scenarios, we assumed that the predator is eradicated rapidly so that its population biomass is set immediately to zero. Each eradication scenario consisted of eradication of only one predator, from any nonbasal trophic level. We did not consider scenarios for the eradication of basal species, since this is an unlikely management action due to the high possibility of secondary extinctions (Dunne and Williams 2009; Staniczenko et al. 2010).

We did not predefine any species to be invasive and therefore candidates for eradication. Hence, we explored scenarios where each predator is individually eradicated. For ecosystems containing more than two species, there are multiple predators that could be eradicated. Specifically, if $TL_{\max}$ is the number of trophic levels in the ecosystem, and S is the common

number of species per trophic level (every trophic level is assumed to have the same number of species in our analysis, see e.g. Fig. 1a), there are $S \times (TL_{\max} - 1)$ nonbasal species that could be eradicated. We ran scenarios for each possible predator being individually eradicated, thereby yielding $S \times (TL_{\max} - 1)$ eradication scenarios per ecosystem. Conversely, there is only one “no action” scenario per ecosystem: letting the ecosystem continue its (non-equilibrium) temporal dynamics beyond the 20 year monitoring period without intervention.

To compare the eradication and no action scenarios, we focused our analysis on the predictions of species population biomasses 10 years into the future ($t = 30$ years) after the monitoring period ($t = 0$ to $t = 20$ years) and proposed eradication ($t = 20$ years). We chose to focus our analysis on a predefined future time because ecosystem management plans are usually drafted with clear, near-future, timeframes in mind, and our chosen timeframe of 10 years is typical for terrestrial ecosystem management (e.g. Director of National Parks 2015). Of course, predictions over longer timescales will likely possess higher uncertainty.

Calculating metrics that quantify the ability of fitted models to make useful predictions

In preliminary simulations we found that predictions of future population biomass often expressed large uncertainty. However, whilst the uncertainty in an individual prediction of a future scenario might be large, we also wanted to identify if the uncertainty in the *difference between scenarios* is also large – as the latter is what is important for management decisions. We also wanted to identify if the data-fitted models are predicting the *correct trends* even if the uncertainty bounds in their predictions are large. Hence we introduced six metrics that quantify the ability of fitted models to make predictions useful for management decisions (Box 1 and Appendix S3); these metrics are summarised below. All six metrics are calculated from the species population biomasses at $t = 30$ years, i.e. ten years after the eradication (or no action) proposed to occur immediately after the 20 year monitoring period. All six metrics are unitless, so that the different biomasses of individual species are scaled out of all the metrics. Each metric is calculated for one species within a particular ecosystem, and is either related to one scenario or a comparison between scenarios, depending on the specific metric used.

The first three metrics we introduced (Box 1) indicate the uncertainty in model predictions without any knowledge of the ecosystem’s true future trajectory – uncertainty in future predictions, uncertainty in eradication impact, and uncertainty in the direction of the

eradication impact. Here, eradication impact is defined as the relative difference in model-predicted future trajectories between the two scenarios of eradication and no action. The last three metrics indicate how different the model predictions are from the ecosystem's true future – difference in future predictions, difference in eradication impact, and difference in the direction of the eradication impact. The six metrics each provide different information about how uncertain the model predictions are, or how different the model predictions are from the true trajectory. All six metrics are non-negative; reducing their values towards 0% indicates that the data yield a more informative fitted model for decision-making. More specifically, metric values less than 10% are excellent while values exceeding 50% are relatively uninformative (except for the uncertainty in the direction of the eradication impact for which a value of 50% is completely uninformative).

We calculated and compared the six metrics for all non-eradicated species in all management scenarios (either eradication or no action), monitoring programs and ecosystems, and grouped the values of the six metrics together by monitoring program and network configuration (i.e. ecosystems with the same number of species per trophic level and number of trophic levels). Individual values of the metrics were aggregated across species and ecosystems (without any stratification of values either by ecosystems or by species position within the network) to identify how these metrics' values are distributed within each combination of monitoring program and network configuration. Ultimately, this analysis addresses the following question: Even if the future predictions of individual species trajectory are highly uncertain, are there particular aspects of ecosystem responses to an eradication which can possibly be predicted with high confidence?

RESULTS

Large uncertainty in future predictions of species population biomass was a common observation amongst the 1000 ecosystems that we investigated. 20 years of synthetic monitoring data was used to inform each modelled ecosystem; and the 10-year future model projections of this ecosystem, following the complete eradication of one predator immediately after the 20 year monitoring period, were analysed. Fig. 1b shows an example of one of our generated ecosystems, measured with the best plausible monitoring program that we considered (annual measurements of all species for 20 years with 10% measurement error). For the true trajectory of this ecosystem

without any management intervention (red lines in Fig. 1b), 20 years of monitoring data was sufficient for the ecosystem to be approaching but not yet reaching equilibrium. For the model predictions (shaded areas) based on the monitoring data (dots), the uncertainty in future projections following a species eradication was sufficiently large that it is unclear if this eradication will be net beneficial or detrimental to the remaining species. The estimated probability distributions of model parameters for this ecosystem (Fig. 2) also indicated that several interaction strengths were unresolvable with this data.

Uncertainty in future population predictions varied widely between species and ecosystems. To give some sense of how the species responses in the ecosystem shown in Fig. 1b compare to our general results from multiple network configurations and monitoring program qualities, we show box and whisker plots capturing the interquartile range (box) and 95% central credible interval (whiskers) of the uncertainty in future predictions in Appendix S5. For example, for 100 ecosystems of the same structure and subjected to the same monitoring program as Fig. 1b, uncertainty in future predictions for the eradication scenario had a median of 21%, interquartile range (box) of 10-44% and 95% central credible interval (whiskers) of 3-217% (second column of Fig. S5.6b in Appendix S5, upper limit not shown). Hence, uncertainty in future predictions could be low or extremely high, depending on the species and ecosystem, even with an excellent monitoring program. As expected, reducing monitoring accuracy or frequency increased the uncertainty in future predictions (Appendix S5).

Reducing measurement error from 40% to 10% reduced model uncertainty more effectively than increasing monitoring frequency from once every four years (quadrennially) to annually (Fig. 3). Hence, precise and infrequent monitoring may be of greater value than imprecise and frequent monitoring, but we caution that this conclusion strongly depends on the possible trade-off between measurement accuracy and frequency in a given study. The trade-off may also depend on other factors not considered here, such as environmental stochasticity, demographic stochasticity, or uncertainty regarding the network structure itself.

For the extreme best-case scenario of annual monitoring with 1% measurement error, prediction accuracy increased dramatically but did not always lead to highly constrained predictions (Appendix S5). For example, for the ecosystems with the largest number of species (nine) that we investigated, the median uncertainty in future predictions of species population biomass after a proposed eradication still exceeded 10% (first column of Fig. S5.10b in

Appendix S5). Uncertainty in future predictions may therefore be an unavoidable situation even with excellent data, but in reality, management decisions still need to be made.

To investigate the usefulness of imperfect data for model calibration and subsequent predictions to inform management decisions, we next focused on what could be achieved with the worst plausible monitoring program we considered (quadrennial measurements with 40% error), across multiple metrics of uncertainty and model-data difference. We first summarise our results for ecosystems possessing three trophic levels and two species per trophic level (Fig. 4) and then discuss applicability of the key result obtained across all ten network configurations we investigated (between two and nine species, Fig. 5).

Both the uncertainty in future predictions, and the difference between model predictions and true trajectories, were higher for eradication scenarios (Fig. 4b,f) than for scenarios involving no intervention (Fig. 4a,e). This occurs because the species in the ecosystem continue their previous trajectories if no management action is undertaken, whereas an eradication “jolts” the species into different trajectories (compare blue and red future predictions in Fig. 1b).

We next sought to identify if the model predictions of the eradication impact – that is, the *relative* difference between scenarios of eradication vs no action – also could possess high uncertainty and large difference from their true values. Contrary to our expectations, we found that predictions of eradication impact carried similar uncertainty (Fig. 4c) and similar difference between model and true values (Fig. 4g) to the individual model-predicted future trajectories (Fig. 4a,b,e,f). To further elucidate this result, we visually inspected many of the thousands of trajectory figures generated by our simulations (of which Fig. 1b is a representative example). We observed that several ecosystems were approaching equilibrium densities within the 20-year monitoring period (see, e.g., Fig. 1b), and thus the uncertainty in the difference between scenarios is potentially being dominated by the uncertainty in the eradication scenario. This result therefore may not hold in ecosystems which are undergoing rapid population fluctuations, but for ecosystems with negligibly or gradually changing species populations it is unsurprising that the impact of an ecosystem perturbation is likely to be less predictable than if the ecosystem experiences no such perturbation.

The final two metrics that we investigated were the uncertainty (Fig. 4d) and model-data difference (Fig. 4h) in the *direction* (either increase or decrease) of the predicted eradication impact. The direction of the eradication impact identifies whether a species’ future population

biomass, after the eradication, will be higher or lower than its future population if no action is undertaken. Unlike the other three uncertainty metrics (Fig. 4a-c), the uncertainty in the direction of the eradication impact (Fig. 4d) cannot exceed 50%, the latter of which indicates a completely uninformative prediction (in this case there is equal probability of an increase or decrease in a species' future population biomass due to the eradication compared to no action, see Appendix S3). Fig. 4d shows that model predictions for the direction of the eradication impact can range from very confident (0%) to completely uninformative (50%).

