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

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**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

87 optimal decision ultimately depends on the predicted outcomes for actions that could be enacted

88 (Possingham et al. 2001), so it is critical to identify whether or not these outcomes will be

89 unclear because of uncertainty in the predictions.

90      In this paper, we investigate what useful information about interaction strengths, and their

91 subsequent effects on future projections, can be gleaned from dynamic ecosystem models fitted

92 to imperfect monitoring data. We fit Lotka-Volterra models to synthetic data generated from

93 known underlying population trajectories for deterministic ecosystems with known network

94 structure. Uncertainty in interaction strength estimates is rigorously calculated using Bayesian

95 inference (Wolf et al. 2017), and this uncertainty is propagated through to ecosystem responses

96 to management decisions. Our work therefore extends previous modelling efforts that have

97 predicted species responses to disturbances given uncertain interaction strengths (Novak et al.

98 2011), by specifically connecting the uncertainty in interaction strength estimates back to the

99 monitoring data used to inform these estimates. Furthermore, instead of just focusing on model

100 prediction accuracy, our analysis goes one step further to investigate the relative difference

101 between future predictions with or without an intervention to guide decision-makers as to

102 whether the intervention should be applied or not. We are not aware of other work that has

103 quantitatively propagated information gleaned from time-series data all the way through to the

104 potential impact of different management decisions. Overall we demonstrate that, despite the

105 issues in estimating parameter values characterising the ecosystem, there is a potential pathway

106 to generate useful predictions for decision-making.

107

108    **METHODS**

109    **Overview**

110    Our method includes three distinct steps: (1) generation of thousands of synthetic ecosystem

111    population time-series data following deterministic Lotka-Volterra dynamics with measurement

112    noise added, (2) fitting Lotka-Volterra models to this simulated data using Bayesian inference

113    (Girolami 2008), and (3) investigating how well the fitted models predict ecosystem responses to

114    a specific management intervention – rapid eradication of one species. These three steps are

115    summarised below; technical details are provided in Appendices S1-S3.

116

117    **Generating the simulated data**

118    We generated virtual ecosystems by modelling the changes in biomass over time, of all species

119    in the ecosystem, via deterministic Lotka-Volterra equations (Murray 2002),

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = r_i y_i(t) + \sum_{j=1}^{N} \alpha_{ij} y_i(t) y_j(t), \tag{1}$$

121    where $y_i(t)$ is the total population biomass (in units of biomass/area) of species $i$ at time $t$ (in

122    years), $r_i$ is the intrinsic net growth rate (yr$^{-1}$) of species $i$, and $\alpha_{ij}$ is the strength of the per-capita

123    interaction between species $i$ and $j$ (in units of (biomass/area)$^{-1}$ yr$^{-1}$). Each ecosystem we

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

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

126        The Lotka-Volterra systems we investigate are deterministic (e.g. Narwani et al. 2017), and

127    therefore possess no process noise. This is a large assumption, but we stress here that the present

128    work is a first attempt (to our knowledge) to quantitatively propagate information gleaned from

129    time-series data all the way through to the potential impact of different management decisions.

130 Combining the analysis presented here with an investigation of the effect of process noise on

131 accuracy of future projections is therefore a clear future step for this research.

132 We generated 1000 ecosystems, each with their own species interaction strengths and

133 network structure, following mathematical procedures detailed and justified in Appendix S1.

134 Briefly, these ecosystems consist of between two and nine species each, organised into one of ten

135 different network configurations: two to five trophic levels with one species per trophic level,

136 two to four trophic levels with two species per trophic level, two to three trophic levels with

137 three species per trophic level, or two trophic levels with four species per trophic level. We refer

138 to these as network configurations (instead of calling them network structures) to indicate that

139 (1) they only group together ecosystems with the same number of species per trophic level and

140 the same number of trophic levels, and (2) ecosystems within the same network configuration

141 can express different interconnections between species (i.e. different network structure). For each

142 network configuration we assumed that there is an equal number of species at each trophic level,

143 which is not a particularly restrictive condition for the small networks we consider ($\leq 9$ species)

144 but may not be a reasonable assumption for the much larger networks that characterise many

145 real-world ecosystems. The assumption of species richness uniformity across trophic levels was

146 made to keep the number of different network configurations tested in our analysis down to a

147 practical number (ten), and there are a plethora of other network configurations that could have

148 also been chosen. Real-world ecosystems may possess decreased numbers of species at higher

149 trophic levels, although uniformity of species richness across trophic level has been observed,

150 especially in terrestrial food webs (Turney & Buddle 2016). In keeping with these observations,

151 parameterisation of the food webs generated in this paper was based primarily on terrestrial

152 systems (Baker et al. 2017; see also Appendix S1).

153        We generated 100 different ecosystems for each of the ten network configurations,

154        thereby yielding the 1000 different ecosystems. As an example, Fig. 1a shows one of the network

155        configurations considered in our analysis. We generated ecosystems with predator-prey

156        interactions only, although we recognise that this common assumption in food web models

157        overlooks other potentially important interaction types (Berlow et al. 2004; Kéfi et al. 2012;

158        Pilosof et al. 2017). We initiate each ecosystem's dynamics to start away from equilibrium.

159        For each of the 1000 ecosystems, we sampled imperfect measurements of their

160        population trajectories to simulate monitoring programs of 20 year duration. This was

161        accomplished by adding temporally-uncorrelated Gaussian noise to the deterministic ecosystem

162        trajectories, to simulate measurement error. To investigate how monitoring accuracy and

163        frequency affects ecosystem predictions, we simulated ten monitoring programs per ecosystem

164        which differed in how often and accurately species population biomasses were measured. Nine

165        of the monitoring programs we investigated are practically achievable: observations every one,

166        two or four years, with measurement error $\delta$ of 10%, 20% or 40% (Marion 1995; Petit et al.

167        1995; Crall et al. 2011). We also simulated a tenth monitoring program with yearly

168        measurements and 1% error to investigate an extreme best-case scenario. Measurement error was

169        assumed to follow a truncated normal distribution, with a lower bound of zero (to avoid negative

170        biomass observations), and standard deviation of 1%, 10%, 20% or 40% of the true value of the

171        species population biomass. Both the true and observed noisy values of species population

172        biomass were retained for comparison in our analysis.

