30. Predicting Malleefowl dynamics using decision theory and qualitative ecosystem modelling

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Abstract

Conservation management often needs to answer urgent questions without knowing everything about how an ecosystem operates. Rather than ask for more time or resources to resolve this uncertainty, the field of decision theory gives managers the tools to make informed decisions using the current understanding of the ecosystem and its dynamics. Australia's mallee ecosystems and the Malleefowl (*Leipoa ocellata*) are both threatened and poorly understood. Although experts can readily describe the qualitative interactions between the ecosystem components, and although they have decades of observations and understanding of the ecosystem to draw on, it is not clear how to convert this information into the types of data required by decision theory tools. In this paper, I describe an approach that can potentially convert expert opinions into explicit and quantitative decision theory models. Building on cause-and-effect model frameworks developed by Parks Victoria, a series of expert elicitation exercises is used to describe both the model structure and parameterisation of an ecosystem model, without experts having to directly engage with the mathematical components of such models. As well as an outline of the methods, I provide preliminary results from two sets of expert workshops aimed at understanding and managing the threatened Malleefowl.

Introduction

Arid and semi-arid ecosystems contain some of the continent's most fragile and threatened species and communities (Millennium Ecosystem Assessment 2005, UNEP 2006). Australian is the globe's driest inhabited continent, with 70% of the land area being either arid or semi-arid, and this landscape contains some of the nation's most recognisable, unique, and threatened biodiversity (Stafford-Smith 1995). Australia has experienced one of the fastest rates of vertebrate extinction in modern history (Short and Smith 1994, Cardillo and Bromham 2001), and the biodiversity impacts of European colonisation have fallen disproportionately on low rainfall regions (Burbidge and McKenzie 1989, Stafford-Smith 1995, Sattler and Creighton 2002, McKenzie *et al.* 2007, Morton *et al.* 2011). In the coming years, the effects of anthropogenic climate change will be acutely felt in semi-arid and arid zones, and on these regions' uniquely adapted biodiversity. Without rapid and extensive management intervention, high post-colonial extinction rates will therefore continue.

The mallee is a fascinating and widely-appreciated semi-arid ecosystem in Australia, and one that has historically experienced severe environmental degradation and habitat loss. The Malleefowl (*Leipoa ocellata*) is one of the many species from the mallee whose populations have declined drastically since the arrival of European colonists, and whose range has contracted substantially (Benshemesh 1992, 1994, 2007, Parsons 2008). The species is now listed as threatened in every state that it occurs, and regarded as Vulnerable nationally. The Malleefowl is threatened by a range of factors (Woinarski and Recher 1997, Benshemesh 2007, Bode and Brennan 2011). These include inappropriate fire regimes, habitat loss and degradation, over-grazing, introduced species, and climate change that have also contributed to the decline or extinction of many other native species, including most medium sized (i.e., "critical weight range") vertebrates that are, like the Malleefowl, the preferred prey of invasive predators (Johnson 2006, Chisholm and Taylor 2007, 2010).

While the declining condition of Malleefowl and their fragile ecosystem is undeniable, realising this fact does not explain how these declines can be arrested and reversed. Despite more than one hundred years of research into the conservation of the species (Mellor 1911, North 1917, Frith 1959, Priddel and Wheeler 2004, Parsons 2009, Wheeler and Priddel 2009, Bode and Brennan 2011), it is not clear what management interventions will reverse their decline. For example, recent debates over more than two decades of Malleefowl monitoring data across Australia have questioned the conventional wisdoms that foxes (*Vulpes vulpes*) are a key threat to the species, and that poison baiting can improve the populations' viability (Benshemesh *et al.* 2007, Bode and Brennan 2011, Garnett 2012, Walsh *et al.* 2012). This uncertainty is not surprising – dryland ecosystems like the mallee are intrinsically difficult to understand due to their complex ecosystem structure, and their high spatial and temporal variability. These uncertainties will be compounded by the unpredictable results of future climate change. Managers in the mallee are therefore faced with a difficult situation – immediate action is required if further losses are to be averted, however, existing uncertainties obscure the choice of the most appropriate intervention.

Conservation management, a "crisis discipline", constantly confronts iterations of this difficult question: how should urgent action be taken with incomplete information? The field itself – an amalgam of practical management theory and ecological science – embodies the tension between a scientific desire to understand complex systems through further research, and practical need to act quickly, while funding and time remain. Pervasive uncertainty can no longer be seen as an excuse for delaying action until certainty is reached (Walters 1986, McLain and Lee 1996, Benshemesh and Bode 2011), since delays bring threatened species closer to extinction (Grantham *et al.* 2009), and may simply represent an unconscious desire to avoid facing invidious questions (Martin *et al.* 2012b). Conservation is therefore increasingly turning to quantitative decision theory to resolve the conflict. Decision theory approaches explicitly characterise and quantify the nature of key uncertainties, and also the benefits expected from either additional research or immediate action. As a consequence, decision theory allows managers to balance these competing factors, and thus to make decisions that maximise the "average" outcome. Among many other examples, decision theory has been used to make recommendations about the sustainable harvesting of wild species (Reed 1979, Hyberg 1987); the translocation of threatened species (Tenhumberg *et al.* 2004); the construction of predator exclusion fences (Bode and Wintle 2010, Bode *et al.* 2012); the eradication of invasive species from islands (Brooke *et al.* 2007, Bode *et al.* 2013) and their suppression in mainland landscapes (Baker and Bode 2013); and the effective reintroduction of captive-bred individuals from highly-threatened species (Runge *et al.* 2011).

