

1 **TITLE**

2 Revealing beliefs: using ensemble ecosystem modelling to extrapolate expert beliefs to novel
3 ecological scenarios.

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20

21 SUMMARY

- 22 1. Ecosystem-based management requires predictive models of ecosystem dynamics. There
23 are typically insufficient empirical data available to parameterise these complex models,
24 and so decision-makers commonly rely on beliefs elicited from experts. However, such
25 expert beliefs are necessarily limited because (1) only a small proportion of ecosystem
26 components and dynamics have been observed; (2) uncertainty about ecosystem
27 dynamics can result in contradictory expert judgements; and; (3) elicitation time and
28 resources are limited.
- 29 2. We use an ensemble of dynamic ecosystem models to extrapolate a limited set of stated
30 expert beliefs into a wider range of revealed beliefs about how the ecosystem will respond
31 to perturbations and management. Importantly, the method captures the expert
32 uncertainty and propagates it through to predictions. We demonstrate this process and its
33 potential value by applying it to the conservation of the threatened malleefowl (*Leipoa*
34 *ocellata*) in the Murray mallee ecosystems of southern Australia.
- 35 3. In two workshops, we asked experts to construct a qualitative ecosystem interaction
36 network and to describe their beliefs about how the ecosystem will respond to particular
37 perturbations. We used this information to constrain an ensemble of 10^9 community
38 models, leaving a subset that could reproduce stated expert beliefs. We then interrogated
39 this ensemble of models to reveal experts' implicit beliefs about management scenarios
40 that were not a part of the initial elicitation exercises.
- 41 4. Our method uses straightforward questions to efficiently elicit expert beliefs, and then
42 applies a flexible modelling approach to reveal those experts' beliefs about the dynamics
43 of the entire ecosystem. It allows rapid planning of ecosystem based management
44 informed by expert judgement, and provides a basis for value-of-information analyses and
45 adaptive management.

46 INTRODUCTION

47 Ecological management relies heavily on expert beliefs (Kuhnert *et al.* 2010; Burgman *et al.*
48 2011; Martin *et al.* 2012). Ecological systems are incredibly complex, with thousands of
49 species interacting across space and time (Turchin 2003), and the time and resources
50 available to study them are severely constrained. As a consequence, ecological communities
51 and their dynamics are poorly understood (Lawton 1999; Kuhnert *et al.* 2010). Conservation
52 managers nevertheless need to respond to multiple threats, often before experimental or
53 observational evidence can be systematically collected. Expert beliefs allow managers to
54 rapidly assess which management problems are most important, and which actions will best
55 mitigate their effects (Kuhnert *et al.* 2010; Martin *et al.* 2012).

56 Unfortunately, while expert beliefs can offer decision-makers timely information, they have
57 two key limitations. First, expert beliefs are incomplete, in the sense that they do not
58 systematically describe all the components and dynamics of an ecosystem. Experts have
59 generally only observed a small subset of possible dynamics and by definition cannot have
60 observed novel circumstances (e.g., responses to untested management interventions).
61 Second, expert beliefs are always uncertain. While structured elicitation methods can reduce
62 the magnitude of uncertainty, uncertain beliefs about system dynamics are inevitable
63 (Kuhnert *et al.* 2010; Martin *et al.* 2012; Wintle *et al.* 2013). We stress that these factors are
64 not exclusive to elicited expert beliefs, but they do limit the utility of expert opinion for
65 conservation decision-making. Furthermore, because elicitation is time-consuming and expert
66 experience is limited, the solution is not simply to elicit more information (Kuhnert *et al.*
67 2010).

68 Expert beliefs are particularly limited when managing whole ecosystems. Conservation is
69 increasingly moving from a single-species focus to the management of whole ecosystems
70 (Garrett 1992; Grumbine 1994). This reflects a more expansive definition of conservation

71 value that includes a greater range of biodiversity (Margules & Pressey 2000), the
72 increasingly appreciated economic value of ecosystem processes and functions (Armsworth &
73 Roughgarden 2001), and an awareness of how complex and indirect ecosystem interactions
74 can determine the consequences of conservation actions (Raymond *et al.* 2010). As the
75 components of an ecosystem being considered (its biotic and abiotic factors) increase in
76 number, the number of ecosystem interactions and processes that need to be understood
77 increase nonlinearly. We therefore need a method that can rapidly predict a wide range of
78 ecosystem dynamics on the basis of uncertain and incomplete expert beliefs. This is the
79 primary goal of this paper.

80 At the centre of this method will be an ecosystem model. Most ecosystems can be readily
81 described by a network of interactions among ecosystem elements (Pimm *et al.* 1991). These
82 qualitative models describe direct relationships between important ecosystem components
83 (species, or environmental & anthropogenic drivers) using cause-and-effect connections, but
84 without specifying the magnitude or functional form of the relationship (Levins 1974). A
85 single *qualitative* network can therefore be represented by a very large set of *quantitative*
86 community models. Rather than choose any particular model in this set (e.g., the best-fit to
87 known data), we represent the interaction network by a very large ensemble of models. Most
88 importantly, we ensure that each model in this ensemble can recreate any stated beliefs that
89 we have been able to elicit from experts. The resulting model ensemble can be used to make
90 predictions about any aspect of ecosystem dynamics, in response to any modelled
91 perturbation or management action.