173

174  **Calibrating a model to the synthetic data**

175  Models were fitted to the observed noisy data using Bayesian inference (Girolami 2008),

176  implemented by a posterior-simulation method called Sequential Monte Carlo (SMC) sampling

177  (Doucet et al. 2000), a class of methods which is related to and overlaps with particle filtering

178  (Doucet and Johansen 2009). SMC sampling is seeing increasing usage for a diverse range of

179  applications (Drovandi & Pettitt 2011; Jeremiah et al. 2012; Lawson et al. 2018; Sisson et al.

180  2018). Our SMC sampler (Appendix S2) is adapted from ideas presented in Jeremiah et al.

181  (2012) and Del Moral et al. (2012).

182      In our application, SMC sampling estimates the joint posterior probability distribution for

183  the model parameters $\left\{ y_{i0}, r_i, \alpha_{ij}, \delta : i, j = 1, ..., N \right\}$ in each simulated ecosystem, which includes

184  estimation of initial species population biomass $y_{i0}$, growth rates $r_i$, interaction strengths $\alpha_{ij}$,

185  measurement noise $\delta$ and the uncertainty in all of these quantities. This approach quantifies

186  parameter uncertainty and propagates this uncertainty into scenario predictions via a model

187  ensemble, thereby building upon a recently introduced ensemble ecosystem modelling

188  framework (Baker et al. 2017, 2019). Using this method, we can compare the ecosystem

189  parameters' true values to their probability distributions obtained from model-data fitting, to

190  identify how much information about ecosystem parameter values can be gained from the

191  synthetic data. For the primary analysis of this paper, we apply SMC sampling to estimate the

192  posterior 10,000 times: for ten monitoring programs of different measurement frequency and

193  accuracy, applied to 100 ecosystems each for ten different network configurations. (We also

194  estimated 600 additional posteriors, in an extension of our analysis to investigate the effects of

195  structural uncertainty, as detailed in Appendix S8.) We then use the full posterior, in each of

196  these cases, to simulate the impact of management interventions on the ecosystem.

197

**Predicting ecosystem response to a species eradication**

199  The ultimate goal of our model fitting to imperfect measurements of generated ecosystems, is to

200  identify – in the best-case scenario of known network structure, negligible process noise, and

201  ecosystem dynamics adhering precisely to the models that we fit – whether any ecological

202  consequences of a management action, specifically eradication, can be reasonably predicted

203  using models calibrated to time-series data. This analysis therefore identifies if it is possible for

204  data-calibrated models to be useful for informing management decisions. To address this goal,

205  we considered two classes of scenarios for each of the 10,000 combinations of ecosystems and

206  monitoring programs: (1) completely eradicating a predator immediately after the 20 year

207  monitoring period, and (2) no action. For eradication scenarios, we assumed that the predator is

208  eradicated rapidly so that its population biomass is set immediately to zero. Each eradication

209  scenario consisted of eradication of only one predator, from any nonbasal trophic level. We did

210  not consider scenarios for the eradication of basal species, since this is an unlikely management

211  action due to the high possibility of secondary extinctions (Dunne and Williams 2009;

212  Staniczenko et al. 2010).

213      We did not predefine any species to be invasive and therefore candidates for eradication.

214  Hence, we explored scenarios where each predator is individually eradicated. For ecosystems

215  containing more than two species, there are multiple predators that could be eradicated.

216  Specifically, if $TL_{max}$ is the number of trophic levels in the ecosystem, and $S$ is the common

217  number of species per trophic level (every trophic level is assumed to have the same number of

218  species in our analysis, see e.g. Fig. 1a), there are $S \times (TL_{max} - 1)$ nonbasal species that could be

219  eradicated. We ran scenarios for each possible predator being individually eradicated, thereby

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220   yielding $S \times (TL_{max} - 1)$ eradication scenarios per ecosystem. Conversely, there is only one "no

221   action" scenario per ecosystem: letting the ecosystem continue its (non-equilibrium) temporal

222   dynamics beyond the 20 year monitoring period without intervention.

223       To compare the eradication and no action scenarios, we focused our analysis on the

224   predictions of species population biomasses 10 years into the future ($t = 30$ years) after the

225   monitoring period ($t = 0$ to $t = 20$ years) and proposed eradication ($t = 20$ years). We chose to

226   focus our analysis on a predefined future time because ecosystem management plans are usually

227   drafted with clear, near-future, timeframes in mind, and our chosen timeframe of 10 years is

228   typical for terrestrial ecosystem management (e.g. Director of National Parks 2015). Of course,

229   predictions over longer timescales will likely possess higher uncertainty.

230

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

232   In preliminary simulations we found that predictions of future population biomass often

233   expressed large uncertainty. However, whilst the uncertainty in an individual prediction of a

234   future scenario might be large, we also wanted to identify if the uncertainty in the *difference*

235   *between scenarios* is also large – as the latter is what is important for management decisions. We

236   also wanted to identify if the data-fitted models are predicting the *correct trends* even if the

237   uncertainty bounds in their predictions are large. Hence we introduced six metrics that quantify

238   the ability of fitted models to make predictions useful for management decisions (Box 1 and

239   Appendix S3); these metrics are summarised below. All six metrics are calculated from the

240   species population biomasses at $t = 30$ years, i.e. ten years after the eradication (or no action)

241   proposed to occur immediately after the 20 year monitoring period. All six metrics are unitless,

242   so that the different biomasses of individual species are scaled out of all the metrics. Each metric

243    is calculated for one species within a particular ecosystem, and is either related to one scenario or

244    a comparison between scenarios, depending on the specific metric used.

245         The first three metrics we introduced (Box 1) indicate the uncertainty in model

246    predictions without any knowledge of the ecosystem's true future trajectory – uncertainty in

247    future predictions, uncertainty in eradication impact, and uncertainty in the direction of the

248    eradication impact. Here, eradication impact is defined as the relative difference in model-

249    predicted future trajectories between the two scenarios of eradication and no action. The last

250    three metrics indicate how different the model predictions are from the ecosystem's true future –

251    difference in future predictions, difference in eradication impact, and difference in the direction

252    of the eradication impact. The six metrics each provide different information about how

253    uncertain the model predictions are, or how different the model predictions are from the true

254    trajectory. All six metrics are non-negative; reducing their values towards 0% indicates that the

255    data yield a more informative fitted model for decision-making. More specifically, metric values

256    less than 10% are excellent while values exceeding 50% are relatively uninformative (except for

257    the uncertainty in the direction of the eradication impact for which a value of 50% is completely

258    uninformative).