Each of the decision theory examples listed in the previous paragraph is centrally concerned with decision-making under uncertainty. However, in every case the ecological system being managed is either relatively simple, or has been simplified for the purpose of analysis. This is true of decision theory as a broader field, perhaps because many of its applications have been interested in the management of single species– principally natural resource management questions concerning forestry, fisheries and game species management. A few notable exceptions exist in marine conservation and fisheries (Kellner *et al.* 2011, Hastings *et al.* 2014). However, these are often for only a handful (i.e., less than five) interacting species, and the techniques used are unlikely to be feasible in larger systems. Managing ecosystems that include dozens of key species (and therefore inevitably contain large amounts of uncertainty) remains an open question in both decision theory and conservation management.

The main limitation is not necessarily the ability to create ecosystem models that reflect the number of species in the real system, and the complex network of their interactions. Ecologists and conservation managers can readily and rapidly construct qualitative models that describe how the components in the system are connected. For example, Parks Victoria have created "Conceptual Ecosystem Models" for every one of Victoria's ecosystems, including the Mallee (White 2012). Although these ecosystem descriptions are not necessarily new (they are derived from food web theory), their use by management agencies is unusual. Constructing, publishing and using these ecosystem models are a considerable advance in the formal representation of complex ecological systems by managers. By explicitly describing the workings and dynamics of the ecosystem, these models provide a mechanism for translating individual understanding into shared institutional knowledge, and offer a foundation and language for discussion, debates and decisions.

However, despite their strengths, these tools have limited scope as predictive tools, because they are currently only qualitative. We call them qualitative because they describe what eats what, what competes with what, which species support each other, and which compete with each other. They are not quantitative because they do not specify how much of species i is eaten by species j. The main limitation is the inability to turn these qualitative models into quantitative models that will make precise predictions about the effects of an intervention. Qualitative models are useful tools for formalising our understanding of a system, but they cannot predict the consequences of actions. With only a qualitative understanding of a system, a particular conservation intervention (e.g. fox baiting or fencing) could have either positive or negative consequences on a species of interest (Levins 1974, Dambacher *et al.* 2003, Raymond *et al.* 2010).

Although there are tools available that can turn qualitative models into predictive quantitative models, the process requires a large amount of data. Unfortunately, while the ecological community has a very large amount of data available to it, much of it resides in the experiences of individual ecologists, land managers and natural historians. These data are inaccessible to most quantitative modellers because they are difficult to convert into specific numbers – growth rates, interaction strengths etc. Modellers have attempted to resolve this issue by asking ecosystem experts to estimate the numerical value of these parameters, but the process is difficult and painful because the relevant experts do not understand the system in these terms (Dexter *et al.* 2012). In this paper, I describe a novel method for collecting such data on mallee ecosystems, and converting it into quantitative model parameters. Essentially, I propose methods for turning experience and data into numbers, predictions and decision theory models. The method draws on the understanding and experiences of experts on mallee ecosystems and Malleefowl using a two-step elicitation process. This process first involves the creation of qualitative ecosystem models of cause-and-effect, and then involves eliciting information that can be used to parameterise these models using indirect methods. I finish by illustrating how the elicited data will be used to parameterise the models.

Methods and Results

Our method contains four steps: two elicitation workshops, and a parameterisation analysis. The purpose of the first elicitation workshop is to construct a qualitative model of mallee ecosystem dynamics. This model describes the key components of the mallee ecosystem, and indicates how they are connected through a series of directed, cause-and-effect linkages. The second elicitation workshop is aimed at creating quantitative information about the dynamics of the linked components of the mallee ecosystem, by mining the experiences of the participants. The final step is to join the results of these two workshops into a quantitative ecosystem model. The qualitative model of Malleefowl dynamics that was elicited in the first workshop will be formulated as a mechanistic mathematical model of the mallee ecosystem. Then, the information on dynamics elicited in the second workshop will be used to constrain the enormous uncertainty present in this quantitative model through a series of training steps. The actions involved in each of these steps is described in detail below.

Step 1: Eliciting the cause-and-effect models

To make predictions about the consequences of interventions into the mallee ecosystem, a quantitative model of that ecosystem needs to be formulated. The first step in this process is to describe the broad, qualitative structure of that model. The result is known as a “cause-and-effect” model, or a “qualitative model”. It describes the major components of the ecosystem, and how they are connected. These connections are not described in a very precise way; instead, each component is linked to other components using connections that are only described very broadly: predation, competition, etc. This information is much less precise than quantitative relationships, but it is much easier to elicit from experts in that ecosystem.