However, promisingly, the model-data difference in eradication impact direction (Fig. 4h) was less than 50% for more than 75% of the individual species responses across all eradication scenarios and ecosystems: this indicates that the majority of the model ensemble (by weight) predicts the correct eradication impact direction >75% of the time. We obtained this result for ecosystems with three trophic levels and two species per trophic level, subjected to a monitoring program with the lowest measurement accuracy (40%) and frequency (quadrennially) that we investigated. Whilst 75% confidence still leaves considerable room for error, especially since 50% confidence for this metric indicates a completely uninformative prediction, this probability is high enough to suggest that sufficient knowledge and monitoring data for an ecosystem may permit calibrated models to make predictions that are practically useful for informing decisions.

Expanding this latter analysis to consider individual species responses across all of the different network configurations we tested (two to nine species) instead of just ecosystems with three trophic levels and two species per trophic level, we found that the direction of eradication impact could be predicted correctly more than 70% of the time in all of our tested network configurations (Fig. 5). For this metric, 50% correct indicates an uninformative result (random prediction of the direction of eradication impact being either an increase or a decrease), so 70% correct classifications is not optimal but could still be of value for decision-makers. We used two different methods to identify if the model was predicting the correct direction of eradication impact (one method shown in Fig. 5; both methods shown in Appendix S6). We reached the same conclusion regardless of the method used to predict the eradication impact direction; for both methods we did not consider ecosystems or species positions within the network separately, but rather aggregated results across all species' potential responses to all possible predator eradications across all ecosystems possessing the same network configuration and monitoring

program. We also found (unsurprisingly) that improving monitoring accuracy and/or frequency can increase the proportion of correct predictions for the direction of eradication impact (Appendix S6).

We undertook additional analysis to disentangle the impacts of trophic level and closeness of response species to the eradicated species on the proportion of correct model predictions for the direction of eradication impact (Appendix S7). This analysis indicated that eradication impacts on individual species depend strongly on network structure; thus such analyses are well-suited for future investigation of specific case study systems.

Finally, we investigated how misspecification of network structure (by assuming all species on different trophic levels are involved in predator-prey interactions with each other) affects model prediction accuracy (Appendix S8). We found that accuracy in predicting the direction of eradication impact reduced, but remained above 65% in all our tested configurations (Figure S8.1). This result (>65%), obtained with the worst plausible monitoring program we considered, is getting closer to completely uninformative (50%), which emphasises the importance of assuming network structures that are as close to correct as possible. In fact, in certain cases, monitoring data of low frequency and accuracy can sometimes not be sufficient to compensate for misspecified network structures (Figure S8.2). These results highlight that comprehensive monitoring data is of best use for model predictions when it is coupled with expert knowledge regarding which species interactions are actually present in the network.

DISCUSSION

Forecasting for decision-making should not wait for a well-constrained model

Predicting the future of an ecosystem is a prerequisite for decision-making (Petchey et al. 2015), but is often avoided in ecology due to concerns about biological complexity (Dietze et al. 2018). Here, we demonstrated that model predictions of future trajectory for ecosystem food webs can carry high uncertainty even if there is excellent time-series data available from a monitoring program. Despite this uncertainty, the models can potentially be useful to inform management decisions, if precise population predictions are not critical to the decisions. To obtain this conclusion, we assessed the predictive proficiency of the fitted ecological models (Pennekamp et al. 2017), and found that even in the most infrequent and imprecise monitoring programs tested, these models had >70% confidence in predicting whether species population biomasses, ten

years after an eradication action, will be higher or lower than if no action is undertaken. (To avoid misinterpretation, we reiterate here that 50% confidence indicates an uninformative prediction, so 70% correct classifications is not optimal but could still be of value for decision-makers.) This finding was obtained in the best-case scenario, whereby the model structure accurately reflects the ecosystem dynamics, and there is no stochasticity in the ecosystem apart from measurement noise. At the very least, our analysis suggests that it is possible, for dynamic models calibrated to time-series data, to provide useful predictions for decision-making. More generally, approaches such as ours that formally account for uncertainty propagation are advantageous because they can predict the probability of an undesirable outcome (Regan et al. 2005; Tunney et al. 2017). Our results therefore support the view that we do not need to wait until ecological models are well-constrained in their predictions before we start forecasting (Dietze et al. 2018; Houlahan et al. 2017); even a model that is not particularly well-constrained in its predictions can potentially be used for management decisions. We recognise that accepting the predictions of a model will always be a value judgement for the decision-maker. However, at the very least, it is of benefit to provide decision-makers with model predictions, including uncertainty, for them to decide on how to act on this information.

Monitoring accuracy versus frequency

Improving the accuracy of monitoring from 40% to 10% reduced model uncertainty more effectively than increasing measurement frequency from quadrennial to annual (Fig. 3 and Appendix S5). This result echoes other authors' findings that reduced sampling visits with greater coverage (thereby increasing monitoring accuracy) may be of greater benefit than frequently sampling fewer sites (Roy et al. 2007), and that skipping certain monitoring time points to improve the remaining abundance estimates can be beneficial (Humbert et al. 2009). However, there is a potential tradeoff here, because higher monitoring frequency increases the chances of detecting unexpected ecological responses (Keith et al. 2014). Regardless of the monitoring program used, our approach is able to predict the potential benefits for forecasting from increased monitoring accuracy versus frequency, as decision-makers may not have the resources to do both. Hence our analysis has the potential to predict the data quality needed to answer a given research or management question, which is a current need suggested within the community ecology literature (Delmas et al. 2019). This is especially pertinent since monitoring

is a substantial investment that requires careful consideration of the benefits versus the costs (McDonald-Madden et al. 2010).

Comparison to previous research in community ecology

Our work adds to the ecological network literature focused on fitting models to time-series data (Ives et al. 2003; Certain et al. 2018), consideration of uncertainty sources (Mutshinda et al. 2009) and propagating parameter uncertainty through to predictions following perturbations (Aufderheide et al. 2013; Novak et al. 2011). In the context of this prior work, our key contribution is to demonstrate how different aspects of time-series data alter forecast uncertainty, and ultimately how this uncertainty affects the utility of model forecasts to help environmental managers decide which ecosystem interventions to implement. Similarly to Novak et al. (2011) we find clear relationships between uncertainty in interaction strengths and the proportion of correct predictions, but our work goes one step further by connecting this uncertainty in interaction strengths back to the informativeness of the measured data. Unlike Novak et al. (2011) we did not investigate how connectance affects uncertainty in interaction strengths, because of the small size of the networks we investigated (Section S1.2.3). We also performed additional analysis to investigate the effects of network structure misspecification on our results (Appendix S8); recent work by other authors has addressed the effects of model misspecification as well (Certain et al. 2018).

Similarly to us, other authors have focused on what information can be gleaned from time-series data (Cenci & Saavedra 2018), but with stochastic autoregressive models (e.g. Ives et al. 2003; Ives et al. 2010; Hampton et al. 2013; Ovaskainen et al. 2017; Certain et al. 2018) used more commonly than deterministic Lotka-Volterra models (e.g. Narwani et al. 2017). Autoregressive models explicitly account for demographic stochasticity, although in practice this process noise may be difficult to distinguish from observation error (Certain et al. 2018).

Generalising our results to real ecosystem networks

Forecasting dynamics in complex ecosystems is challenging, but may be of great benefit for informing management decisions in these systems. Our work investigates this problem in small predator-prey networks with known structure. However, in real ecosystems we may not know their network structure, and these systems can be far more complex, involving many other

interaction types (Arim & Marquet 2004; Berlow et al. 2004; Ruscoe et al. 2011; Plein et al. 2017), variability in interaction strengths (Navarrete & Berlow 2006; Ushio et al. 2018), process noise (Wood 2010) and age or size structure (Law et al. 2016). The ecosystems we investigated had high connectance (Section S1.2.3), and thus a relatively large number of interaction strengths needed to be estimated in our generated ecosystems. The lower connectance of the larger ecosystems expected in nature might counteract the reduced confidence in future predictions expected in these more complex systems, but only if there is knowledge of which species interactions are present or absent (as was assumed here).

We considered ecosystems that follow deterministic Lotka-Volterra equations, as this is a relatively ubiquitous approach for investigating community ecology dynamics (e.g. Roberts 1974; Jansen & Kokkoris 2003; Stone 2016). Extrapolation of our key results regarding the ability of calibrated models to predict management outcomes may vary in ecological communities with different dynamics. Future work could also investigate the relative importance of different sources of uncertainty (measurement noise, environmental and demographic stochasticity, model structure uncertainty and network structure uncertainty) on predicting management outcomes, following on from prior studies analysing stochasticity sources (Mutshinda et al. 2009) and robustness to parametric assumptions (Certain et al. 2018). Resolving these different sources of uncertainty is a logical next step to improve the precision of future ecological forecasts.

CONCLUSION

Even with excellent data and sophisticated model calibration techniques, it may not be possible to resolve all species interaction strengths, but this should not prevent fitted models from being used to inform management decisions. At the very least, it may be possible to predict whether a management action, in this case, eradication, will cause a net positive or negative impact on a species' population. This information might be sufficient for managers to act upon even if uncertainty in future ecosystem projections is large. In short, we do not need to wait for models to produce well-constrained predictions before we start using them to inform decisions that improve environmental outcomes.