259         We calculated and compared the six metrics for all non-eradicated species in all

260    management scenarios (either eradication or no action), monitoring programs and ecosystems,

261    and grouped the values of the six metrics together by monitoring program and network

262    configuration (i.e. ecosystems with the same number of species per trophic level and number of

263    trophic levels). Individual values of the metrics were aggregated across species and ecosystems

264    (without any stratification of values either by ecosystems or by species position within the

265    network) to identify how these metrics' values are distributed within each combination of

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266 monitoring program and network configuration. Ultimately, this analysis addresses the following

267 question: Even if the future predictions of individual species trajectory are highly uncertain, are

268 there particular aspects of ecosystem responses to an eradication which can possibly be predicted

269 with high confidence?

270

271 **RESULTS**

272 Large uncertainty in future predictions of species population biomass was a common observation

273 amongst the 1000 ecosystems that we investigated. 20 years of synthetic monitoring data was

274 used to inform each modelled ecosystem; and the 10-year future model projections of this

275 ecosystem, following the complete eradication of one predator immediately after the 20 year

276 monitoring period, were analysed. Fig. 1b shows an example of one of our generated ecosystems,

277 measured with the best plausible monitoring program that we considered (annual measurements

278 of all species for 20 years with 10% measurement error). For the true trajectory of this ecosystem

279 without any management intervention (red lines in Fig. 1b), 20 years of monitoring data was

280 sufficient for the ecosystem to be approaching but not yet reaching equilibrium. For the model

281 predictions (shaded areas) based on the monitoring data (dots), the uncertainty in future

282 projections following a species eradication was sufficiently large that it is unclear if this

283 eradication will be net beneficial or detrimental to the remaining species. The estimated

284 probability distributions of model parameters for this ecosystem (Fig. 2) also indicated that

285 several interaction strengths were unresolvable with this data.

286     Uncertainty in future population predictions varied widely between species and

287 ecosystems. To give some sense of how the species responses in the ecosystem shown in Fig. 1b

288 compare to our general results from multiple network configurations and monitoring program

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289    qualities, we show box and whisker plots capturing the interquartile range (box) and 95% central

290    credible interval (whiskers) of the uncertainty in future predictions in Appendix S5. For example,

291    for 100 ecosystems of the same structure and subjected to the same monitoring program as Fig.

292    1b, uncertainty in future predictions for the eradication scenario had a median of 21%,

293    interquartile range (box) of 10-44% and 95% central credible interval (whiskers) of 3-217%

294    (second column of Fig. S5.6b in Appendix S5, upper limit not shown). Hence, uncertainty in

295    future predictions could be low or extremely high, depending on the species and ecosystem, even

296    with an excellent monitoring program. As expected, reducing monitoring accuracy or frequency

297    increased the uncertainty in future predictions (Appendix S5).

298         Reducing measurement error from 40% to 10% reduced model uncertainty more

299    effectively than increasing monitoring frequency from once every four years (quadrennially) to

300    annually (Fig. 3). Hence, precise and infrequent monitoring may be of greater value than

301    imprecise and frequent monitoring, but we caution that this conclusion strongly depends on the

302    possible trade-off between measurement accuracy and frequency in a given study. The trade-off

303    may also depend on other factors not considered here, such as environmental stochasticity,

304    demographic stochasticity, or uncertainty regarding the network structure itself.

305         For the extreme best-case scenario of annual monitoring with 1% measurement error,

306    prediction accuracy increased dramatically but did not always lead to highly constrained

307    predictions (Appendix S5). For example, for the ecosystems with the largest number of species

308    (nine) that we investigated, the median uncertainty in future predictions of species population

309    biomass after a proposed eradication still exceeded 10% (first column of Fig. S5.10b in

310    Appendix S5). Uncertainty in future predictions may therefore be an unavoidable situation even

311    with excellent data, but in reality, management decisions still need to be made.

312    To investigate the usefulness of imperfect data for model calibration and subsequent

313    predictions to inform management decisions, we next focused on what could be achieved with

314    the worst plausible monitoring program we considered (quadrennial measurements with 40%

315    error), across multiple metrics of uncertainty and model-data difference. We first summarise our

316    results for ecosystems possessing three trophic levels and two species per trophic level (Fig. 4)

317    and then discuss applicability of the key result obtained across all ten network configurations we

318    investigated (between two and nine species, Fig. 5).

319    Both the uncertainty in future predictions, and the difference between model predictions

320    and true trajectories, were higher for eradication scenarios (Fig. 4b,f) than for scenarios

321    involving no intervention (Fig. 4a,e). This occurs because the species in the ecosystem continue

322    their previous trajectories if no management action is undertaken, whereas an eradication "jolts"

323    the species into different trajectories (compare blue and red future predictions in Fig. 1b).

324    We next sought to identify if the model predictions of the eradication impact – that is, the

325    *relative* difference between scenarios of eradication vs no action – also could possess high

326    uncertainty and large difference from their true values. Contrary to our expectations, we found

327    that predictions of eradication impact carried similar uncertainty (Fig. 4c) and similar difference

328    between model and true values (Fig. 4g) to the individual model-predicted future trajectories

329    (Fig. 4a,b,e,f). To further elucidate this result, we visually inspected many of the thousands of

330    trajectory figures generated by our simulations (of which Fig. 1b is a representative example).

331    We observed that several ecosystems were approaching equilibrium densities within the 20-year

332    monitoring period (see, e.g., Fig. 1b), and thus the uncertainty in the difference between

333    scenarios is potentially being dominated by the uncertainty in the eradication scenario. This

334    result therefore may not hold in ecosystems which are undergoing rapid population fluctuations,

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335  but for ecosystems with negligibly or gradually changing species populations it is unsurprising

336  that the impact of an ecosystem perturbation is likely to be less predictable than if the ecosystem

337  experiences no such perturbation.

338      The final two metrics that we investigated were the uncertainty (Fig. 4d) and model-data

339  difference (Fig. 4h) in the *direction* (either increase or decrease) of the predicted eradication

340  impact. The direction of the eradication impact identifies whether a species' future population

341  biomass, after the eradication, will be higher or lower than its future population if no action is

342  undertaken. Unlike the other three uncertainty metrics (Fig. 4a-c), the uncertainty in the direction

343  of the eradication impact (Fig. 4d) cannot exceed 50%, the latter of which indicates a completely

344  uninformative prediction (in this case there is equal probability of an increase or decrease in a

345  species' future population biomass due to the eradication compared to no action, see Appendix

346  S3). Fig. 4d shows that model predictions for the direction of the eradication impact can range

347  from very confident (0%) to completely uninformative (50%).