A workshop was convened in October 2012 at the University of Melbourne that comprised 22 individuals with expertise on mallee ecosystems, with a particular emphasis on the Malleefowl species itself. Participants included expert ecologists, managers from the state and federal government, university researchers, and stakeholders from the Malleefowl conservation community. These individuals were asked to list and describe all of the important elements in the mallee ecosystem, particularly those that are likely to have a direct or indirect effect on the Malleefowl species. These components included the key species (e.g. Malleefowl, foxes, goats, kangaroos), threats (e.g. fire, habitat loss), environmental variables (e.g. rainfall, temperature), and ecological processes (e.g. dispersal).

After each group enumerated the primary components of the ecosystem, participants were asked to join these components via cause-and-effect linkages. Essentially, they were asked to identify which of the components had a direct effect on any other component, and then to describe whether that effect was positive or negative. Direct effects exclude impacts that are mediated by another component (these are indirect effects). For example, foxes have a direct effect on Malleefowl, because individual foxes consume individual Malleefowl. If a room contained nothing but a fox and a Malleefowl, predation could still occur. In contrast, the effect of rabbits on Malleefowl will be indirect. Rabbits could impact Malleefowl by either providing resources that increase the population of foxes in the environment, or by damaging the quality of the vegetation that Malleefowl require for resources and shelter. These are both indirect effects (and would therefore not be included in our model), since their impacts on Malleefowl require the presence of another component. Returning to our room: if a rabbit and a Malleefowl were placed inside it alone, there would be no negative effects on the Malleefowl.

Once all these direct cause-and-effect linkages were identified, the component lists were translated into a qualitative model of the mallee ecosystem, with a focus on the Malleefowl (Figure 1). Diagrams of the model were returned to and discussed within the group to verify that it captured participants' beliefs about cause-and-effect, and to add in any remaining interactions not captured. These qualitative models are useful goals and products in their own right. The process of constructing them helps to formalise and capture beliefs about how ecosystems operate, and how their different components impact key management objectives (e.g. Malleefowl abundances). Moreover, explicitly capturing these beliefs in an easily communicated format (a cause-and-effect network), can help stakeholders understand each other's beliefs about the ecosystem, and identify precisely where they differ.

These cause-and-effect models are also an important foundational step towards the goal of making quantitative predictions, and thereby applying decision theory to the problem of Malleefowl management. As mentioned in the introduction, because they have extensive and complicated indirect interaction networks, cause-and-effect models cannot predict precisely what the effect of a given action will be, until the connections themselves are defined more precisely and quantitatively. To move towards this goal, following the workshop, the qualitative model shown in Figure 1 was converted into an equivalent quantitative form. Specifically, the qualitative model was translated into a sign-structured interaction matrix (Table 1). Then, the network nodes and interactions were expressed as a deterministic series of coupled differential equations of Lotka-Volterra form (May 1972):

$$\frac{dN_i}{dt} = \left[r_i + \sum_{j=1}^{S} \frac{\alpha_{ji} N_j}{K_i} \right] N_i$$

(Equation 1)

where N_i is the size of the population of species i, K_i is the carrying capacity of the environment for species i, r_i is the intrinsic growth rate of species i, α_{ji} is the per-capita effect of species j on species i, and S is the total number of species in the model (encapsulated in Table 1). The role of the ecosystem model described by the workshop was to constrain the matrix of interaction terms α_{ji}. Specifically, if the workshop participants did not connect nodes 2 and 3 directly (e.g. where 2 indicates Malleefowl and 3 indicates rabbits), then they were implying that $\alpha_{23} = \alpha_{32} = 0$. In contrast, if they drew an arrow with a negative sign from node 2 to node 1 (e.g. where 2 indicates Malleefowl and 1 indicates foxes), they were implying that $\alpha_{21} > 0$ and $\alpha_{12} < 0$. As a consequence, the interaction network described by the participants can therefore be considered equivalent to a sign-specified Lotka-Volterra interaction matrix (see Figure 2 for a simple example). The consequence is that there is a mechanism through which the dynamics of the ecosystem can be predicted using the model in Equation 1, and the specifications of the elicited interaction network (Figure 1, Table 1).

Table 1. Interaction matrix describing the direction and connection between ecosystem components shown in Figure 1. This table is equivalent to both the conceptual model in the Figure, and to the Lotka-Volterra systems used to generate the ecosystem dynamics in Figure 3 and Figure 4.