ACKNOWLEDGEMENTS

The corresponding author thanks Brodie A. J. Lawson, Chris C. Drovandi, Matias Quiroz and Robert Salomone for fruitful discussions regarding the application of Bayesian inference to differential equation models. Nigel Bean, Phillip Staniczenko, and several students and researchers from the School of Earth and Environmental Sciences, The University of Queensland, are thanked for their comments on an earlier version of the manuscript. The authors wish to acknowledge The University of Queensland's Research Computing Centre (RCC) for its support in this research, and also thank Gloria M. Monsalve-Bravo for her technical assistance with running the simulations. This work was funded by the Australian Research Council (ARC) Linkage Grant LP160100496, and ideas for this paper were initiated from a 2017 workshop on Novel Methods for Modelling Complex Dynamic Ecological Systems jointly funded by the ARC Centre of Excellence in Environmental Decisions and the ARC Centre of Excellence for Mathematical and Statistical Frontiers (ACEMS). SAS is directly supported by ACEMS. CMB is the recipient of a John Stocker Fellowship from the Science and Industry Endowment Fund. EMM's contribution was funded by an ARC Future Fellowship FT170100140. The authors also thank three anonymous reviewers whose comments greatly improved the manuscript.

REFERENCES

- Angulo, M.T., Moreno, J.A., Lippner, G., Barabási, A.-L. & Liu, Y.-Y. (2017). Fundamental limitations of network reconstruction from temporal data. *J. R. Soc. Interface*, 14, 20160966.
- Arim, M. & Marquet, P.A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.*, 7, 557-564.
- Arnoldi, J.-F., Bideault, A., Loreau, M. & Haegeman, B. (2018). How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. *J. Theor. Biol.*, 436, 79-92.
- Attayde, J.L. & Hansson, L.-A. (2001). Press perturbation experiments and the indeterminacy of ecological interactions: effects of taxonomic resolution and experimental duration. *Oikos*, 92, 235-244.
- Aufderheide, H., Rudolf, L., Gross, T. & Lafferty, K. D. (2013). How to predict community responses to perturbations in the face of imperfect knowledge and network complexity. *Proc. R. Soc. B*, 280, 20132355.

525 Baker, C.M., Gordon, A. & Bode, M. (2017). Ensemble ecosystem modeling for predicting
 526 ecosystem response to predator reintroduction. *Conserv. Biol.*, 31, 376-384.

527 Baker, C.M., Holden, M.H., Plein, M., McCarthy, M.A. & Possingham, H.P. (2018). Informing
 528 network management using fuzzy cognitive maps. *Biol. Conserv.*, 224, 122-128.

529 Baker, C.M., Bode, M., Dexter, N., Lindenmayer, D.B., Foster, C., MacGregor, C. *et al.* (2019).
 530 A novel approach to assessing the ecosystem-wide impacts of reintroductions. *Ecol. Appl.*,
 531 29, e01811.

532 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M. *et al.*
 533 (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, 73,
 534 585-598.

535 Cenci, S. & Saavedra, S. (2018). Uncertainty quantification of the effects of biotic interactions
 536 on community dynamics from nonlinear time-series data. *J. R. Soc. Interface*, 15,
 537 20180695.

538 Certain, G., Barraquand, F. & Gårdmark, A. (2018). How do MAR(1) models cope with hidden
 539 nonlinearities in ecological dynamics?. *Methods Ecol. Evol.*, 9, 1975-1995.

540 Crall, A.W., Newman, G.J., Stohlgren, T.J., Holfelder, K.A., Graham, J. & Waller, D.M. (2011).
 541 Assessing citizen science data quality: an invasive species case study. *Conserv. Lett.*, 4,
 542 433-442.

543 Dambacher, J. M., Gaughan, D. J., Rochet, M.-J., Rossignol, P. A. & Trenkel, V. M. (2009).
 544 Qualitative modelling and indicators of exploited ecosystems. *Fish Fish.*, 10, 305-322.

545 Dambacher, J. M., Li, H. W. & Rossignol, P. A. (2002). Relevance of community structure in
 546 assessing indeterminacy of ecological predictions. *Ecology*, 83, 1372-1385.

547 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J. *et al.*
 548 (2019). Analysing ecological networks of species interactions. *Biol. Rev.*, 94, 16-36.

549 Del Moral, P., Doucet, A. & Jasra, A. (2012). An adaptive sequential Monte Carlo method for
 550 approximate Bayesian computation. *Stat. Comput.*, 22, 1009-1020.

551 Dietze, M.C., Fox, A., Beck-Johnson, L.M., Betancourt, J.L., Hooten, M.B., Jarnevich, C.S. *et al.*
 552 (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges.
 553 *P. Natl. Acad. Sci. USA*, 115, 1424-1432.

- Director of National Parks (2015). *Booderee National Park Management Plan 2015-2025*. Available at: <https://www.environment.gov.au/resource/booderee-national-park-management-plan-2015-2025>. Last accessed 13 November 2019.
- Doucet, A., Godsill, S. & Andrieu, C. (2000). On sequential Monte Carlo sampling methods for Bayesian filtering. *Stat. Comput.*, 10, 197-208.
- Doucet, A. & Johnansen, A.M. (2009). A tutorial on particle filtering and smoothing: fifteen years later. Chapter in: Crisan, D. & Rozovskii, B. (editors) *The Oxford Handbook of Nonlinear Filtering*, Oxford University Press, pp. 656-704.
- Drovandi, C.C. & Pettitt, A.N. (2011). Estimation of parameters for macroparasite evolution using approximate Bayesian computation. *Biometrics*, 67, 225-233.
- Dunne, J.A. & Williams, R.J. (2009). Cascading extinctions and community collapse in model food webs. *Phil. Trans. R. Soc. B*, 364, 1711-1723.
- Fischhoff, B. & Davis, A.L. (2014). Communicating scientific uncertainty. *Proc. Natl. Acad. Sci. USA*, 111, 13644-13671,
- Girolami, M. (2008). Bayesian inference for differential equations. *Theor. Comput. Sci.*, 408, 4-16.
- Gross, T. & Feudel, U. (2006). Generalized models as a universal approach to the analysis of nonlinear dynamical systems. *Phys. Rev. E*, 73, 016205.
- Hampton, S. E., Holmes, E. E., Scheef, L. P., Scheuerell, M. D., Katz, S. L., Pendleton, D. E. *et al.* (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, 94, 2663-2669.
- Houlahan, J.E., McKinney, S.T., Anderson, T.M. & McGill, B.J. (2017). The prior of prediction in ecological understanding. *Oikos*, 126, 1-7.
- Humbert, J.-Y., Mills, L.S., Horne, J.S. & Dennis, B. (2009). A better way to estimate population trends. *Oikos*, 118, 1940-1946.
- Iles, A. C. & Novak, M. (2016). Complexity increases predictability in allometrically constrained food webs. *Am. Nat.*, 188, 87-98.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F. *et al.* (2008). Review: Ecological networks – beyond food webs. *J. Anim. Ecol.*, 78, 253-269.
- Ives, A. R., Abbott, K. C. & Ziebarth, N. L. (2010). Analysis of ecological time series with ARMA(p,q) models. *Ecology*, 91, 858-871.

- Ives, A. R., Dennis, B., Cottingham, K. L. & Carpenter, S. R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73, 301-330.
- Jansen, V. A. A. & Kokkoris, G. D. (2003). Complexity and stability revisited. *Ecol. Lett.*, 6, 498-502.
- Jeremiah, E., Sisson, S.A., Sharma, A. & Marshall, L. (2012). Efficient hydrological parameter optimization with Sequential Monte Carlo sampling. *Environ. Modell. Softw.*, 38, 283-295.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A. *et al.* (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett.*, 15, 291-300.
- Keith, D., Lindenmayer, D., Lowe, A., Russell-Smith, J., Barrett, S., Enright, N. *et al.* (2014). Heathlands. Chapter in: Lindenmayer, D., Burns, E., Thurgate, E. & Lowe, A. (editors) *Biodiversity and Environmental Change: Monitoring, Challenges and Direction*, CSIRO Publishing, pp 286-379.
- Kück, H., de Freitas, N. & Doucet, A. (2006). SMC samplers for Bayesian optimal nonlinear design. *2006 IEEE Nonlinear Statistical Signal Processing Workshop*. doi: 10.1109/NSSPW.2006.4378829.
- Law, R., Plank, M.J. & Kolding, J. (2016). Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish Fish.*, 17, 281-302.
- Lawson, B.A.J., Drovandi, C.C., Cusimano, N., Burrage, P., Rodriguez, B., Burrage, K. (2018). Unlocking datasets by calibrating populations of models to data density: A study in atrial electrophysiology. *Sci. Adv.*, 4, e1701676.
- Levins, R. (1974). The qualitative analysis of partially specified systems. *Ann. NY Acad. Sci.*, 231, 123-138.
- Marion, J.L. (1995). Capabilities and management utility of recreation impact monitoring programs. *Environ. Manage.*, 19, 763-771.
- McDonald-Madden, E., Baxter, P.W., Fuller, R.A., Martin, T.G., Game, E.T., Montambault, J. & Possingham, H.P. (2010). Monitoring does not always count. *Trends Ecol. Evol.*, 25, 547-550.
- Montoya, J.M., Pimm, S.L., Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259-264.
- Murray, J.D. (2002). *Mathematical biology I: an introduction*. Springer, New York.