348      However, promisingly, the model-data difference in eradication impact direction (Fig.

349  4h) was less than 50% for more than 75% of the individual species responses across all

350  eradication scenarios and ecosystems: this indicates that the majority of the model ensemble (by

351  weight) predicts the correct eradication impact direction >75% of the time. We obtained this

352  result for ecosystems with three trophic levels and two species per trophic level, subjected to a

353  monitoring program with the lowest measurement accuracy (40%) and frequency (quadrennially)

354  that we investigated. Whilst 75% confidence still leaves considerable room for error, especially

355  since 50% confidence for this metric indicates a completely uninformative prediction, this

356  probability is high enough to suggest that sufficient knowledge and monitoring data for an

357 ecosystem may permit calibrated models to make predictions that are practically useful for

358 informing decisions.

359     Expanding this latter analysis to consider individual species responses across all of the

360 different network configurations we tested (two to nine species) instead of just ecosystems with

361 three trophic levels and two species per trophic level, we found that the direction of eradication

362 impact could be predicted correctly more than 70% of the time in all of our tested network

363 configurations (Fig. 5). For this metric, 50% correct indicates an uninformative result (random

364 prediction of the direction of eradication impact being either an increase or a decrease), so 70%

365 correct classifications is not optimal but could still be of value for decision-makers. We used two

366 different methods to identify if the model was predicting the correct direction of eradication

367 impact (one method shown in Fig. 5; both methods shown in Appendix S6). We reached the

368 same conclusion regardless of the method used to predict the eradication impact direction; for

369 both methods we did not consider ecosystems or species positions within the network separately,

370 but rather aggregated results across all species' potential responses to all possible predator

371 eradications across all ecosystems possessing the same network configuration and monitoring

372 program. We also found (unsurprisingly) that improving monitoring accuracy and/or frequency

373 can increase the proportion of correct predictions for the direction of eradication impact

374 (Appendix S6).

375     We undertook additional analysis to disentangle the impacts of trophic level and

376 closeness of response species to the eradicated species on the proportion of correct model

377 predictions for the direction of eradication impact (Appendix S7). This analysis indicated that

378 eradication impacts on individual species depend strongly on network structure; thus such

379 analyses are well-suited for future investigation of specific case study systems.

380    Finally, we investigated how misspecification of network structure (by assuming all

381    species on different trophic levels are involved in predator-prey interactions with each other)

382    affects model prediction accuracy (Appendix S8). We found that accuracy in predicting the

383    direction of eradication impact reduced, but remained above 65% in all our tested configurations

384    (Figure S8.1). This result (>65%), obtained with the worst plausible monitoring program we

385    considered, is getting closer to completely uninformative (50%), which emphasises the

386    importance of assuming network structures that are as close to correct as possible. In fact, in

387    certain cases, monitoring data of low frequency and accuracy can sometimes not be sufficient to

388    compensate for misspecified network structures (Figure S8.2). These results highlight that

389    comprehensive monitoring data is of best use for model predictions when it is coupled with

390    expert knowledge regarding which species interactions are actually present in the network.

391

392    **DISCUSSION**

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

394    Predicting the future of an ecosystem is a prerequisite for decision-making (Petchey et al. 2015),

395    but is often avoided in ecology due to concerns about biological complexity (Dietze et al. 2018).

396    Here, we demonstrated that model predictions of future trajectory for ecosystem food webs can

397    carry high uncertainty even if there is excellent time-series data available from a monitoring

398    program. Despite this uncertainty, the models can potentially be useful to inform management

399    decisions, if precise population predictions are not critical to the decisions. To obtain this

400    conclusion, we assessed the predictive proficiency of the fitted ecological models (Pennekamp et

401    al. 2017), and found that even in the most infrequent and imprecise monitoring programs tested,

402    these models had >70% confidence in predicting whether species population biomasses, ten

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403     years after an eradication action, will be higher or lower than if no action is undertaken. (To

404     avoid misinterpretation, we reiterate here that 50% confidence indicates an uninformative

405     prediction, so 70% correct classifications is not optimal but could still be of value for decision-

406     makers.) This finding was obtained in the best-case scenario, whereby the model structure

407     accurately reflects the ecosystem dynamics, and there is no stochasticity in the ecosystem apart

408     from measurement noise. At the very least, our analysis suggests that it is possible, for dynamic

409     models calibrated to time-series data, to provide useful predictions for decision-making. More

410     generally, approaches such as ours that formally account for uncertainty propagation are

411     advantageous because they can predict the probability of an undesirable outcome (Regan et al.

412     2005; Tunney et al. 2017). Our results therefore support the view that we do not need to wait

413     until ecological models are well-constrained in their predictions before we start forecasting

414     (Dietze et al. 2018; Houlahan et al. 2017); even a model that is not particularly well-constrained

415     in its predictions can potentially be used for management decisions. We recognise that accepting

416     the predictions of a model will always be a value judgement for the decision-maker. However, at

417     the very least, it is of benefit to provide decision-makers with model predictions, including

418     uncertainty, for them to decide on how to act on this information.

419

420     **Monitoring accuracy versus frequency**

421     Improving the accuracy of monitoring from 40% to 10% reduced model uncertainty more

422     effectively than increasing measurement frequency from quadrennial to annual (Fig. 3 and

423     Appendix S5). This result echoes other authors' findings that reduced sampling visits with

424     greater coverage (thereby increasing monitoring accuracy) may be of greater benefit than

425     frequently sampling fewer sites (Roy et al. 2007), and that skipping certain monitoring time

426    points to improve the remaining abundance estimates can be beneficial (Humbert et al. 2009).

427    However, there is a potential tradeoff here, because higher monitoring frequency increases the

428    chances of detecting unexpected ecological responses (Keith et al. 2014). Regardless of the

429    monitoring program used, our approach is able to predict the potential benefits for forecasting

430    from increased monitoring accuracy versus frequency, as decision-makers may not have the

431    resources to do both. Hence our analysis has the potential to predict the data quality needed to

432    answer a given research or management question, which is a current need suggested within the

433    community ecology literature (Delmas et al. 2019). This is especially pertinent since monitoring

434    is a substantial investment that requires careful consideration of the benefits versus the costs

435    (McDonald-Madden et al. 2010).

436

437    **Comparison to previous research in community ecology**

438    Our work adds to the ecological network literature focused on fitting models to time-series data

439    (Ives et al. 2003; Certain et al. 2018), consideration of uncertainty sources (Mutshinda et al.