	1. Rain	2. Temp	3. Fire	4. Dingoes	5. Foxes	6. Cats	7. Varanids	8. Raptors	9. Goats	10. Kangaroos	11. Rabbits	12. Seedlings	13. Vegetation	14. Malleefowl
1. Rainfall	-1	0	-1	0	0	0	0	0	1	0	0	1	1	1
2. Temp	0	-1	1	0	0	0	0	0	0	0	0	1	1	2
3. Fire	0	0	-1	1	1	1	1	1	-1	-1	-1	-1	-1	-1
4. Dingos	0	0	0	-1	-1	-1	-1	0	-1	-1	-1	0	0	-1
5. Foxes	0	0	0	0	-1	-1	-1	0	-1	-1	-1	0	0	-1
6. Cats	0	0	0	0	0	-1	-1	0	0	0	-1	0	0	-1
7. Varanids	0	0	0	0	0	0	-1	0	0	0	-1	0	0	-1
8. Raptors	0	0	0	0	-1	-1	-1	-1	0	0	-1	0	0	-1
9. Goats	0	0	0	1	1	0	0	0	-1	0	0	-1	-1	0
10. Kangar	0	0	0	1	2	0	0	1	0	-1	0	-1	-1	0
11. Rabbits	0	0	0	1	1	1	1	1	0	0	-1	-1	-1	0
12. Seedlg	0	0	1	0	0	0	0	0	1	1	1	-1	1	1
13. Veg^n	0	0	1	-1	-1	-1	-1	-1	1	1	1	1	-1	1
14. MalleeF	0	0	0	0	1	1	1	1	0	0	0	0	0	-1

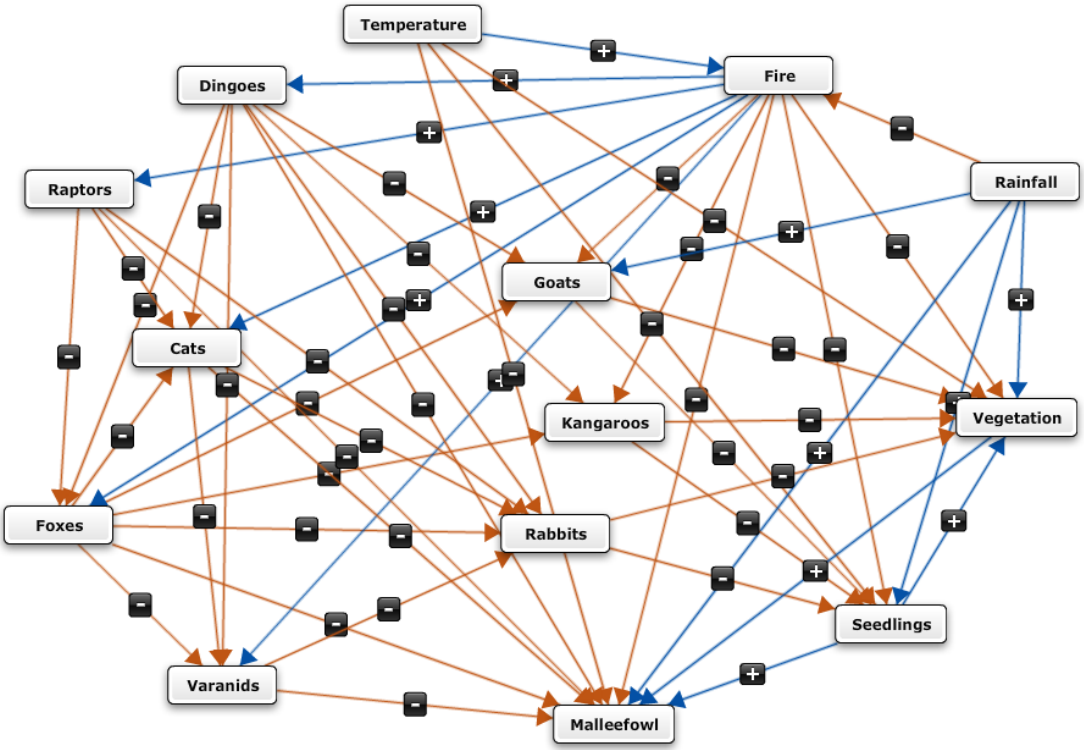
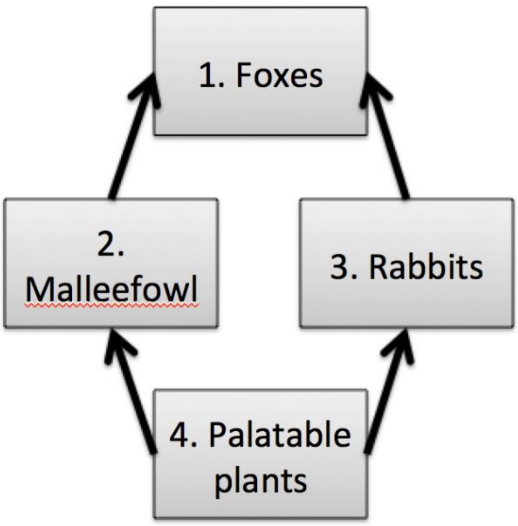