- Mutshinda, C. M., O'Hara, R. B. & Woiwod, I. P. (2009). What drives community dynamics?. *Proc. R. Soc. B*, 276, 2923-2929.
- Narwani, A., Bentlage, B., Alexandrou, M. A., Fritschie, K. J., Delwiche, C., Oakley, T. H. *et al.* (2017). Ecological interactions and coexistence are predicted by gene expression similarity in freshwater green algae. *J. Ecol.*, 105, 580-591.
- Navarrete, S.A. & Berlow, E.L. (2006). Variable interaction strengths stabilize marine community pattern. *Ecol. Lett.*, 9, 526-536.
- Novak, M., Wootton, J. T., Doak, D. F., Emmerson, M., Estes, J. A. & Tinker, M. T. (2011). Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. *Ecology*, 92, 836-846.
- Novak, M., Yeakel, J. D., Noble, A. E., Doak, D. F., Emmerson, M., Estes, J. A. *et al.* (2016). Characterizing species interactions to understand press perturbations: what is the community matrix? *Annu. Rev. Ecol. Evol. Syst.*, 47, 409-432.
- Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B.-E. *et al.* (2017). How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proc. R. Soc. B*, 284, 20170768.
- Pennekamp, F., Adamson, M.W., Petchey, O.L., Poggiale, J.-C., Aguiar, M., Kooi, B.W. *et al.* (2017). The practice of prediction: What can ecologists learn from applied, ecology-related fields? *Ecol. Complex.*, 32, 156-167.
- Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M. *et al.* (2015). The ecological forecast horizon, and examples of its uses and determinants. *Ecol. Lett.*, 18, 597-611.
- Petit, D.R., Petit, L.J., Saab, V.A. & Martin, T.E. (1995). Fixed-radius point counts in forests: factors influencing effectiveness and efficiency. In: C. J. Ralph, S. Droege & J. Sauer (editors). *Monitoring bird population trends by point counts (USDA Forest Service General Technical Report PSW-GTW-149)*, pp. 49-56. Albany, CA.
- Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nat. Ecol. Evol.*, 1, 0101.
- Plein, N., Morris, W. K., Moir, M. L. & Veski, P. A. (2017). Identifying species at coextinction risk when detection is imperfect: Model evaluation and case study. *PLoS One*, 12, e0183351.

- Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. & Pulliam, H.R. (2001). Making smart conservation decisions. *Conservation biology: research priorities for the next decade*, 225-244.
- Raymond, B., McInnes, J., Dambacher, J.M., Way, S. & Bergstrom, D.M. (2011). Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *J. Appl. Ecol.*, 48, 181-191.
- Regan, H.M., Ben-Haim, Y., Langford, B., Wilson, W.G., Lundberg, P., Andelman, S.J. & Burgman, M.A. (2005). Robust decision-making under severe uncertainty for conservation management. *Ecol. Appl.*, 15, 1471-1477.
- Roberts, A. (1974). The stability of a feasible random ecosystem. *Nature*, 251, 607-608.
- Roy, D.B., Rothery, P. & Brereton, T. (2007). Reduced-effort schemes for monitoring butterfly populations. *J. Appl. Ecol.*, 44, 993-1000.
- Ruscoe, W.A., Ramsey, D.S.L., Pech, R.P., Sweetapple, P.J., Yockney, I., Barron, M.C. *et al.* (2011). Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecol. Lett.*, 14, 1035-1042.
- Sisson, S.A., Fan, Y. & Beaumont, M.A. (2018). *Handbook of Approximate Bayesian Computation*. Chapman & Hall / CRC Press, Boca Raton, Florida.
- Staniczenko, P.P.A., Lewis, O.T., Jones, N.S. & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecol. Lett.*, 13, 891-899.
- Stone, L. (2016). The Google matrix controls the stability of structured ecological and biological networks. *Nat. Comm.*, 7, 12857.
- Turney, S. & Buddle, C. M. (2016). Pyramids of species richness: the determinants and distribution of species diversity across trophic levels. *Oikos*, 125, 1224-1232.
- Tunney, T.D., Carpenter, S.R. & Vander Zanden, M.J. (2017). The consistency of a species' response to press perturbations with high food web uncertainty. *Ecology*, 98, 1859-1868.
- Ushio, M., Hsieh, C.-H., Masuda, R., Deyle, E.R., Ye, H., Chang, C.-W. *et al.* (2018). Fluctuating interaction network and time-varying stability of a natural fish community. *Nature*, 554, 360-363.
- Wolf, C., Novak, M. & Gitelman, A. I. (2017). Bayesian characterization of uncertainty in species interaction strengths. *Oecologia*, 184, 327-339.

Wood, S.N. (2010). Statistical inference for noisy nonlinear ecological dynamic systems. *Nature*, 466, 1102-1104.

Yodzis, P. (1988). The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, 69, 508-515.

SUPPORTING INFORMATION

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

FIGURE CAPTIONS

Figure 1. (a) An ecosystem network configuration possessing three trophic levels with two species per trophic level. Arrows represent predator-prey links, with the arrowhead directed towards the predator. Predator-prey interactions given by dashed arrows only exist in our generated networks if the predator feeds on more than one trophic level (see Appendix S1 for further details). (b) One of the ecosystems generated from the network configuration shown in (a), monitored annually with a measurement error of 10%, over a 20 year period. An eradication of species 1 immediately after the 20 year monitoring period is proposed in this example. The true ecosystem trajectory without any intervention is shown with a red line, and the true ecosystem trajectory if species 1 is eradicated is shown with a blue line. Data from the simulated monitoring program is shown as black dots. This data is used to inform the SMC-fitted model: projections without any intervention are shown in red shaded areas, and projections if species 1 is eradicated are shown in blue shaded areas. For these model projections, dark and light shaded areas represent the 68% and 95% central credible intervals of the predictions, respectively. Notice that there is large uncertainty in future predictions, especially for the eradication scenario (blue shaded areas).

Figure 2. Probability distributions (shaded regions) for four of the 22 interaction strengths obtained from SMC sampling for the ecosystem and sampled data shown in Fig. 1b. Dashed vertical lines represent the true parameter values. Insets show the associated interaction; for example, parameter $\alpha_{3,2}$ (top) represents the effect of the interaction between species 2 and 3 (black arrow) on species 3 (black circle). Uniform prior distributions enclosed by the x -axis

limits were assumed for all parameters. The y-axes represent relative rather than absolute probabilities, rescaled so that the density function's maximum is one. Probability distributions for all parameters of this ecosystem, and technical details for constructing these distributions, are provided in Appendix S4. Notice that the data helped to estimate interaction strengths $\alpha_{3,5}$ and $\alpha_{3,6}$ but was not particularly informative for $\alpha_{3,2}$ or $\alpha_{4,2}$. Appendix S4 also shows that informativeness of data for interaction strengths is not necessarily related to trophic level (see e.g. distributions for parameters $\alpha_{2,3}$ and $\alpha_{5,4}$ in Appendix S4).

Figure 3. Uncertainty in future predictions, across 100 randomly generated ecosystems with 3 trophic levels and 2 species per trophic level. Uncertainty in future predictions for eradication scenarios (blue boxplots) include all possible nonbasal species eradications (four per ecosystem in this case). Boxes represent the interquartile range and whiskers enclose the 95% central interval. The “baseline monitoring program” indicates model predictions informed by 20 years of species population data monitored quadrennially with 40% measurement error. The other two columns show the reduction in uncertainty due to either a four-fold increase in measurement frequency (annual monitoring) or a four-fold increase in measurement accuracy (10% measurement error), relative to the baseline monitoring program. Notice that increasing monitoring accuracy is better than increasing monitoring frequency by the same factor, if the goal is to reduce uncertainty in model predictions.

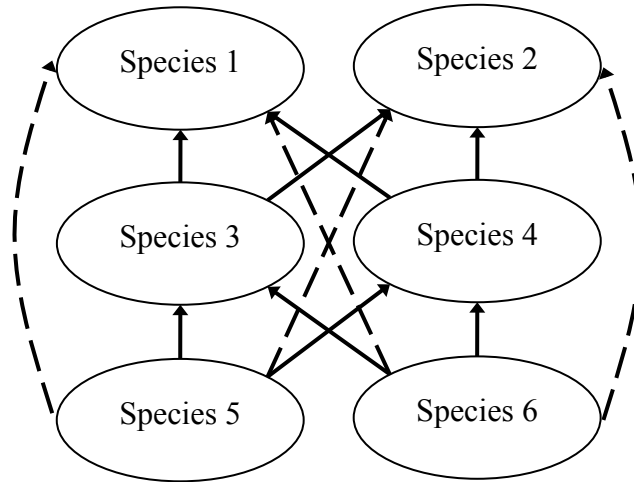
Figure 4. Model uncertainty, and difference between the model and true underlying data, quantified in several different ways (see Methods and Appendix S3), across 100 randomly generated ecosystems with 3 trophic levels and 2 species per trophic level, given a 20 year monitoring program that measures all species quadrennially with 40% measurement error. Red and blue boxplots indicate the “no action” and “eradication” scenarios, respectively; black boxplots show metrics calculated from comparing these two scenarios. Boxplots (a) and (b) present the same information as the two “baseline monitoring program” boxplots shown in Fig. 3. For metrics shown in this figure that are calculated from the eradication scenario results, all possible nonbasal species eradications are considered (four per ecosystem in this case). Boxes represent the interquartile range and whiskers enclose the 95% central interval. Whiskers whose upper vertical bars are not shown indicate that the 95% central interval includes metric values

that exceed 100% (indicating the possibility of a very uninformative prediction). Notice that the third quartile for the direction of the eradication impact (right-most column) is less than 50%. This indicates that the model's predictions of the direction of change (increase or decrease) in a species' future population biomass due to a proposed eradication, compared to the future population biomass if no action is undertaken, are correct at least 75% of the time for ecosystems with 3 trophic levels and 2 species per trophic level (see also Fig. 5).