440    2009) and propagating parameter uncertainty through to predictions following perturbations

441    (Aufderheide et al. 2013; Novak et al. 2011). In the context of this prior work, our key

442    contribution is to demonstrate how different aspects of time-series data alter forecast uncertainty,

443    and ultimately how this uncertainty affects the utility of model forecasts to help environmental

444    managers decide which ecosystem interventions to implement. Similarly to Novak et al. (2011)

445    we find clear relationships between uncertainty in interaction strengths and the proportion of

446    correct predictions, but our work goes one step further by connecting this uncertainty in

447    interaction strengths back to the informativeness of the measured data. Unlike Novak et al.

448    (2011) we did not investigate how connectance affects uncertainty in interaction strengths,

449   because of the small size of the networks we investigated (Section S1.2.3). We also performed

450   additional analysis to investigate the effects of network structure misspecification on our results

451   (Appendix S8); recent work by other authors has addressed the effects of model misspecification

452   as well (Certain et al. 2018).

453        Similarly to us, other authors have focused on what information can be gleaned from

454   time-series data (Cenci & Saavedra 2018), but with stochastic autoregressive models (e.g. Ives et

455   al. 2003; Ives et al. 2010; Hampton et al. 2013; Ovaskainen et al. 2017; Certain et al. 2018) used

456   more commonly than deterministic Lotka-Volterra models (e.g. Narwani et al. 2017).

457   Autoregressive models explicitly account for demographic stochasticity, although in practice this

458   process noise may be difficult to distinguish from observation error (Certain et al. 2018).

459

460   **Generalising our results to real ecosystem networks**

461   Forecasting dynamics in complex ecosystems is challenging, but may be of great benefit for

462   informing management decisions in these systems. Our work investigates this problem in small

463   predator-prey networks with known structure. However, in real ecosystems we may not know

464   their network structure, and these systems can be far more complex, involving many other

465   interaction types (Arim & Marquet 2004; Berlow et al. 2004; Ruscoe et al. 2011; Plein et al.

466   2017), variability in interaction strengths (Navarrete & Berlow 2006; Ushio et al. 2018), process

467   noise (Wood 2010) and age or size structure (Law et al. 2016). The ecosystems we investigated

468   had high connectance (Section S1.2.3), and thus a relatively large number of interaction strengths

469   needed to be estimated in our generated ecosystems. The lower connectance of the larger

470   ecosystems expected in nature might counteract the reduced confidence in future predictions

20

471   expected in these more complex systems, but only if there is knowledge of which species

472   interactions are present or absent (as was assumed here).

473       We considered ecosystems that follow deterministic Lotka-Volterra equations, as this is a

474   relatively ubiquitous approach for investigating community ecology dynamics (e.g. Roberts

475   1974; Jansen & Kokkoris 2003; Stone 2016). Extrapolation of our key results regarding the

476   ability of calibrated models to predict management outcomes may vary in ecological

477   communities with different dynamics. Future work could also investigate the relative importance

478   of different sources of uncertainty (measurement noise, environmental and demographic

479   stochasticity, model structure uncertainty and network structure uncertainty) on predicting

480   management outcomes, following on from prior studies analysing stochasticity sources

481   (Mutshinda et al. 2009) and robustness to parametric assumptions (Certain et al. 2018).

482   Resolving these different sources of uncertainty is a logical next step to improve the precision of

483   future ecological forecasts.

484

485   **CONCLUSION**

486   Even with excellent data and sophisticated model calibration techniques, it may not be possible

487   to resolve all species interaction strengths, but this should not prevent fitted models from being

488   used to inform management decisions. At the very least, it may be possible to predict whether a

489   management action, in this case, eradication, will cause a net positive or negative impact on a

490   species' population. This information might be sufficient for managers to act upon even if

491   uncertainty in future ecosystem projections is large. In short, we do not need to wait for models

492   to produce well-constrained predictions before we start using them to inform decisions that

493   improve environmental outcomes.

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677

678   **SUPPORTING INFORMATION**

679   Additional supporting information may be found online in the Supporting Information section at

680   the end of the article.

681

682   **FIGURE CAPTIONS**

683   **Figure 1.** (a) An ecosystem network configuration possessing three trophic levels with two

684   species per trophic level. Arrows represent predator-prey links, with the arrowhead directed

685   towards the predator. Predator-prey interactions given by dashed arrows only exist in our

686   generated networks if the predator feeds on more than one trophic level (see Appendix S1 for

687   further details). (b) One of the ecosystems generated from the network configuration shown in

688   (a), monitored annually with a measurement error of 10%, over a 20 year period. An eradication

689   of species 1 immediately after the 20 year monitoring period is proposed in this example. The

690   true ecosystem trajectory without any intervention is shown with a red line, and the true

691   ecosystem trajectory if species 1 is eradicated is shown with a blue line. Data from the simulated

692   monitoring program is shown as black dots. This data is used to inform the SMC-fitted model:

693   projections without any intervention are shown in red shaded areas, and projections if species 1

694    is eradicated are shown in blue shaded areas. For these model projections, dark and light shaded

695    areas represent the 68% and 95% central credible intervals of the predictions, respectively.

696    Notice that there is large uncertainty in future predictions, especially for the eradication scenario

697    (blue shaded areas).

698

699    **Figure 2.** Probability distributions (shaded regions) for four of the 22 interaction strengths

700    obtained from SMC sampling for the ecosystem and sampled data shown in Fig. 1b. Dashed

701    vertical lines represent the true parameter values. Insets show the associated interaction; for

702    example, parameter $\alpha_{3,2}$ (top) represents the effect of the interaction between species 2 and 3

703    (black arrow) on species 3 (black circle). Uniform prior distributions enclosed by the *x*-axis

704    limits were assumed for all parameters. The *y*-axes represent relative rather than absolute

705    probabilities, rescaled so that the density function's maximum is one. Probability distributions

706    for all parameters of this ecosystem, and technical details for constructing these distributions, are

707    provided in Appendix S4. Notice that the data helped to estimate interaction strengths $\alpha_{3,5}$ and

708    $\alpha_{3,6}$ but was not particularly informative for $\alpha_{3,2}$ or $\alpha_{4,2}$. Appendix S4 also shows that

709    informativeness of data for interaction strengths is not necessarily related to trophic level (see

710    e.g. distributions for parameters $\alpha_{2,3}$ and $\alpha_{5,4}$ in Appendix S4).