92 We describe and demonstrate this approach for the management of the malleefowl *Leipoa*
93 *ocellata* (Gould 1840), a threatened bird species from Australia's semi-arid and arid zones
94 that has experienced a substantial decline over the last two decades, but for uncertain reasons
95 (Benshemesh 2007; Benshemesh *et al.* 2007). We undertook two workshops to elicit *stated*

96 expert beliefs about the structure and dynamics of mallee ecosystems from a suite of relevant
97 experts. Our method translates these limited and uncertain stated beliefs into a large
98 ensemble of predictive, quantitative ecosystem models. This model ensemble can then be
99 manipulated to answer new questions. The results of these simulations reveal expert beliefs
100 about ecosystem dynamics that are not explicitly stated during the elicitation process. These
101 *revealed* expert beliefs (embodied in the predictions of the model ensemble) can be used to
102 inform management decisions, and guide future research.

103 **MATERIALS AND METHODS**

104 **Expert workshops**

105 Participants at two workshops were chosen to represent a cross-section of expertise on
106 mallee ecosystems, including managers from nongovernmental conservation organisations;
107 government; university researchers; ecological consultants; and conservation volunteers.
108 Remnant mallee is broadly distributed across southern Australia, from New South Wales to
109 Western Australia, but we focused our analyses on the Murray mallee ecosystem (MDD02
110 IBRA subregion) that contains high densities of malleefowl in well-studied populations
111 (Benshemesh 2007). As with any ecosystem, there are a number of competing hypotheses
112 about the drivers of malleefowl decline, which have been variously ascribed to the effects of
113 invasive mammalian predation, herbivore competition, habitat degradation, altered fire
114 regimes and climate change (Benshemesh *et al.* 2007; Bode & Brennan 2011; Garnett 2012;
115 Walsh *et al.* 2012). We sought to include participants who represented a range of perspectives
116 on the relative priority of these threats.

117 The first workshop constructed qualitative ecosystem interaction models. A set of important
118 “ecosystem components” (species, or environmental drivers such as fire and rainfall), were
119 joined by cause-and-effect connections. Connections were drawn if a change in one
120 component was expected to directly cause a change in another component, with the sign of

121 the relationship indicating whether the change in the recipient component will be negative or
122 positive. Only direct interactions were included in the model. For example, if rabbit
123 populations have a positive effect on dingoes through predation, but a potentially negative
124 effect through damage to vegetated habitat, we only included the direct positive interaction,
125 and allowed the model to incorporate the negative effect via links from rabbits to vegetation,
126 and from vegetation to dingoes (Baker *et al.* 2016a). We incorporated structural uncertainty
127 by allowing the experts to define relationships that they believed existed, but were of
128 unknown sign (i.e., they could be either positive or negative), or that they were unsure existed
129 but would be certain of the sign if they did (i.e., they could be zero or positive). A full
130 description of the workshop and the results can be found in *Supplementary Information 1*.

131 The second workshop elicited uncertain information from participants that could be used to
132 constrain the predictions of the qualitative interaction network. In 14 different scenarios, an
133 abiotic or anthropogenic driver from the qualitative model changed by a particular magnitude
134 (e.g., rainfall decreased by 75% for one year), following approximately 10 years of relatively
135 constant ecosystem conditions. We explained that this period of unchanging conditions was to
136 ensure that any large prior perturbations (e.g., a recent fire) were no longer playing a large
137 role in the ecosystem dynamics. Experts were asked to quantitatively describe how a different
138 ecosystem component would respond over the next 5 years, a length of time considered long
139 enough to reveal dynamics over the short- to medium-term. The participants submitted their
140 answers by drawing “envelopes” on a timeseries graph that described their belief and
141 uncertainty about the response (Figure 1). While participants were encouraged to draw
142 envelopes for all scenarios, they were free to not answer questions they felt were beyond
143 their experience or intuition. A full description can be found in *Supplementary Information 2*.

144 When eliciting information from multiple experts, evidence shows that iterative rounds of
145 anonymised feedback between experts (Kuhnert *et al.* 2010) improves the accuracy of

146 estimates (Rowe & Wright 1999). We chose to elicit information from experts independently,
147 in a single round. This allowed us to maximise the number of scenarios we could consider in
148 one workshop, since we are primarily interested in the process of extrapolating from a range
149 of stated beliefs, rather than eliciting the most accurate information.

150 **Ensemble ecosystem modelling**

151 When predicting the future dynamics of a complex, nonlinear system, it is better to base
152 decisions on the ensemble predictions of a large number of plausible models, rather than rely
153 on a single model, even if that single model offers the best fit to the available validation data
154 (Leith 1974). Ensemble prediction is an essential component of modern meteorology and the
155 associated assessment of environmental risks, with the IPCC's multi-model predictions of
156 global climate representing the best-known application of the technique (Stocker 2014). A
157 recent variant of the approach is ensemble ecosystem modelling (EEM; Dexter *et al.* 2012;
158 Gårdmark *et al.* 2013; Bode *et al.* 2015; Hunter *et al.* 2015), which applies the approach to
159 models of ecosystems. Following our two workshops we generated an ensemble of models
160 whose structure matched the beliefs of the first expert workshop, and whose
161 parameterisations were consistent with expert beliefs (see *Supplementary Figure S1* for a
162 schematic overview of the process).