Figure 5. Ability of the fitted models to correctly predict the direction of eradication impact (increase or decrease in a species' future population biomass due to eradication, compared to the future population biomass if no action is undertaken) for the 20 year monitoring program with the most imprecise (40% error) and infrequent (quadrennial) measurements that we investigated. The ability of the model to predict the correct direction of eradication impact was calculated from the proportion of simulations where the model predicted a >50% probability of a species' future population biomass changing in the same direction as the true value (same method as the blue bars in Appendix S6, and the blue and cyan bars in Appendix S7). TL = trophic level.

FIGURES

(a)



(b)

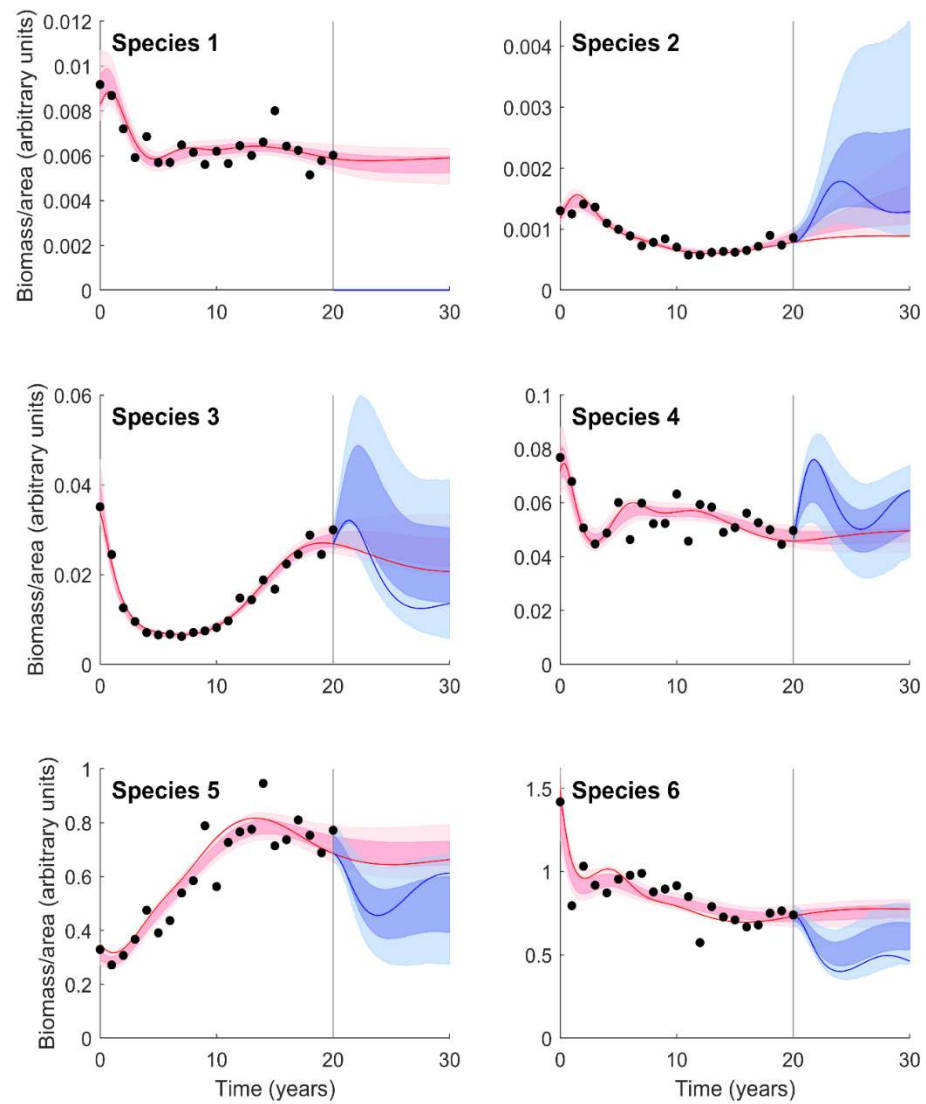


Figure 1.

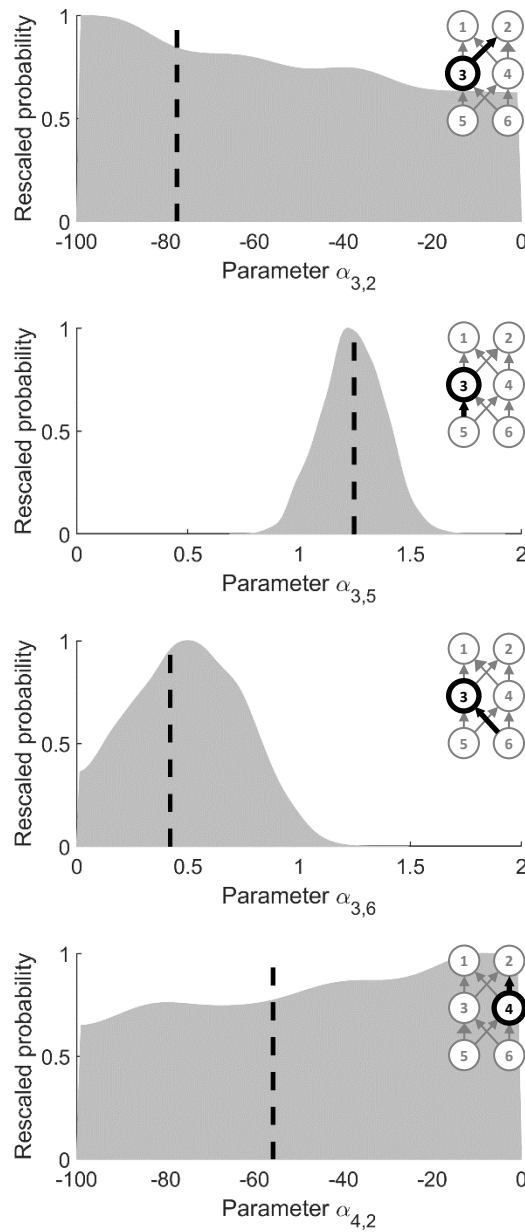


Figure 2.

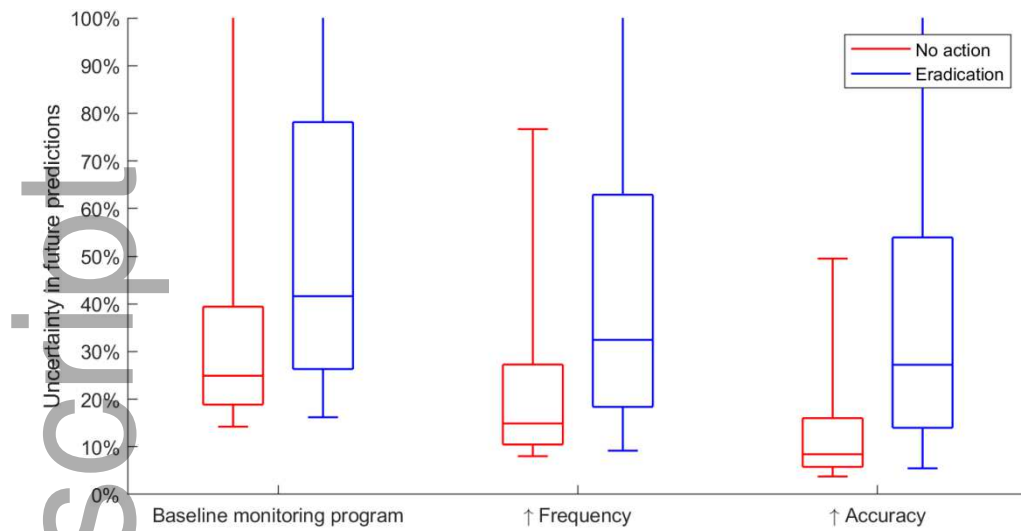


Figure 3.