Figure 1. Conceptual cause-and-effect model of the mallee ecosystem devised in the first workshop. Each labelled node refers to a key ecosystem component considered important by the workshop group. Arrows indicate the direct cause-and-effect connections between the nodes, with the signs and colours (red is negative; blue is positive) indicating whether those connections had a positive or negative effect on the population at the arrow-end of the connecting line. Many negative effects have symmetrical positive effects in the opposite direction (e.g. predation is negative for the prey and positive for the predator). These are not shown here, although they can be seen in Table 1, which is equivalent to this model.



$$\alpha = \begin{bmatrix} - & - & - & 0 \\ + & - & 0 & - \\ + & 0 & - & - \\ 0 & + & + & - \end{bmatrix}$$

Figure 2. Example conceptual model of a four-node ecosystem (left). The Lotka-Volterra interaction matrix corresponding to the conceptual model (right).

Step 2: Eliciting information about the mallee ecosystem dynamics

Models are only as good as the information that goes into them. The purpose of the second workshop was therefore to gather together a set of mallee ecosystem and Malleefowl experts to help train these models for the mallee ecosystem. To this end, 18 participants gathered together at Dubbo Zoo in October 2014 from a range of stakeholder groups. Once again this included expert research ecologists, Malleefowl conservation volunteers, and managers from the state and federal government. These experts were chosen because they had observed Malleefowl and the mallee ecosystem for a long period of time, not because they had particular quantitative skills. As a result, no attempt was made to elicit a priori numerical data from this group. Instead, a structured elicitation process was undertaken where participants were separately asked to choose between a range of options, each of which represented the consequences of a particular set of quantitative assumptions. Through a series of questions and discussions, the quantitative beliefs of the group were indirectly revealed, without participants being required to explicitly express those beliefs in a quantitative form.

Each of the participants was given a series of timeseries graphs that illustrated the response of a hypothetical mallee ecosystem to a particular disturbance (see Figure 3 for an example). These timeseries were called “ecosystem scenarios”. Each ecosystem scenario is defined by only two factors. The first is the dynamics of one particular ecosystem species, shown by coloured lines, the second is the dynamics of a particular ecosystem driver, shown by coloured bars. “Mallee ecosystem” meant a local region made up of approximately 10,000 hectares of mallee habitat that was suitable for Malleefowl, similar to that found in north-western Victoria (i.e. “Murray Mallee”). The habitat quality in the location is not necessarily pristine, but it is still predominantly intact and healthy mallee.

The first part of the timeseries shown in each scenario (the far left hand side) represented the initial conditions present in the area for the ecosystem component. In Figure 3, the chosen component was Malleefowl, but different scenarios involved other ecosystem components as well, chosen from the ecosystem model. These initial conditions represented a “normal year” in the mallee. In this case, normal meant that there hadn’t been any serious events (e.g. fires, droughts, floods, locust outbreaks) for more than five years. The abundance of all the components of the ecosystem are therefore around their normal levels during the initial phase, which we represent as a value of 100% (see the y-axis).

After one year (i.e. at $t = 1$), a perturbation impacts the system. This can be seen by the immediate change in the previously constant bars. In Figure 3 this change was the increase in the amount of rainfall in the first month of the second year (the first year begins at $t = 0$), that continues through until the end of that first year. It is assumed that that there are no other exogenous changes occurring in the system (i.e. that any other changes that occur are the direct or indirect result of this change).

In response to this perturbation, the abundance of the species may also change (although it may not). The scenarios proposed a series of six different hypothetical ways in which the particular ecosystem component could respond (note that this number may vary slightly between scenarios). These different responses represent different descriptions of the underlying ecosystem dynamics, any of which may be true. They were chosen to represent a wide variety of possible outcomes, including populations that increased, decreased, oscillated and were unaffected by the perturbation in the ecosystem driver. As stated earlier, there are no other exogenous perturbations occurring during this timeseries, although the other components of the system are changing, but are not shown.

The task of the workshop participants was to choose which one of the six scenarios accurately represented their personal prediction about how the ecosystem would respond to the perturbation. In each scenario, the participants were asked to consider the scenario, and then to pause and consider (1) The component of the ecosystem that is responding to the perturbation, (2) The role played by that component in the ecosystem, (3) The direction of the response to the perturbation (e.g. increase, no change, cyclic), (4) The magnitude of the response (e.g. 50% increase, doubling in abundance) and (5) The speed with which the species responds to the perturbation (e.g. immediate, or delayed). Once these factors had been considered, the participant was asked to classify each possible outcome as either possible or impossible, or whether they could not be certain. Possible motivations for considering a particular dynamic possible were that the participant may have observed this outcome first hand. Alternatively, they may have heard about this outcome from someone else who observed it themselves. Finally, it is possible that they consider it plausible because it agreed with their understanding of the ecosystem.