163 For EEM, we define a large ensemble of models with a given qualitative structure (in our case,
164 the interaction network identified in our first workshop). We use a system of Lotka-Volterra
165 (LV) equations, where the amount of a component i in an ecosystem at time t (the abundance
166 or density of a species, the volume of rainfall, etc) is defined as $N_i(t)$. This amount changes
167 according to the component's internal dynamics, and its interactions with other components:

$$168 \quad \frac{dN_i}{dt} = r_i N_i + \sum_{j=1}^c a_{ij} N_i N_j$$

170 where C is the number of components in the ecosystem, r_i is a component's intrinsic growth
171 rate, and a_{ij} are interaction coefficients describing the per-unit effect of component j on each
172 unit of component i . The interaction matrix \mathbf{A} (Figure 2a) contains the elements a_{ij} which
173 match the sign structure of elicited interaction networks (Figure 2b). LV models are designed
174 to describe the dynamics and stability of foodwebs (Pimm *et al.* 1991; Turchin 2003) but can
175 be extended to describe abiotic components. An environmental driver such as rainfall is not
176 affected by any other components of the ecosystem ($a_{ij} = 0$ for $i \neq j$). Its intensity is
177 therefore defined by its stable equilibrium value, determined by the ratio of r_i and α_{ii} .

178 We construct an ensemble of 10^9 different models by choosing random values for growth
179 rates and interaction terms. Growth rates are chosen at random from an inverse distribution
180 (i.e., $1/(r_i + 1) \sim U(0,1)$), allowing them to take any positive value. The magnitudes of the
181 interaction coefficients are chosen from unit uniform distributions ($\alpha_{ij} \sim U(0,1)$), with their
182 signs assigned according to expert beliefs. Latin hypercube sampling can generate random
183 numbers that efficiently sample this high-dimensional parameter space. Although the choice
184 of bounded distributions for the interaction coefficients may seem limiting, any LV system can
185 be rescaled to produce an ecosystem model with parameters within these bounds
186 (*Supplementary Information 3*). In addition, simulations show that model predictions are
187 robust to the distributions from which parameters are chosen (Baker *et al.* 2016b).

188 We then use expert beliefs about ecosystem dynamics to constrain the model ensemble. First,
189 we remove any models from the ensemble that are not "viable"; that is, where not all the
190 species that were listed can persist at equilibrium. To assess viability, we calculate the
191 equilibrium state of the ecosystem, and determine whether all species have positive
192 abundances (Baker *et al.* 2016b). In altered ecosystems, it may not be certain whether species
193 that are currently extant will be able coexist over the medium to long term, and in these

194 circumstances the equilibrium coexistence condition will be inappropriate. For example,
195 malleefowl have coexisted with foxes for approximately 190 years, but malleefowl have a
196 10% probability of becoming extinct in the next 100 years (according to IUCN Red List
197 Criterion E for Vulnerable), with foxes listed as a key threatening process. They may therefore
198 be on a long trajectory towards extinction, and unable to persist alongside foxes. In these
199 latter cases, we could simulate the models for the finite length of observed coexistence (e.g.,
200 190 years), rather than calculate equilibrium abundances. We would then remove any models
201 where at least one species declines below a threshold (e.g., malleefowl fall below 0.1% of their
202 initial abundance). Given that all species eventually become extinct, a finite coexistence time
203 is probably a more realistic constraint on the model ensemble, although it is more
204 computationally demanding.

205 Next, we simulate the dynamics of each model in response to the perturbations (described in
206 the second workshop), using the equilibrium as the initial condition. We compare the
207 predicted changes in species' abundance to the uncertain envelopes drawn by the workshop
208 participants, and penalise any models that disagree with the expert beliefs. We measure the
209 "performance" of each model in the ensemble as shown graphically in Figure 1, by calculating
210 the overlap between a model and the expert beliefs: for every time step the model falls within
211 any expert envelope, its performance increases by a constant amount. Intersecting with an
212 envelope for twice as long yields twice the benefit; intersecting two envelopes provides twice
213 as much benefit as intersecting a single envelope. Under this measure of model performance,
214 we include only the best 5% of models in the ensemble, an approach conceptually similar to
215 Approximate Bayesian Computation (Beaumont 2010). Once the best performing models are
216 identified, we calculate the proportional change in Shannon entropy associated with each
217 model coefficient. This change measures the amount of information imparted to each
218 uncertain coefficient by the set of envelope constraints (*Supplementary Figure S2*).

219 **Analyses**

220 The remaining ensemble of models encapsulates the experts' beliefs – revealed as well as
221 stated – about the dynamics of the mallee ecosystem. We undertake two sets of analyses to
222 illustrate the potential of EEM, and the flexibility of revealed expert opinion.

223 Our first set of analyses illustrates how limited stated expert beliefs can be extrapolated to
224 construct revealed expert beliefs. In our second workshop we asked questions about 14
225 different ecosystem perturbation scenarios (*Supplementary Information 2*). We used EEM to
226 answer three additional perturbation questions about malleefowl populations that were
227 purposely not explored in the workshop: (1) How will malleefowl abundance change in
228 response to a 25% increase in dingo abundance over 5 years? (2) How will malleefowl
229 abundance change in response to a 25% increase in the cat population over 5 years? (3) What
230 will be the effect of additional annual migration of malleefowl into a population, equal to 10%
231 of the equilibrium population, as a consequence of either natural dispersal, or a managed
232 release from captive populations? EEM allows us to extrapolate experts' revealed beliefs
233 regarding these three questions, by simulating the response of each model in the ensemble.
234 We then extract and graph the range of malleefowl population responses, with the ecosystem
235 simulated in weekly timesteps for a 5 year period. This time horizon matched the experts'
236 stated beliefs, and is long enough to reflect the approximate timescale of malleefowl funding
237 (e.g., the Malleefowl Management Committee funding lasted 7 years; the Australian Research
238 Council Linkage grant that funded this work lasted 3 years). We repeat each simulation using
239 both the unconstrained and constrained model ensemble (i.e., the set of models before and
240 after we consider the envelopes), contrasting these simulations to illustrate the value of
241 stated expert beliefs.