711

712    **Figure 3.** Uncertainty in future predictions, across 100 randomly generated ecosystems with 3

713    trophic levels and 2 species per trophic level. Uncertainty in future predictions for eradication

714    scenarios (blue boxplots) include all possible nonbasal species eradications (four per ecosystem

715    in this case). Boxes represent the interquartile range and whiskers enclose the 95% central

716    interval. The "baseline monitoring program" indicates model predictions informed by 20 years of

717 species population data monitored quadrennially with 40% measurement error. The other two

718 columns show the reduction in uncertainty due to either a four-fold increase in measurement

719 frequency (annual monitoring) or a four-fold increase in measurement accuracy (10%

720 measurement error), relative to the baseline monitoring program. Notice that increasing

721 monitoring accuracy is better than increasing monitoring frequency by the same factor, if the

722 goal is to reduce uncertainty in model predictions.

723

724 **Figure 4.** Model uncertainty, and difference between the model and true underlying data,

725 quantified in several different ways (see Methods and Appendix S3), across 100 randomly

726 generated ecosystems with 3 trophic levels and 2 species per trophic level, given a 20 year

727 monitoring program that measures all species quadrennially with 40% measurement error. Red

728 and blue boxplots indicate the "no action" and "eradication" scenarios, respectively; black

729 boxplots show metrics calculated from comparing these two scenarios. Boxplots (a) and (b)

730 present the same information as the two "baseline monitoring program" boxplots shown in Fig.

731 3. For metrics shown in this figure that are calculated from the eradication scenario results, all

732 possible nonbasal species eradications are considered (four per ecosystem in this case). Boxes

733 represent the interquartile range and whiskers enclose the 95% central interval. Whiskers whose

734 upper vertical bars are not shown indicate that the 95% central interval includes metric values

735 that exceed 100% (indicating the possibility of a very uninformative prediction). Notice that the

736 third quartile for the direction of the eradication impact (right-most column) is less than 50%.

737 This indicates that the model's predictions of the direction of change (increase or decrease) in a

738 species' future population biomass due to a proposed eradication, compared to the future

32

739    population biomass if no action is undertaken, are correct at least 75% of the time for ecosystems

740    with 3 trophic levels and 2 species per trophic level (see also Fig. 5).

741

742    **Figure 5.** Ability of the fitted models to correctly predict the direction of eradication impact

743    (increase or decrease in a species' future population biomass due to eradication, compared to the

744    future population biomass if no action is undertaken) for the 20 year monitoring program with

745    the most imprecise (40% error) and infrequent (quadrennial) measurements that we investigated.

746    The ability of the model to predict the correct direction of eradication impact was calculated

747    from the proportion of simulations where the model predicted a >50% probability of a species'

748    future population biomass changing in the same direction as the true value (same method as the