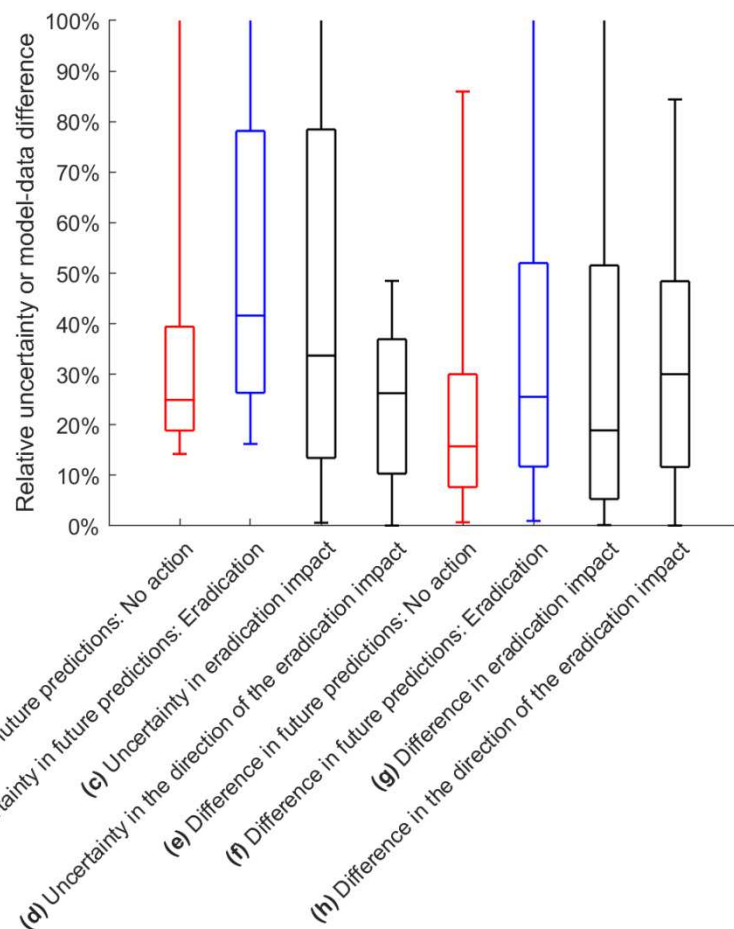


Figure 4.

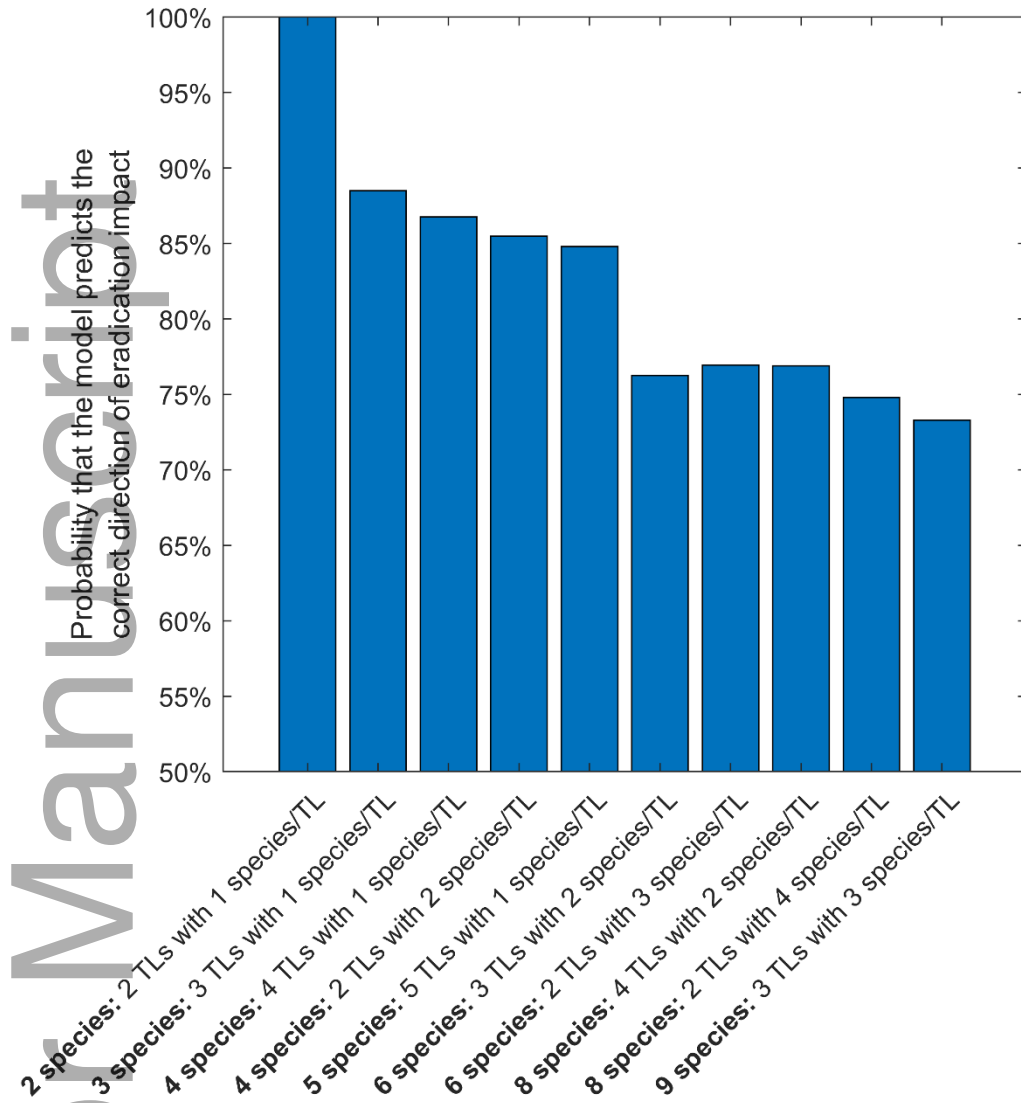


Figure 5.

BOXES

Box 1. Definition of the six metrics used to quantify the ability of fitted models to make predictions useful for management decisions

1. Uncertainty in future predictions (UFP):

$$UFP_{\text{erad}} = \frac{\Delta_{CI} \{y_{\text{model,erad}}(t_{\text{future}})\}}{\text{median} \{y_{\text{model,erad}}(t_{\text{future}})\}} \quad \text{for eradication scenarios, and}$$

$$UFP_{\text{no erad}} = \frac{\Delta_{\text{CI}} \{y_{\text{model,no erad}}(t_{\text{future}})\}}{\text{median}\{y_{\text{model,no erad}}(t_{\text{future}})\}} \quad \text{for the “no action” scenario.}$$

2. Uncertainty in eradication impact (UEI):

$$UEI = \Delta_{\text{CI}} \left\{ \frac{y_{\text{model,erad}}(t_{\text{future}}) - y_{\text{model,no erad}}(t_{\text{future}})}{y_{\text{model,no erad}}(t_{\text{future}})} \right\}$$

3. Uncertainty in the direction of the eradication impact (UDEI):

$$UDEI = \min\{q, 1-q\}, \quad \text{where} \quad q = \overline{H(y_{\text{model,erad}}(t_{\text{future}}) - y_{\text{model,no erad}}(t_{\text{future}}))}$$

4. Difference in future predictions (DFP) between model predictions and true values:

$$DFP_{\text{erad}} = \left| \frac{\text{median}\{y_{\text{model,erad}}(t_{\text{future}})\} - y_{\text{true,erad}}(t_{\text{future}})}{y_{\text{true,erad}}(t_{\text{future}})} \right| \quad \text{for eradication scenarios, and}$$

$$DFP_{\text{no erad}} = \left| \frac{\text{median}\{y_{\text{model,no erad}}(t_{\text{future}})\} - y_{\text{true,no erad}}(t_{\text{future}})}{y_{\text{true,no erad}}(t_{\text{future}})} \right| \quad \text{for the “no action” scenario.}$$

5. Difference in eradication impact (DEI) between model predictions and true values:

$$DEI = \left| \text{median} \left\{ \frac{y_{\text{model,erad}}(t_{\text{future}}) - y_{\text{model,no erad}}(t_{\text{future}})}{y_{\text{model,no erad}}(t_{\text{future}})} \right\} - \frac{y_{\text{true,erad}}(t_{\text{future}}) - y_{\text{true,no erad}}(t_{\text{future}})}{y_{\text{true,no erad}}(t_{\text{future}})} \right|$$

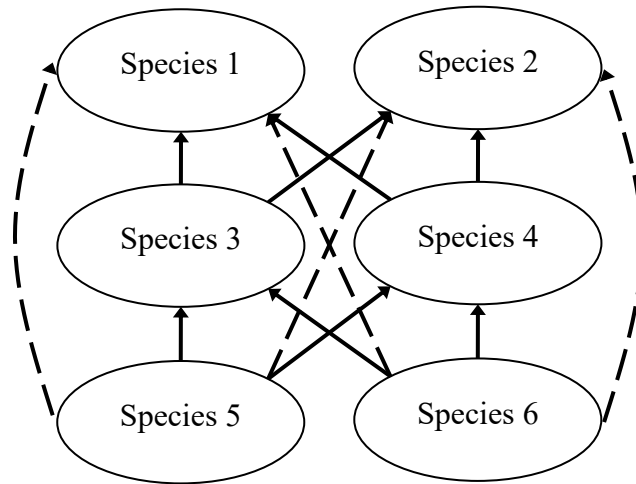
6. Difference in the direction of the eradication impact (DDEI) between model predictions and true values:

$$DDEI = \left| \overline{H(y_{\text{model,erad}}(t_{\text{future}}) - y_{\text{model,no erad}}(t_{\text{future}}))} - \overline{H(y_{\text{true,erad}}(t_{\text{future}}) - y_{\text{true,no erad}}(t_{\text{future}}))} \right|$$