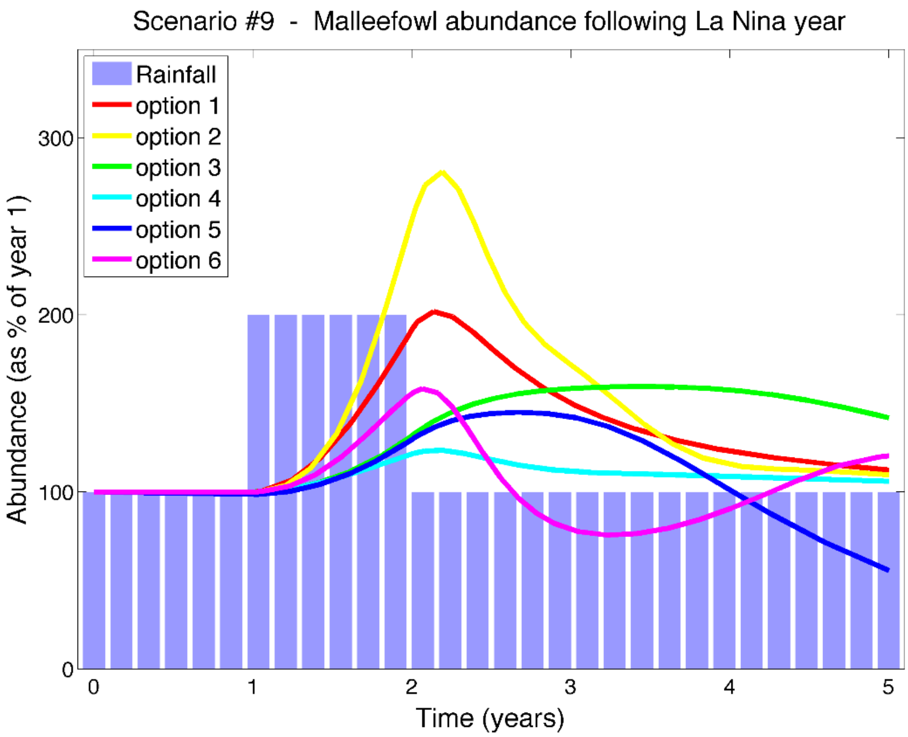


Figure 3. An example ecosystem scenario, as used in the second workshop. Modelled dynamics correspond to Figure 1 and Equation 1. Scenarios are defined by two factors: (1) the dynamics of a particular ecosystem species, shown by coloured lines. Each line offers an alternative response of the species to the perturbation. (2) The dynamics of a particular ecosystem driver, shown by coloured bars. In this case the driver is rainfall. In response to a perturbation in the driver, the abundance of the species may change. Participants were asked to choose between these alternatives, or to offer another option.

The participants were then asked to report their beliefs about each outcome, briefly explaining why they had come to that conclusion. Finally, they were asked to draw their belief about the dynamics onto the graph, indicating how they thought the ecosystem component would respond (their best guess), and also their level of uncertainty around that best guess, drawn using an uncertainty envelope (Figure 4). If they believed that one of the six proposed dynamics was an accurate reflection of their belief, they were asked to expand an uncertainty envelope around that best guess to indicate how unsure they were of what the true dynamics would be. This envelope represented plausible bounds, rather than confidence intervals, and so it was assumed to imply nothing specific about the shape of the participant's belief distribution (i.e. it did not imply that dynamics toward the middle of this envelope were proposed as being more probable than dynamics which were toward the periphery of the envelope).

Figure 4 shows the beliefs of one participant about how Malleefowl populations (defined by all individuals older than 3 months) would respond through time to a 100% increase (i.e. a doubling) of the average rainfall for a single year. The grey envelope described a broad range of responses that the participant thought were within the bounds of possibility. The workshop generated 75 such results, indicating the responses of 14 participants to 15 scenarios, involving four perturbations on six different species (note that not all participants were able to respond to all the scenarios in the time allotted during the workshop). The perturbations were an increase in rainfall for a single year; an intense fox baiting program, a two year period of intense overgrazing, and a severe fire that impacted more than half of the habitat. The responding species were Malleefowl, palatable vegetation, cats, rabbits, kangaroos, and foxes.