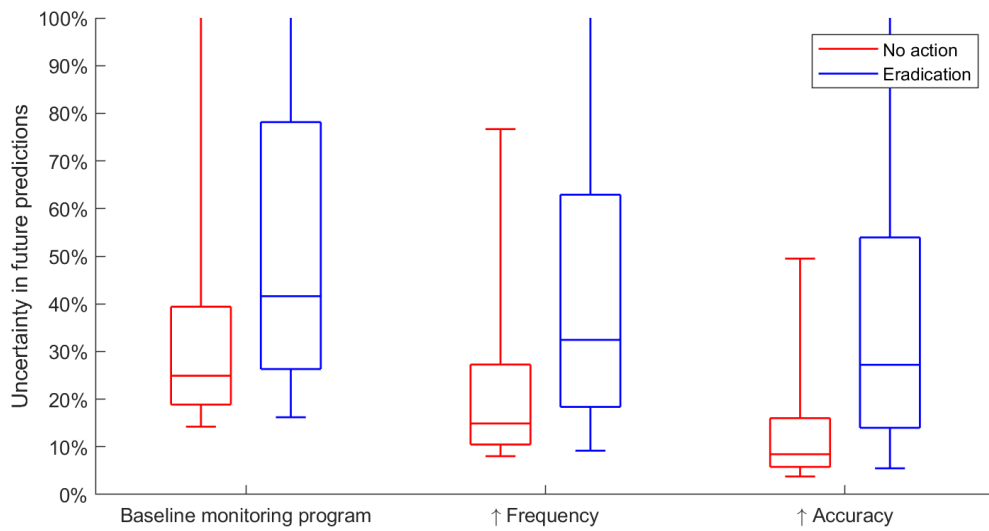749    blue bars in Appendix S6, and the blue and cyan bars in Appendix S7). TL = trophic level.
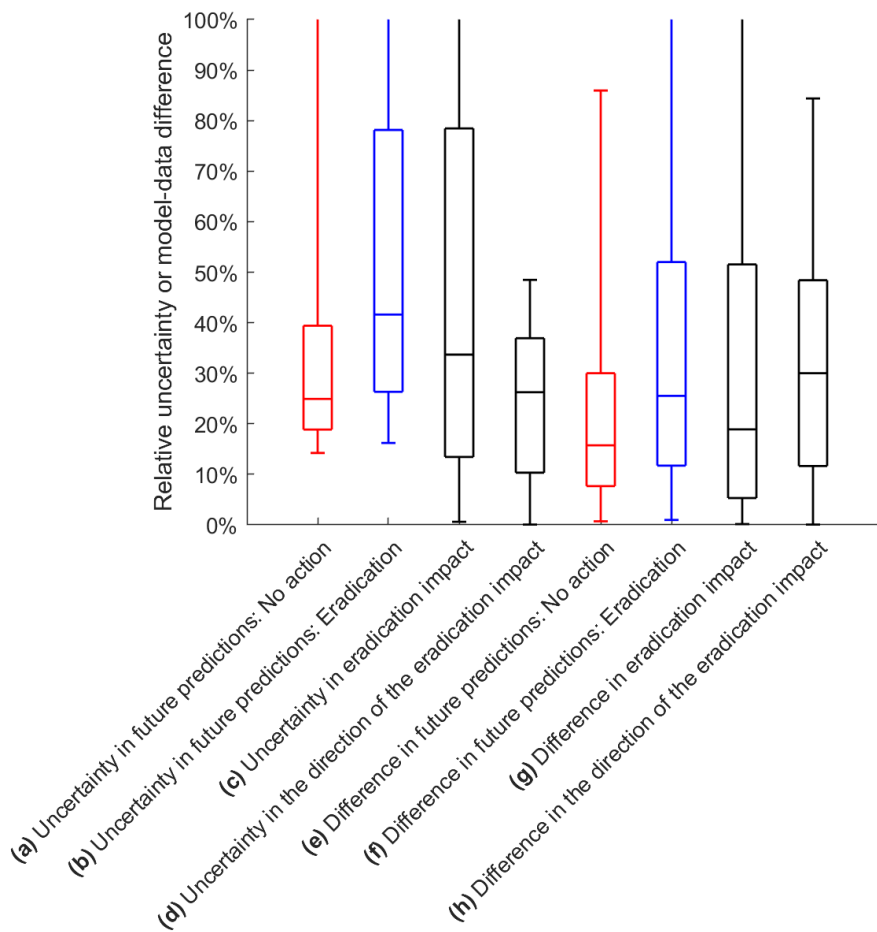
750
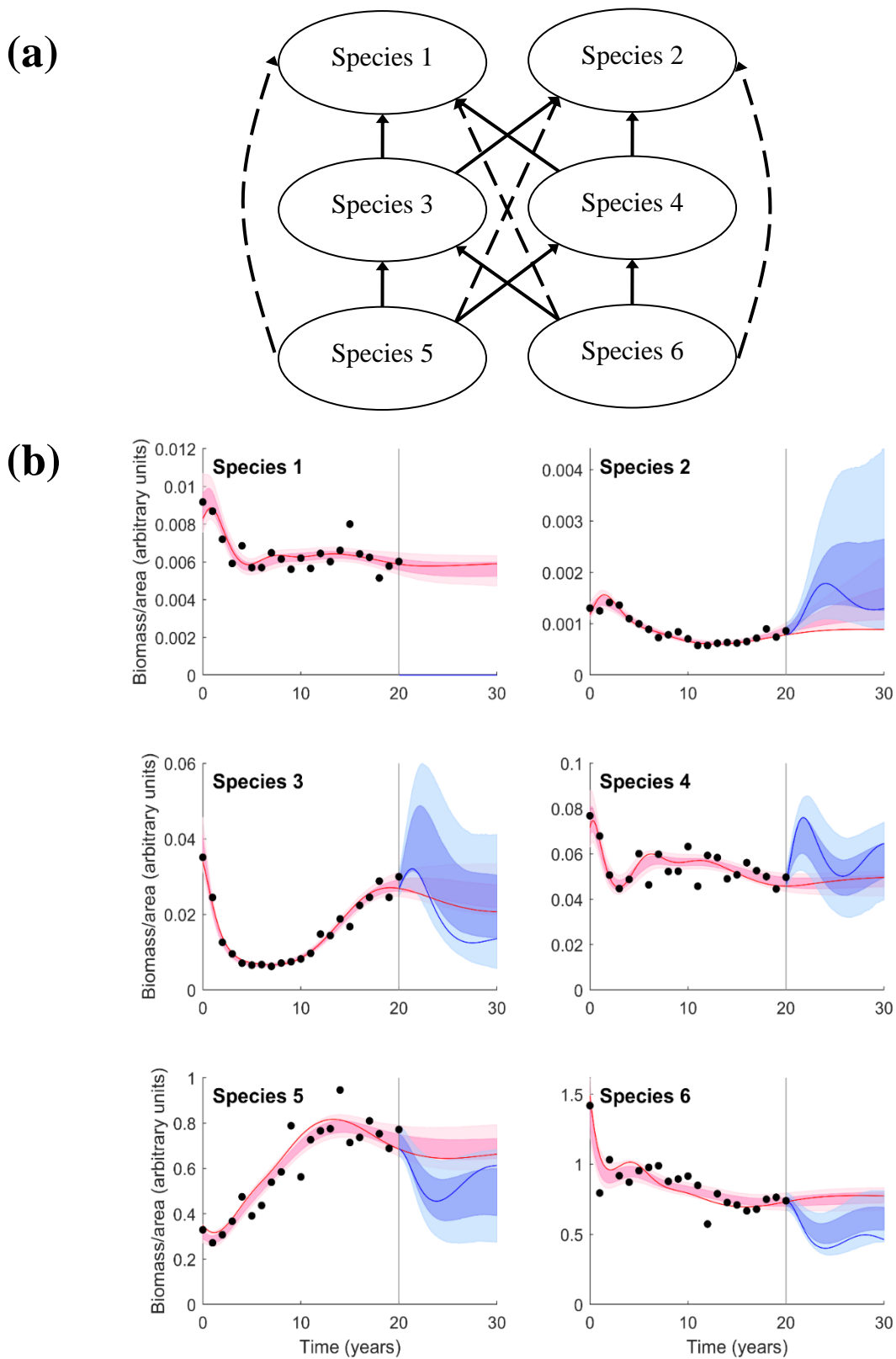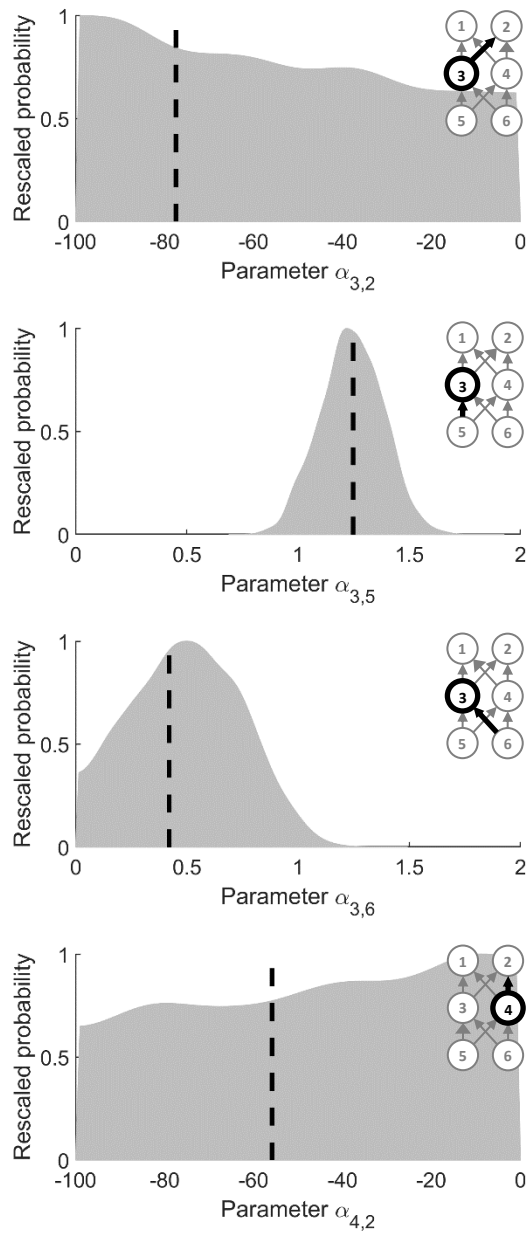
**FIGURES**

Figure 1.