242 Our second set of analyses illustrates how EEM can offer management support that is formal
243 and ecosystem-based, but is also rapid and efficient. The malleefowl National Recovery Plan

244 (NRP; Benshemesh 2007) lists six important threats to malleefowl, and we use the model
245 ensemble to predict the impact of mitigating each in turn over 5 years. The key threats of the
246 NRP and the specific details of our model simulations are: (1) *Habitat loss and fragmentation*.
247 We assume that active restoration results in an exogenous 15% increase in suitable habitat
248 (the seedling & vegetation components). (2) *Competition by grazing herbivores*. We model the
249 effects of reducing feral goats by 30% through mustering, and rabbit populations by 30%
250 through baiting. These are reasonable outcomes for ecosystems like the mallee (Parkes *et al.*
251 1996; Cooke 2010). (3) *Predation by introduced foxes*. We assume that effective baiting can
252 reduce fox populations by 95%, in line with best practice in similar ecosystems (Saunders &
253 McLeod 2007). (4) *Predation by introduced cats*. We model the effects of baiting that targets
254 cat populations, reducing them by 85%. Reductions of this magnitude have been previously
255 achieved in non-insular arid and semi-arid ecosystems (Algar & Burrows 2004). (5) *Fire*
256 *intensity and severity*. Both dimensions of fire affect malleefowl negatively, and we model the
257 effects of currently planned management changes to public land in the Murray mallee, which
258 will increase the area burned by fire by at least 50% from current levels. (6) *Disease and*
259 *inbreeding*. We assumed that these two factors act to reduce population growth rates,
260 generally through increased mortality (Keller 2002). Although it is not clear how these threats
261 would be addressed by managers, we assume that the benefit of managing disease and
262 inbreeding will increase the population growth rate by 10%. In each case, we use EEM to
263 simulate the range of consequences for malleefowl abundance. We note, however, that the
264 results will reflect the above assumptions about management effectiveness, which are only
265 based on a limited literature survey, and will vary with location and management actors.

266 **RESULTS**

267 The first workshop generated three different interaction networks that connected similar
268 ecosystem components in slightly different configurations (*Supplementary Information 1*). For

269 the analyses that follow, we analyse the network produced by the first expert group (Figure
270 2). This network connects 14 ecosystem components with 80 direct interactions (in the
271 matrix, we ignore intraspecific interactions and only consider off-diagonal elements). While
272 this creates a complex interaction network (Figure 2b), it is fewer than half of the 182
273 possible direct connections, and the dynamics of many components are therefore only
274 indirectly coupled. The majority (65%) of these direct interactions were qualitatively certain
275 (either definitely positive or definitely negative), with the remainder being either of uncertain
276 existence but known sign (28.8%), or of unknown existence and sign (6.2%).

277 In the second workshop, we were able to elicit 62 beliefs from 13 experts about 14 ecosystem
278 perturbation scenarios (*Supplementary Figure S6*). Every scenario received between 2 and 7
279 different expert beliefs. The average expert was not able or willing to describe their beliefs
280 about most scenarios, or did not have sufficient time (34% of 182 potential beliefs were
281 elicited). While opinions about some scenarios were quite consistent (e.g., all experts believe
282 that cat abundance will increase during fox baiting), others differed markedly (e.g., fox
283 abundance could increase or decrease during overgrazing).

284 On the basis of the network structure, the viability constraint and the elicited envelopes, we
285 were able to reduce the original set of 10^9 LV models down to an ensemble of approximately
286 10^5 models. The substantial constraints offered by the experts' beliefs (to <0.01%) were
287 heterogeneously distributed across the unknown interaction parameters. The proportional
288 change in Shannon entropy associated with each coefficient indicates that, while three-
289 quarters of the coefficients only experienced a small reduction (<20%) in entropy, the
290 coefficients associated with malleefowl, vegetation, predators and grazers experienced a large
291 (>80%) reduction (*Supplementary Figure S2*). This concentration of information on a few
292 parameters reflects the focus of the elicitation scenarios on the interactions between
293 malleefowl and predators, and between malleefowl, vegetation and herbivores. Despite the

294 reduction in the size of the model ensemble and the increase in information, the retained
295 models are enormously variable. Although all are based on the same interaction network, and
296 can replicate all stated expert beliefs, their parameterisations are vastly different
297 (*Supplementary Figure S3*), and they therefore represent alternative hypotheses about what
298 ecosystem dynamics could generate the stated expert beliefs. Models with as many as 16
299 structural differences were able to recreate the same dynamics. For example, about half of the
300 models retained in the ensemble considered fire to have a positive effect on cat abundance;
301 the other half considered it to have a negative effect. As a result of this variability, the
302 correlation structure of the retained parameterisations is indistinguishable from purely
303 random data, suggesting that the models remaining in the ensemble are dynamically very
304 different from one another. The predictions of these retained models are similarly variable –
305 species' responses to perturbations are generally of ambiguous sign. Thus some of the
306 ensemble predicts increases in a given component, while others predict decreases. The
307 magnitude of the changes also varies by more than an order of magnitude (e.g., some models
308 predict a 10% increase in abundance, some predict a 100% increase).