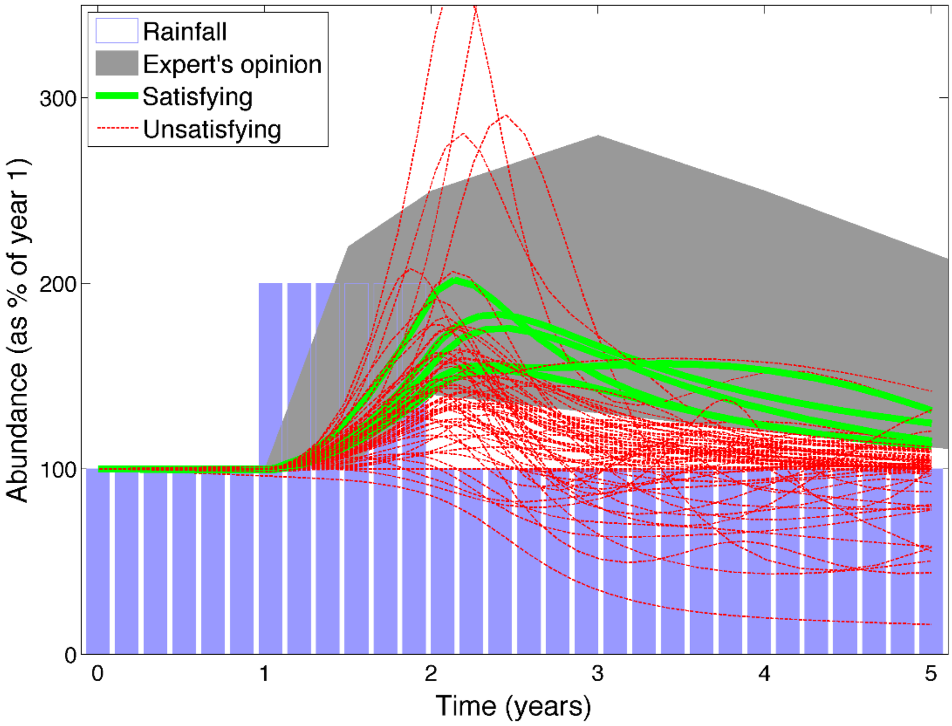


Figure 4. As in Figure 3, the bars indicate the change in an ecosystem driver in the model shown in Figure 1 and Equation 1. However in this figure the grey envelope indicates the opinions of an expert from the workshop. The lines represent predictions of random ecosystems generated by the modelling framework. Green lines correspond to five randomly generated models (the predictions of these five models are shown in green) that agree with the expert opinion. Red lines (that fall outside the envelope) correspond to 50 different randomly generated models that do not agree with the expert, and which would therefore be discarded from further consideration.

Step 3: Parameterising the ecosystem models using the dynamical information

The information elicited from each of these two workshops are interdependent – they concern the same ecosystem and species. The data contained in both was gathered with the purpose of constraining our understanding, and narrowing our predictions about mallee ecosystem dynamics. Our uncertainty about the dynamics of the mallee can be thought of as a very large set of models, which vary in (a) their structure, and (b) their parameterisation. We're initially faced with an enormous number of models, any of which could be true. If this number of models is reduced, our uncertainty about the dynamics of the system is reduced also. The goal of the two workshops is to reduce our uncertainty by removing models from consideration in two different ways.

The first workshop described the key functional components of the complex mallee ecosystem, with a particular focus on identifying those components that would have the greatest impact on Malleefowl populations. It then connected those components that were directly interdependent. Defining the cause-and-effect relationships in an ecosystem dramatically narrows our uncertainty about mallee dynamics. It does this in two ways. First, by identifying a group of approximately 20 important species, functional groups and drivers from an ecosystem that contains many more. Second, by identifying which of those important components interact, and which do not. This latter step is a considerable specification of the system – a dynamical system of 20 components could be described by an effectively infinite number of different cause-and-effect models (each component i could be joined to each component j by either a positive value, a negative value or zero, giving 3,400 options. There are vastly more of these than there are atoms in the observable universe!). From among this vast number of options, the first workshop highlighted a very small subset as being in keeping with our ecological understanding of the mallee.

Even though this structural description of the system reduces the number of potential ecosystem models, an unlimited number of potential ecosystem models still remains. Random number generation can be used to generate any number of these models as follows. Equation 1 can completely describe the dynamics of a system of S species, if $S(S+1)$ parameters are specified. For example, to model the ecosystem shown in Figure 2, Equation 1 needs a specification of 20 different parameters (Table 2; note that the population abundances Ni are variables and not parameters since they will change through time). An ecosystem model can be specified simply by choosing random values for these 20 different parameters. As long as the values are chosen from an unbounded probability density function (e.g. a one-tailed normal distribution, or a lognormal distribution), any ecosystem that can be described by Equation 1 can be randomly generated (in practice, the probability density function from which these values are chosen will influence the relative probability of choosing any particular ecosystem model).

Table 2. Parameters used in the Lotka-Volterra equivalent of the conceptual model shown in Figure 1.