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755                                    Figure 2.
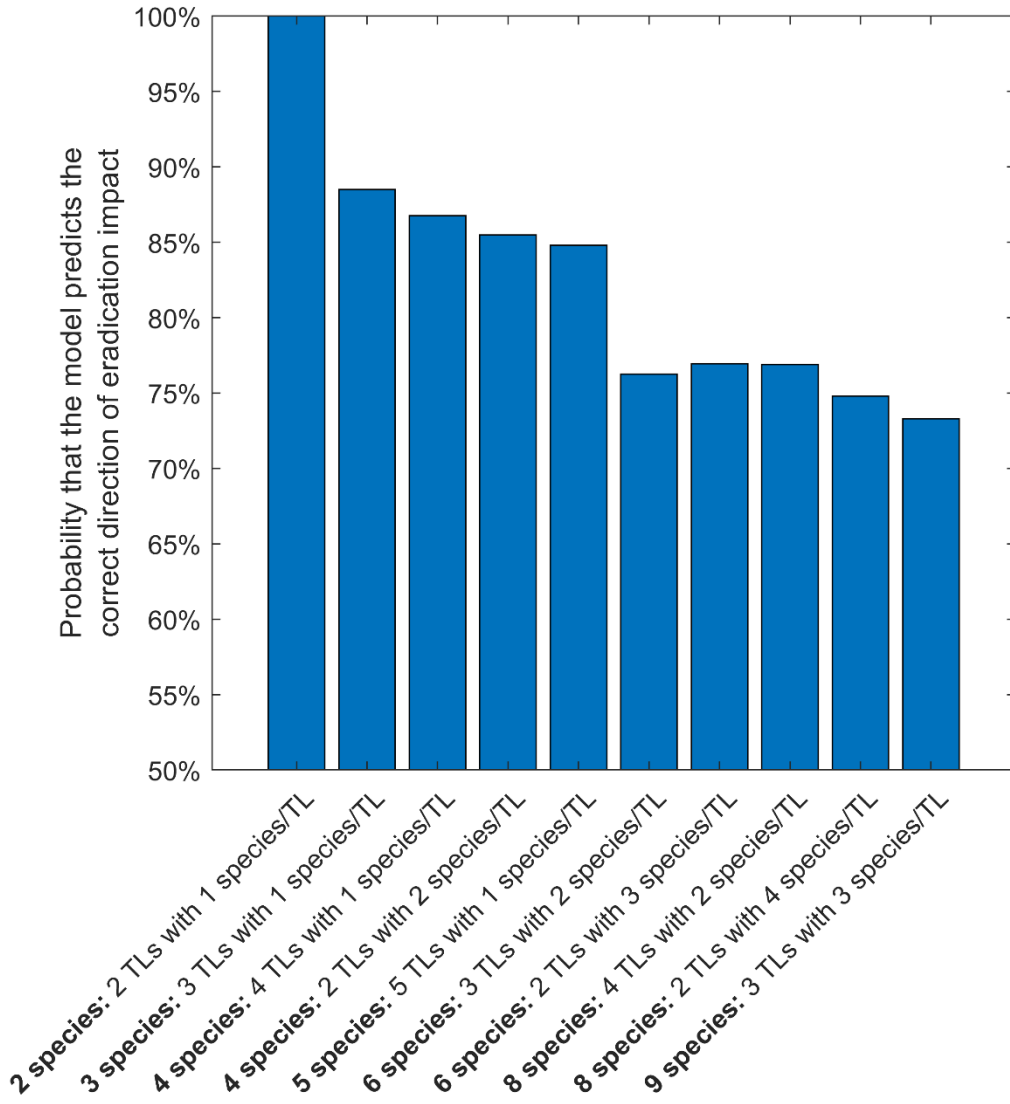
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757                                    Figure 3.



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759                                    Figure 4.

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Figure 5.

**BOXES**

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**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):

$$\text{UFP}_\text{erad} = \frac{\Delta_\text{CI}\left\{ y_\text{model,erad}(t_\text{future}) \right\}}{\text{median}\left\{ y_\text{model,erad}(t_\text{future}) \right\}} \qquad \text{for eradication scenarios, and}$$

$$\text{UFP}_\text{no erad} = \frac{\Delta_\text{CI}\left\{ y_\text{model,no erad}(t_\text{future}) \right\}}{\text{median}\left\{ y_\text{model,no erad}(t_\text{future}) \right\}} \qquad \text{for the "no action" scenario.}$$

2. Uncertainty in eradication impact (UEI):

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

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

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

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

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

$$\text{DFP}_\text{no erad} = \left| \frac{\text{median}\left\{ y_\text{model,no erad}(t_\text{future}) \right\} - y_\text{true,no erad}(t_\text{future})}{y_\text{true,no erad}(t_\text{future})} \right| \qquad \text{for the "no action" scenario.}$$

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

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

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

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

Terminology: $\mathrm{median}\{x\}$ is the median of $x$, $\bar{x}$ is the mean of $x$, and $\Delta_{\mathrm{CI}}\{x\}$ 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. $y_{\mathrm{true,erad}}(t_{\mathrm{future}})$ and $y_{\mathrm{model,erad}}(t_{\mathrm{future}})$ are the true and model-predicted population biomasses, respectively, of a non-eradicated species at some future time $t_{\mathrm{future}}$ 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. $t_{\mathrm{future}} = 30$ years.) Analogously, $y_{\mathrm{true,no\,erad}}(t_{\mathrm{future}})$ and $y_{\mathrm{model,no\,erad}}(t_{\mathrm{future}})$ are the true and model-predicted population biomasses, respectively, of a species at the same future time $t_{\mathrm{future}}$ if no management action is undertaken. Both $y_{\mathrm{true,erad}}(t_{\mathrm{future}})$ and $y_{\mathrm{true,no\,erad}}(t_{\mathrm{future}})$ are

single values, whilst $y_{model,erad}(t_{future})$ and $y_{model,no\ erad}(t_{future})$ 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.

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