309 Despite this variability, the first set of analyses shows that constraining the model ensemble
310 with expert opinions reveals additional and informative expert beliefs. Figure 3 shows the
311 change in malleefowl abundance that would result from an increase in dingo abundance; an
312 increase in cat abundance; and increased malleefowl immigration. The grey envelopes show
313 that the set of viable models is incredibly variable before they are constrained by the stated
314 expert beliefs. This is even true when, as is the case for increased immigration (Figure 3c), the
315 changes have a direct and positive impact on the malleefowl population. The blue envelopes
316 show the revealed expert opinions, which are much narrower than the original set of possible
317 trajectories. An increase in dingoes to the ecosystem will have an uncertain effect on
318 malleefowl abundances, ranging from a decrease of 20% to an increase of 30% (Figure 3a).
319 This range of revealed expert beliefs matches the uncertainty surrounding the effect of top-

320 predators on prey species in the literature, particularly in Australia's semi-arid rangelands
321 (Allen *et al.* 2013). Our other revealed expert beliefs show more confidence in the effects of
322 ecosystem perturbations: if cat populations increase, malleefowl will most likely decline (a 0–
323 15% decrease; Figure 3b); if malleefowl immigration increases, malleefowl populations will
324 also experience a small increase (0–20%; Figure 3c).

325 Our second set of analyses uses EEM to calculate experts' revealed beliefs about the benefits
326 of management actions that affect each NRP threat (Figure 4). The most striking result of
327 these revealed beliefs is their uncertainty. While each management action could benefit
328 malleefowl populations, the combined effect of direct and indirect ecosystem interactions
329 could also result in a perverse negative outcome. Both habitat management and grazing
330 management appear as likely to damage malleefowl populations as they are to benefit them.
331 The revealed beliefs are less ambiguous about the effects of managing cat predation (likely
332 positive) or an increase in fire intensity/frequency (likely negative), but the 95% EEM
333 confidence intervals for both interventions still overlap zero. The sole exception to this
334 qualitative uncertainty is the revealed belief about the positive effects of addressing
335 inbreeding and disease in the populations. Interestingly, the management of foxes is arguably
336 the most commonly undertaken action to benefit malleefowl, and could have the largest
337 positive or the largest negative effects on malleefowl abundance.

338 **DISCUSSION**

339 EEM allows limited stated expert beliefs to be extrapolated, revealing implicit beliefs about
340 the broader dynamics of an ecosystem and its response to perturbations. Our application of
341 these methods to malleefowl conservation produced a quantitative decision-support tool after
342 two workshops and a relatively small amount of computational analysis. The method allows
343 beliefs to be elicited at minimal cost, and therefore reduces burden on experts. It translated
344 expert beliefs into a quantitative tool that we used to rapidly estimate the expected benefit

345 and uncertainty of actions aimed at mitigating each threat. The total cost of the two
346 workshops required to do this was approximately \$10,000 (2015 Australian dollars).

347 The EEM process is computationally demanding but conceptually straightforward, and it
348 offers decision-makers three primary benefits. First, EEM reveals a much broader range of
349 expert beliefs about their ecosystems, without requiring them to answer an enormous
350 number of questions. This process provides a logical and internally-consistent method of
351 extending expertise to new and more complex problems. Once a few expert beliefs have been
352 elicited, the decision-maker can ask an enormous number and range of questions at
353 essentially no cost: expertise on tap. This provides substantial efficiencies: when eliciting
354 information from 13 experts about a 14-component interaction network, there are 2,548
355 single-perturbation questions that can be asked. Our half-day workshop answered 63 of these
356 questions; a desktop computer use EEM to answer the remainder in less than one minute (the
357 model ensemble took approximately one day to create, but this can be pre-computed).

358 Second, we elicited stated beliefs about ecosystem dynamics by asking experts to construct
359 interaction networks, and to draw uncertain envelopes describing the response of different
360 components to perturbations. These forms of elicitation are simple and intuitive since both
361 interaction networks and uncertain timeseries data are common elements of undergraduate
362 biology degrees, ecological reports, and journal articles. In contrast, the alternative method of
363 eliciting information about dynamic networks is to ask individual questions about the model
364 parameters (Kuhnert *et al.* 2009), for example, about per-capita growth rates, interaction
365 coefficients, or conditional probabilities for Bayesian networks (Martin *et al.* 2012). In
366 contrast to our timeseries questions, these require difficult and numerically-precise
367 statements about implicit and unobservable ecological quantities, and impose a high
368 elicitation burden on experts. EEM allows these more difficult quantities to be computed from
369 the envelopes.

370 Third, EEM can consider questions that are difficult or impossible to engage with using
371 standard expert elicitation. Expert observations and beliefs concentrate on a subset of
372 ecosystem components and dynamics: easily-observed species, recent perturbations, previous
373 management actions, and contemporary environmental and climatic conditions. If we accept
374 that ecosystems are in part driven by the deterministic interactions of a connected system
375 with consistent dynamics, then observed phenomena can offer insights into unobserved
376 events. Thus EEM allows us to extend stated expert beliefs to a much broader set of
377 predictions about ecosystem dynamics and management actions. We expect that such
378 predictions will be uncertain, and accept that they will often be ambiguous (e.g., Figure 4).

379 Our analyses demonstrate that an EEM approach, constrained by a reasonable number of
380 stated expert beliefs, can provide useful predictions about the performance of different
381 management actions (Figure 4). For example, the beliefs elicited from experts indicate that
382 managing diseases or cat abundance are very likely to improve malleefowl populations, and
383 that an increase in fire intensity and severity is likely to produce a negative impact. In
384 contrast, the most commonly undertaken management action on behalf of malleefowl – fox
385 baiting – has an entirely uncertain impact, although it could potentially offer the greatest
386 benefits. These results concur with the deep uncertainty highlighted by previous modelling
387 and empirical studies on fox predation (Walsh *et al.* 2012) and fire dynamics (Benshemesh
388 2007). They reveal that, despite more than a century of conservation research on malleefowl
389 (Mellor 1911), we remain deeply uncertain about the impact of management actions on this
390 threatened species.