Parameter symbol	Parameter interpretation (all effect parameters are per-capita *i*, per-capita *j*)
r_1	The growth rate of foxes
r_2	The growth rate of Malleefowl
r_3	The growth rate of rabbits
r_4	The growth rate of palatable plants
α_{11}	The effect of foxes on foxes (density dependence, and therefore negative)
α_{12}	The effect of foxes on Malleefowl (predation, and therefore negative)
α_{13}	The effect of foxes on rabbits (predation, and therefore negative)
α_{14}	The effect of foxes on palatable plants (no effect, and therefore zero)
α_{21}	The effect of Malleefowl on foxes (preyed upon, and therefore positive)
α_{22}	The effect of Malleefowl on Malleefowl (density dependence, and therefore negative)
α_{23}	The effect of Malleefowl on rabbits (no effect, and therefore zero)
α_{24}	The effect of Malleefowl on palatable plants (herbivory, and therefore negative)
α_{31}	The effect of rabbits on foxes (preyed upon, and therefore positive)
α_{32}	The effect of rabbits on Malleefowl (no effect, and therefore zero)
α_{33}	The effect of rabbits on rabbits (density dependence, and therefore negative)
α_{34}	The effect of rabbits on palatable plants (herbivory, and therefore negative)
α_{41}	The effect of palatable plants on foxes (no direct effect, and therefore negative)
α_{42}	The effect of palatable plants on Malleefowl (potentially consumed and used for reproduction, and therefore negative)
α_{43}	The effect of palatable plants on rabbits (consumed, and therefore positive)
α_{44}	The effect of palatable plants on palatable plants (density dependence, and therefore negative)
N_1	The population density of foxes
N_2	The population density of Malleefowl
N_3	The population density of rabbits
N_4	The population density of palatable plants

Most of these randomly generated models will be incorrect, even though they match the structure of the mallee ecosystem. The purpose of the second workshop was to provide a method for identifying and discarding incorrect ecosystem models. The envelopes described by the experts for each scenario can be directly compared to the output of one of our ecosystem models. When a model is randomly generated, the envelopes allow us to consider whether that model satisfies the opinions of our different experts. If it does not, then it is removed from consideration. If it does, then it is saved into a pool of satisfying models, where it will await comparison with the next envelope. If enough different envelopes are applied, that pool will only contain models of the mallee ecosystem that can recreate a wide range of plausible mallee ecosystem dynamics.

Figure 4 illustrates this process for one of the envelopes created during the workshop, by a single expert. The grey region captures the uncertain beliefs of one particular expert about the response of Malleefowl to a year of higher-than-average rain. The different lines illustrate the predictions of 50 different ecosystem models (Equation 1), parameterised in accordance with the cause-and-effect model structure. Most of these different ecosystem models do not agree with the expert's opinion (the red dashed lines), and are therefore discarded from further consideration. However, five of the options considered did fit entirely within the expert's envelope (the solid green lines). These models would then be returned to the plausible set for further consideration.

Discussion and future directions

The results shown in this paper are only the partial outputs of two workshops. In their entirety, the first workshop constructed three ecosystem models, while the second workshop produced 75 envelopes. However, while very preliminary, these results do demonstrate that the two forms of data are not incompatible (Figure 4). The construction of the ecosystem models, and their comparison with the expert information remains incomplete at the time of this writing because both steps are computationally very time-consuming. The methods described here are extensions of ideas first devised by Richard Levins in the 1970s (Levins 1974), but which remained beyond the scope of computational tools until only the last decade (Raymond *et al.* 2010). Therefore, expanding them to multiple ecosystem models and multiple expert opinions will involve entry into novel scientific waters.

As well as offering useful tools for the management of both Malleefowl and mallee ecosystems, these methods raise a number of interesting conceptual issues and offer new analytic perspectives from which to consider them. Parameterising the expert-derived ecosystem models with the expert-derived dynamical envelopes demands a large degree of consistency between two very different expert representations of the ecosystem. The first is a cause-and-effect model of the ecosystem, similar to a food web. The second is a partial description of the ecosystem dynamics' response to exogenous perturbations. This method therefore offers an interesting and quite novel integration of the two fields.

Finally, by performing the elicitation of both models and envelopes multiple times, the method is also testing the consistency of different descriptions and understandings of how the ecosystem operates. The degree to which these different understandings align is an interesting question, since consistency among experts is currently a matter of some debate and importance in applied ecology and conservation management (Kuhnert *et al.* 2010, Burgman *et al.* 2011, Martin *et al.* 2012a). Furthermore, given that there will inevitably be some degree of disagreement between the experts, it will be interesting to see whether a single quantitative model of the ecosystem will nevertheless be able to satisfy all, or a large proportion of experts.

As described in the introduction, conservation management involves the difficult process of making urgent decisions under uncertainty. Qualitative descriptions of ecosystem structure are readily available, as illustrated by this project's ability to elicit three different ecosystem models in a week-long workshop, and by Parks Victoria's creation of ecosystem models for all 16 of the state's natural ecosystem groups. The dynamical envelopes elicited in the second workshop also represent readily available information on ecosystems. The fact that it was possible to elicit 75 different time-series predictions from a group of 14 participants in approximately three hours attests to the large amount of latent information held by experts in land management, research and natural history. It also illustrates how this approach, which emphasises simple graphical descriptions of different ecological scenarios, represents a much less painful form of expert elicitation (painful for both the experts and the elicitors) than asking them to numerically estimate parameters. This is despite the fact that both methods are providing essentially the same information. The approach described in this paper therefore has the potential to play an important role in future ecosystem management if the results prove interesting – even more so if they prove useful.

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