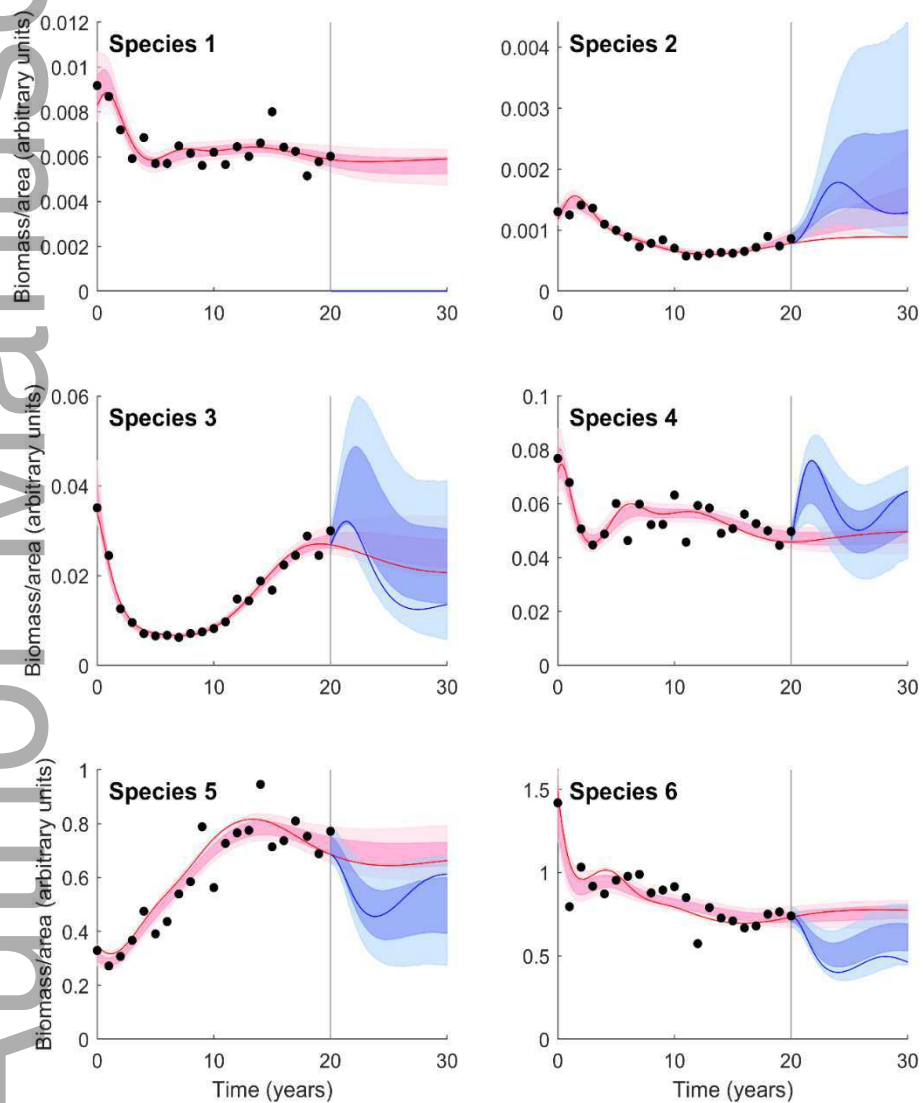
Terminology: $\text{median}\{x\}$ is the median of x , $\bar{x}$ is the mean of x , and $\Delta_{\text{CI}}\{x\}$ is half the difference between the upper and lower bounds of the 68% central credible interval for x . All of these calculations are applied to the model ensemble obtained from posterior simulation and may require internal weighting if each member of the posterior sample does

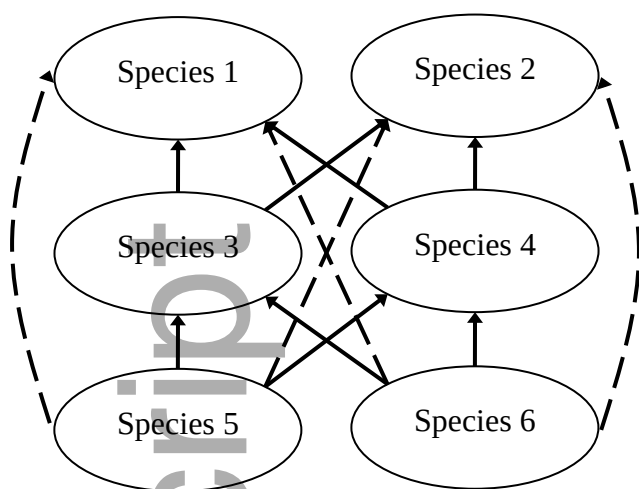
not have the same probability (e.g. using weighted mean instead of mean, etc.). $H(x)$ is the Heaviside step function, equal to one if $x > 0$ and zero otherwise. $y_{\text{true,erad}}(t_{\text{future}})$ and $y_{\text{model,erad}}(t_{\text{future}})$ are the true and model-predicted population biomasses, respectively, of a non-eradicated species at some future time t_{future} following the eradication of another species at some earlier time. (In our simulations the eradication occurred at the end of a 20 year monitoring period, and the future time of interest was 10 years later, i.e. $t_{\text{future}} = 30$ years.) Analogously, $y_{\text{true,no erad}}(t_{\text{future}})$ and $y_{\text{model,no erad}}(t_{\text{future}})$ are the true and model-predicted population biomasses, respectively, of a species at the same future time t_{future} if no management action is undertaken. Both $y_{\text{true,erad}}(t_{\text{future}})$ and $y_{\text{true,no erad}}(t_{\text{future}})$ are single values, whilst $y_{\text{model,erad}}(t_{\text{future}})$ and $y_{\text{model,no erad}}(t_{\text{future}})$ both represent probability distributions obtained from posterior simulation. Further details on all metrics are provided in Appendix S3. Notice that each metric provides different information about how well the fitted model is predicting the future of a species in response to a proposed eradication action.

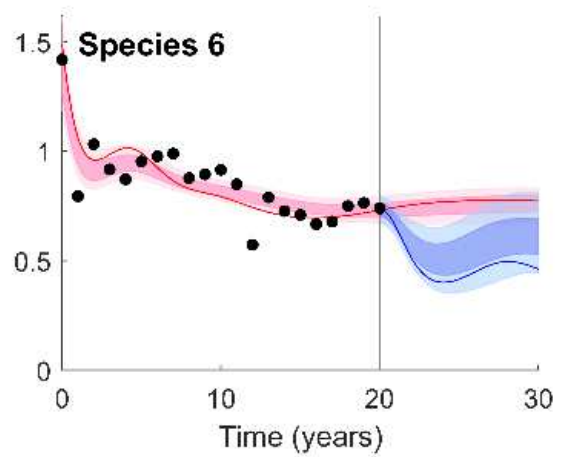
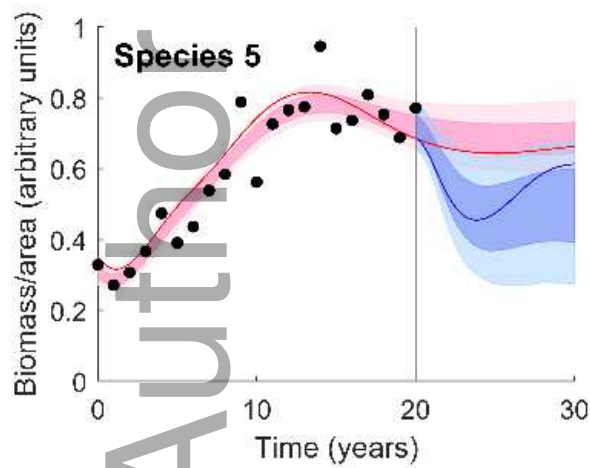
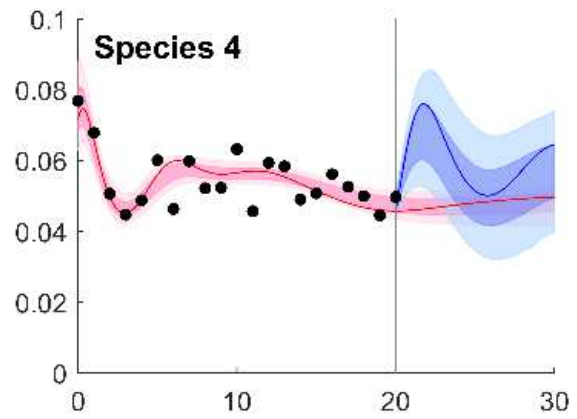
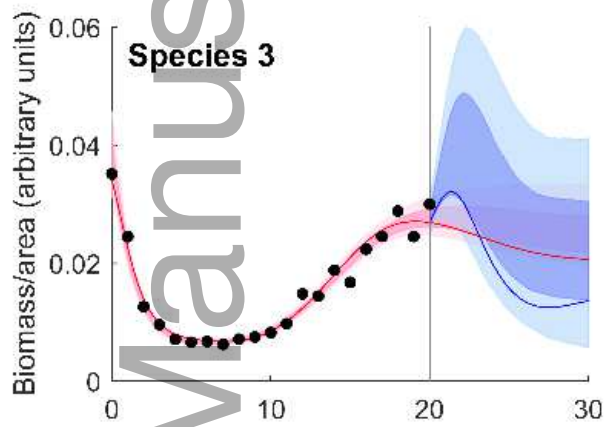
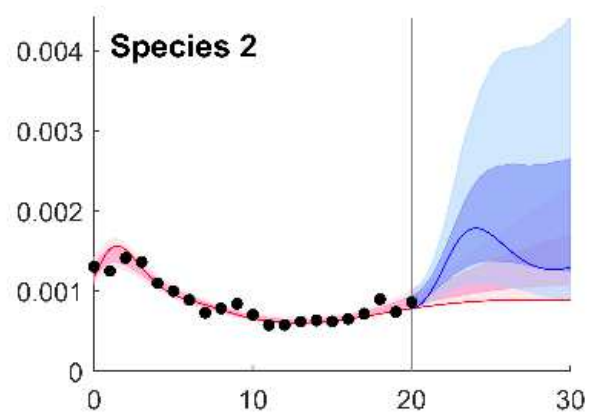
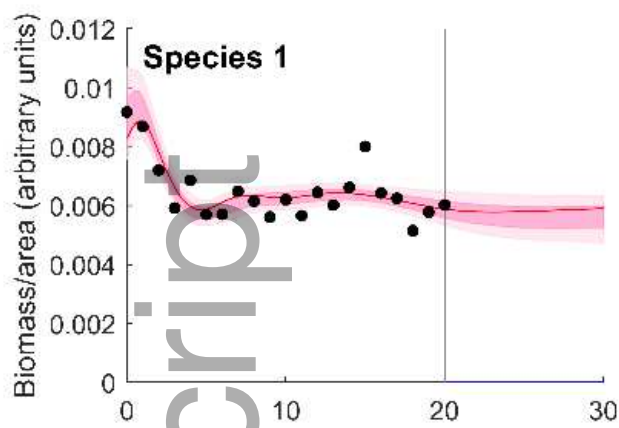
(a)