391 Even when constrained by the expert-elicited timeseries, the forecasts made by our model
392 ensemble are enormously variable, to the point of being qualitatively uncertain (Figure 3, 4).
393 This variation is partly the result of over-fitting – we are estimating 108 free parameters
394 using timeseries data on 14 perturbations – but this does not necessarily mean that our

395 models are too complicated. The interaction network is complex (Figure 2), and so our models
396 must also be complex if they aim to offer a fulsome mechanistic explanation of how ecosystem
397 structure drives dynamics. Explicitly modelling the complexity of the interaction network is
398 valuable for two reasons. First, management outcomes are often heavily affected by indirect
399 interactions with the broader network (Raymond *et al.* 2010; Dexter *et al.* 2012; Buckley &
400 Han 2014). Our ensemble offers a range of models that reproduce the stated expert beliefs,
401 but offer competing hypotheses about which direct and indirect interactions produced them
402 (*Supplementary Figure S3*). These competing hypotheses make different predictions about
403 future dynamics, and this is partly responsible for the highly variable predictions. Second, in
404 addition to forecasting future dynamics, a central goal of this method is to extrapolate from a
405 limited set of stated beliefs, to create revealed beliefs about the broader ecosystem. A more
406 parsimonious model might offer more accurate predictions about the future dynamics of
407 observed ecosystem components, but it would be unable to extrapolate across the ecosystem.
408 Although we do not detail the required steps here, a model ensemble can answer a much
409 wider range of questions. To give a few examples for malleefowl conservation:

- 410 • The mallee contains threatened species other than malleefowl. Will management actions
411 that benefit malleefowl (e.g., particular fire regimes) detrimentally affect the viability of
412 other species (Driscoll *et al.* 2016)? EEM models the future dynamics of multiple species
413 simultaneously, identifying conservation trade-offs.
- 414 • The varying amount of uncertainty in different future predictions (Figure 3 & 4), and
415 model parameters (*Supplementary Figure S2 & S3*) could be used to undertake a value-of-
416 information analysis (Runge *et al.* 2011), focusing research on reducing uncertainties that
417 most strongly hamper sound decision making and consequent improvements in outcomes.
- 418 • Monitoring data – particularly when gathered in response to perturbations or
419 management interventions – can be used with EEM in the same manner as the stated

420 expert beliefs: to further constrain the model ensemble. Applied iteratively with VOI,
421 managers can use the EEM method to undertake short-term active adaptive management
422 (Benshemesh & Bode 2011), that explicitly considers ecosystem interactions.

423 Ecosystem dynamics are often modelled with sets of ordinary differential equations (Turchin
424 2003), and there are reasons to believe that our formulation may offer robust insights into
425 future dynamics. However, two factors in particular should be kept in mind when interpreting
426 the results: ecosystems are unlikely to be perfectly represented by the functional forms of the
427 Lotka-Volterra equations, and ecosystem dynamics are stochastic and spatial. This is
428 particularly true in arid environments, where stochastic and spatially-explicit models of
429 environmental covariates are generally considered essential (Cadenhead *et al.* 2015). Despite
430 these problematic assumptions, there are reasons to hope that EEM can offer useful
431 predictions. First, we asked our experts to describe dynamics in the vicinity of the ecosystems'
432 equilibrium point, and over short time periods (5 years). In this set of states, the precise
433 functional form of the models (e.g., Lotka-Volterra) is much less important, since many
434 different functional forms share the same dynamics (Raymond *et al.* 2010; Melbourne-
435 Thomas *et al.* 2012). It may be appropriate to further account for this issue by eliciting and
436 predicting dynamics over shorter time periods; by discounting the performance of models in
437 the more distant future; by constructing model ensembles using more than one functional
438 form; or by constructing models with alternative plausible interaction structures. Although
439 we elicited three different interaction networks, their structure was very similar, as experts
440 were allowed to move freely between the groups. This non-independence makes the three
441 networks unsuitable for a structural sensitivity analysis. Second, although we model a
442 stochastic ecosystem with an ensemble of deterministic models, the technique of ensemble
443 modelling was adopted in meteorology precisely because it reduces inaccuracies caused by
444 sub-grid-scale stochasticity and unmeasured variation in initial conditions (Leith 1974). We
445 attempt to further reduce the influence of stochasticity by modelling ecosystem components

446 with large abundances, as demographic stochasticity will have a smaller effect on the
447 dynamics of large numbers of individuals (Gustafsson & Sternad 2013).

448 EEM is part of a field of ideas for making predictions about complex, uncertain, nonlinear
449 systems. The approach is heavily based on ideas from qualitative modelling (QM) in both its
450 loop-analysis (Levins 1974; Dambacher *et al.* 2003) and computational forms (Raymond *et al.*
451 2010; Dexter *et al.* 2012; Melbourne-Thomas *et al.* 2012). These QM approaches will offer
452 complementary or superior perspectives to EEM for many problems, particularly when
453 smaller interaction networks are sufficient (loop QM), or when elicited constraints and
454 predictions concern short-term and small-magnitude perturbations (computational QM).
455 “Sloppy modelling” analyses, which are increasingly influential in physics and systems
456 biology, are another parallel set of ideas. This approach can offer deeper insights into the
457 most important components and parameters in the system, rather than simply predicting the
458 consequences of perturbations (Gutenkunst *et al.* 2007). Finally, model ensembles have
459 proven invaluable in geophysical fluid dynamics (Leith 1974) and complex and nonlinear
460 statistical modelling (Beaumont 2010). Both the motivation and justification for this approach
461 to prediction can be found in reviews of these fields, as can a range of extensions that will add
462 strength and robustness to our approach.