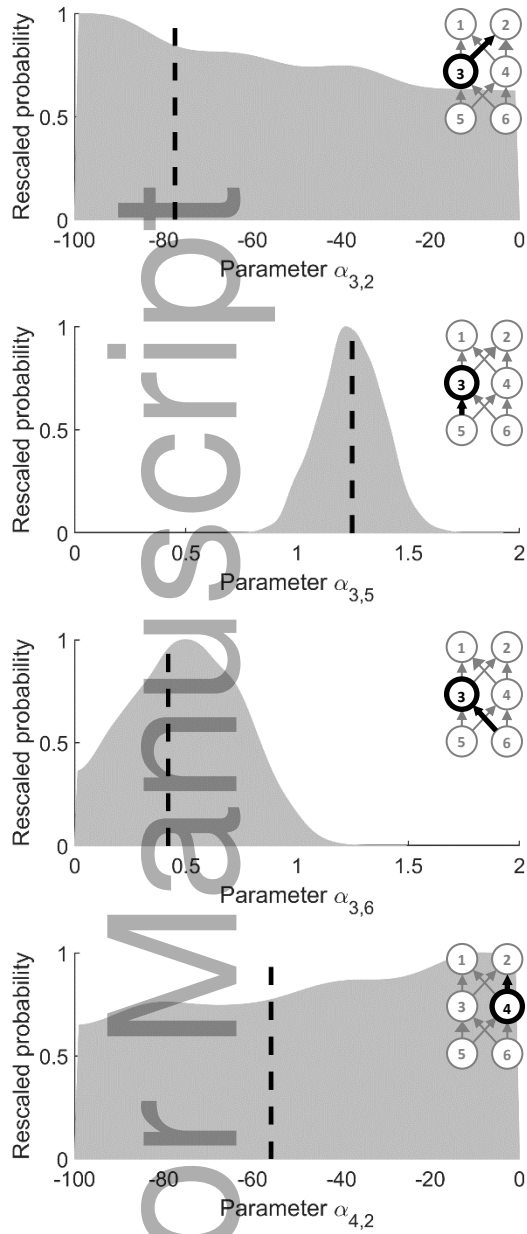
(b)

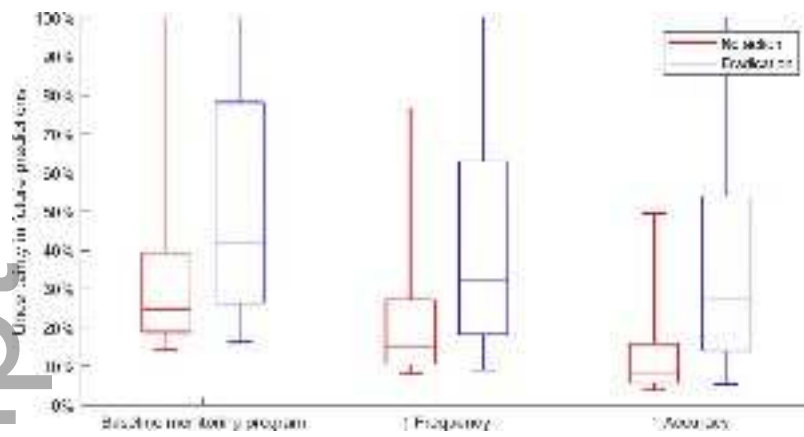




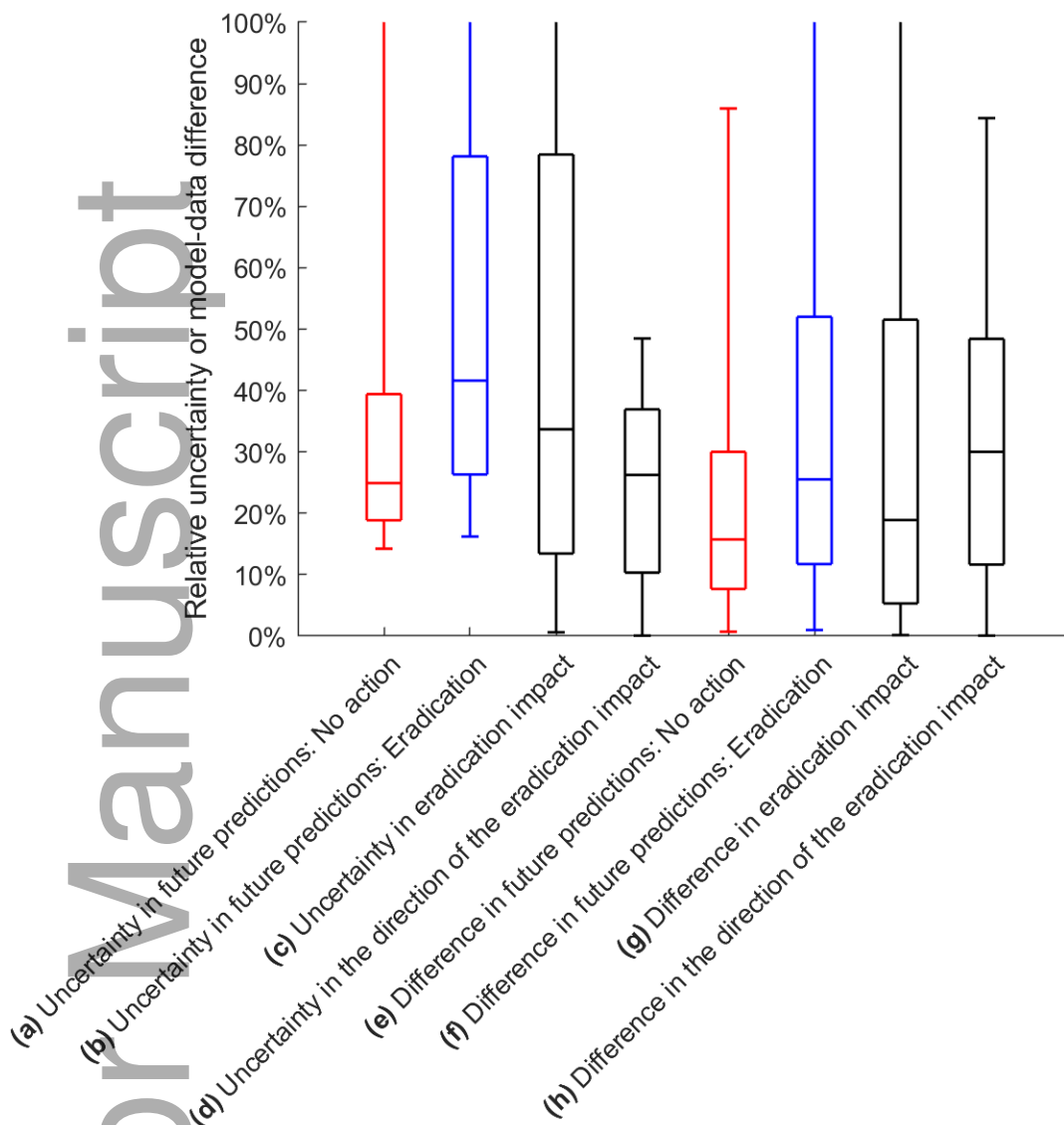


ele_13465_f1b.png





ele_13465_f3.png



ele_13465_f4.png