463 Resource and time constraints force conservation science to make important management
464 decisions on the basis of limited information. Expert beliefs provide essential guidance in the
465 face of such logistical constraints, but the elicited information is limited and uncertain.
466 Conservation is also increasingly focused on making decisions that consider the highly
467 interconnected nature of ecosystems, and the indirect and counter-intuitive dynamics that
468 these connections create. Ecologists can construct interaction networks that outline such
469 dynamics, but these cannot make the necessary quantitative predictions. Ensemble Ecosystem
470 Modelling offers one solution to both these problems. By merging expert beliefs and

471 qualitative modelling, EEM can systematically extrapolate a limited number of stated expert
472 beliefs into a broader range of revealed implicit beliefs. Not only does this make expert-
473 supported decisions more efficient and quantitative, it also provides a framework for
474 extending them into unobserved future scenarios and untested management actions. The
475 method therefore allows management options to be quickly and defensibly prioritised, and
476 does so using a framework that explicitly takes ecosystem interactions and indirect effects
477 into account. EEM therefore helps to address three key obstacles to effective conservation
478 action: complex ecosystem interactions, limited information, and limited resources.

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487 **DATA ACCESSIBILITY**

488 This manuscript does not contain any data.

489 **AUTHOR CONTRIBUTIONS**

490 All authors conceived the ideas, held the workshops, interpreted the results, and drafted the
491 manuscript. MB and CB developed the methods. MB undertook the analysis. All authors gave
492 final approval for publication.

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601

602 **SUPPORTING INFORMATION**

603 Additional supporting information can be found online in the supporting information tab for
604 this article:

605 **Supplementary Information 1:** Methods for eliciting interaction networks.

606 **Supplementary Information 2:** Methods for eliciting ecosystem dynamics.

607 **Supplementary Information 3:** Rescaling methods for Lotka-Volterra systems.

608 **Supplementary Table S1:** Participants and affiliations at the first workshop.

609 **Supplementary Table S2:** Participants and affiliations at the second workshop.

610 **Supplementary Figure S1:** Schematic overview of belief modelling process.

611 **Supplementary Figure S2:** Information contained in stated expert beliefs.

612 **Supplementary Figure S3:** Similarity of satisfactory ecosystem models.

613 **Supplementary Figure S4:** Example ecosystem scenario shown to workshop participants.

614 **Supplementary Figure S5:** Example ecosystem scenario with expert opinion superimposed.

615 **Supplementary Figure S6:** All ecosystem scenarios with all stated expert beliefs

616 superimposed.

617

618 **FIGURE LEGENDS**

619 **Figure 1:** Envelope method for eliciting expert beliefs and constraining the model ensemble.
620 Grey shaded area indicates a 3 year period of overgrazing of mallee habitat, where native and
621 introduced herbivore abundance was 200% of its long-term average. Experts were asked to
622 draw envelopes that described their belief in the dynamics of the fox populations (y-axis)
623 during this window. Two experts chose to answer this question; the coloured envelopes
624 indicates their uncertain beliefs. The lines indicate the predictions of 4 viable models in the
625 ensemble. One (green) is able to entirely replicate at least one expert belief; two (blue lines)
626 are able to partly replicate the beliefs; one (black line) is unable to recreate them at all.

627 **Figure 2:** (a) Sign-structured interaction matrix elicited during the first workshop. Elements
628 of the matrix indicate the qualitative direct impact that an increase in the component on the
629 row would have on a component on the column. For example, an increase in rabbit abundance
630 (row 11) will have a direct positive impact (+1) on fox abundance (column 5). +1 indicates a
631 definite positive direct effect; -1 indicates a definite negative; 0 indicate a definite zero direct
632 impact; +2 indicates either positive or zero; -2 indicates either negative or zero; 3 indicates
633 either positive or negative. All diagonal values are negative to indicate density-dependence.
634 (b) Graphical description of the interaction network shown above. This is the format in which

635 information on the structure of the interaction network was elicited from experts. Arrows
636 indicate direct interactions with the sign indicated at the mid-point of each arrow.

637 **Figure 3.** Change in malleefowl abundance predicted by the unconstrained model ensemble
638 (“unc”: grey lines, with grey region enclosing 95% of the ensemble predictions) and expert
639 belief-constrained ensemble (“con”: blue lines and 95% region), following a perturbation
640 made to another ecosystem component (black line). (a) Malleefowl abundance changes during
641 a 25% increase in dingo abundance over 5 years. (b) Malleefowl abundance changes during a
642 25% increase in cat abundance over 5 years. (c) Malleefowl abundance changes during
643 increased malleefowl immigration equal to 10% of the equilibrium population annually.

644 **Figure 4:** Predictions of the model ensemble when management interventions of reasonable
645 intensity are applied to the 6 main threats in the malleefowl National Recovery Plan. Upper 6
646 plots show the relative change in malleefowl populations through time when each action is
647 taken (shown in title), for a random sample of 200 models from the constrained ensemble.
648 The lower plot synopsis the relative change of malleefowl population after 5 years (95%
649 confidence intervals of final populations, with the mean shown by a circle).

650 **Supplementary Figure S1:** Schematic overview of how Ensemble Ecosystem Modelling
651 (EEM) can be used to translate stated expert beliefs into revealed beliefs. The left-hand
652 column describes the steps taken, the right hand column indicates where the information
653 from each step is sourced from, the central column provides a diagrammatic flow-chart of the
654 process.

655 Step 1 is to elicit a **qualitative ecosystem interaction network** from experts, which lists
656 important ecosystem components and their direct cause-and-effect relationships. Step 2 is to
657 transform this qualitative model into a large ensemble of **initial quantitative Lotka-Volterra**
658 **(LV) models**, indicated by the black squares. Each model comprises a set of equations
659 corresponding to the components of the interaction network, with the parameters chosen at
660 random. Step 3 is to elicit a set of **stated belief envelopes** from experts, which describe their
661 beliefs about how a particular ecosystem component will respond to a perturbation in a
662 different ecosystem component. The degree of uncertainty surrounding this belief is indicated
663 by the width of the envelopes. Step 4 is to use these stated belief envelopes to retain only
664 those models in the ensemble that most closely recreate expert beliefs about system dynamics
665 (green arrows), discarding any models which do not replicate these beliefs (red arrows). The
666 envelopes therefore act as a filter or constraint on the model ensemble. The **remaining**
667 **quantitative LV models** represent an ensemble of quantitative ecosystem models that

668 concur with both sets of expert beliefs: the interaction structure of the qualitative networks,
669 and the dynamic responses of the different envelopes. Step 5 is to interrogate the remaining
670 ensemble of models, to produce implicit **revealed beliefs** about the ecosystem. These will
671 include its response to perturbations, the relative priority of different management options,
672 and the relative uncertainty surrounding different ecosystem processes and components.

673 **Supplementary Figure S2:** Information contained in the stated expert beliefs, expressed by
674 the change in Shannon entropy H of the interaction coefficients. To calculate H , we collect the
675 values of each coefficient into 20 bins of width 0.05, where n_i is the number of coefficients
676 between $0.05(i - 1)$ and $0.05i$. We then normalise these bins so that $p_i = n_i / \sum n_i$, and use
677 Shannon's definition:

$$678 \quad H = - \sum_{i=1}^{20} p_i \log_2 p_i.$$

679 The initial information associated with each coefficient (selected from a uniform distribution)
680 is approximately $H = 4.32$. Once the expert beliefs are used to constrain the model ensemble,
681 we are left with a subset of coefficient values with a lower or equal entropy. The decrease in
682 entropy reflects the decrease in uncertainty caused by the constraints. Upper panel shows the
683 proportional change in entropy for the distributions of each parameter in the interaction
684 matrix (Figure 2a). A small proportion of coefficients have gained a large amount of
685 information from the constraint process, while the majority have experienced a small
686 improvement. The two lower panels detail two examples from the upper panel. Red bars
687 indicate the original coefficient values in the unconstrained model ensemble (uniformly
688 distributed); grey bars indicate the distribution in the constrained model. In the lower left
689 hand panel (the direct effect of rainfall on fires), the constraints indicate that the coefficient is
690 likely to be closer to one than zero. In the lower right hand panel (the direct effect of dingoes
691 on kangaroo abundance), the model constraints offered little information, and the coefficient
692 distribution remains relatively unchanged.

693 **Supplementary Figure S3:** (a–c) Scatter plots of interaction coefficient parameters for three
694 randomly selected pairs of models that satisfy all stated expert beliefs. Blue markers
695 represent the value of interaction parameter (e.g., $\alpha_{4,6}$ measures the per-capita / per-capita
696 effect of dingoes on cats) in the two models. Red circles highlight structurally uncertain
697 parameters. Note that the raw parameter correlation will appear artificially high because the
698 signs of the different parameters are generally known. We therefore report the correlation of
699 the absolute value of the parameters. (d) Scatter plot of the correlation results for 500

700 randomly selected model pairs. The black markers indicate Pearson's correlation coefficient
701 (y-axis), and the significance of the correlation observed (x-axis). Green shaded area indicates
702 the null expectation if these parameters were simply random numbers selected from a
703 uniform distribution $U(0,1)$. The two sets of correlation statistics are indistinguishable,
704 indicating that the retained models in the ensemble are highly variable, and do not offer a
705 single description of the ecosystem dynamics.

706 **Supplementary Figure S4:** An example ecosystem scenario, as used in the second workshop.
707 Modelled dynamics correspond to a model based on Figure 2. Scenarios are defined by two
708 factors: (1) the dynamics of a particular ecosystem species, shown by coloured lines. Each line
709 offers an alternative response of the species to the perturbation. (2) The dynamics of a
710 particular ecosystem driver, shown by coloured bars. In this case the driver is rainfall. In
711 response to a perturbation in the driver, the abundance of the species may change. Experts
712 were asked to choose between these alternatives, or to offer another option.

713 **Supplementary Figure S5:** As in *Supplementary Figure S4*, the bars indicate the change in an
714 ecosystem driver. However in this figure the grey envelope indicates the opinions of an expert
715 from the workshop.

716 **Supplementary Figure S6:** The aggregated results of the expert answers to each
717 perturbation scenario (indicated in the title). Each expert has an assigned colour, and these
718 are transparently overlaid on the timeseries to assess where experts agree and disagree on
719 the likely consequences of an ecosystem perturbation. Note that since not all experts
720 answered all questions, each scenario has a different number of responses.

721

722