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Predicting the ecosystem-wide impacts of eradication with limited information using a qualitative modelling approach.



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ABSTRACT

Conservation-motivated eradications may cause unexpected perverse effects, and these undesirable consequences can be difficult to predict due to the paucity of information on species interactions. A probabilistic qualitative approach, which does not require extensive model parameterization, is becoming increasingly accepted and applied to conservation scenarios when information is limited. However, recent work has criticized this approach on philosophical grounds and proposed an alternative non-probabilistic Boolean analysis method. which circumvents the philosophical difficulties. There is a need for exploring the ability of this novel approach for informing conservation decisions. To do so, we applied the first real-world test of the non-probabilistic Boolean approach using a case study of management of Felis catus (feral cat) and Rattus rattus (black rat) on Christmas Island. We also applied the probabilistic approach as a contrast. Our modeling results showed that the probabilistic approach generated ambiguous outcomes, making it impractical to draw management recommendations. In contrast, the non-probabilistic Boolean approach revealed interpretable rules governing species responses, suggesting that while cat management alone is a risky strategy, the risk of negative effects of cat management on native species can be reduced by the addition of rat management. Thus, given limited resources, in combination with cat management it is prudent to prioritize rat management efforts in the habitats of potentially impacted native species of high concern and value. We conclude that the Boolean approach can be very useful when little information is available to model an ecological system and that it provides a way of identifying the potential risks and benefits of management strategies, enabling better informed conservation decision-making in the face of limited knowledge.

1. Introduction

Conservation-motivated eradications have proved effective in ameliorating impacts on the environment (Howald et al., 2007; Nogales et al., 2004; Ratcliffe et al., 2010), however, because of the complex indirect feedbacks between species in an ecosystem, unexpected outcomes can also occur (Bergstrom et al., 2009; Rayner et al., 2007). Invasive species can integrate into an invaded ecosystem, and consequently some invaders can play a dual role in an ecosystem, negatively impacting some native species while assuming important, otherwise unfulfilled, ecological functions (Schlaepfer et al., 2011; Zavaleta et al., 2001). Elimination of invasive species does not therefore guarantee ecosystem benefits, but can instead cause adverse indirect effects to native species (e.g. through trophic cascades)

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(Bergstrom et al., 2009; Oppel et al., 2014; Rayner et al., 2007). In order for potential undesirable consequences to be included in the decision to eradicate, or to inform concurrent management interventions, we need an approach to predict potential management outcomes at an ecosystem-level.

Understanding ecosystem wide outcomes of species removal is an active area of theoretical food web research. Topological models have been used to examine the role of network properties (Dunne et al., 2002; Tylianakis et al., 2010); and small population dynamic models (typically 3 – 4 species) have demonstrated how the removal of higher order predators can release pressure on lower order predators and enhance potential for cascading ecosystem outcomes (e.g. meso-predator release) (Bode et al., 2015; Courchamp et al., 1999; Tompkins and Veltman, 2006). These theoretical works provide valuable insights into how larger models, that have been designed with a specific ecosystem and management scenario in mind, may behave. For more complex systems, large food web models of system dynamics can predict indirect effects of species removal (Montoya et al., 2009; Schmitz, 1997). However, these models require a large amount of data to parameterize (Montoya et al., 2009), including the interaction strengths between all species. Such information is usually completely unknown and is extremely difficult to obtain for practical, economic and ethical reasons (Eklöf et al., 2013; Montoya et al., 2009; Schmitz, 1997).

Given that population dynamic models are difficult to parameterize, modelers have turned to a qualitative approach, which seeks instead to obtain probabilistic model predictions. One approach, based on a Monte Carlo simulation, circumvents ignorance of interaction-strengths by sampling values from an uninformative prior, and interprets the resulting proportion of different species responses (positive or negative) a prediction of their probability of occurring as (e.g. Raymond et al. (2011)). Given the ability of this approach to work with limited system information, it has been applied to various practical conservation scenarios, such as: predicting ecosystem response to invasive species management (Raymond et al., 2011), assisting understanding of the mechanism of ecosystem change under regional climate warming (Melbourne-Thomas et al., 2013), and evaluating community impacts of the climate-driven species redistribution (Marzloff et al., 2016). However, recent work has criticized the approach on philosophical grounds, showing there are often multiple equally defensible ways of defining parameter spaces and sampling them, such that contradictory probabilities can be obtained for the same predicted outcome (Kristensen et al., 2019). A partial view of the multiple plausible outcomes could lead to poorly informed decisions or confusion on how to act.

Kristensen et al. (2019) proposed a non-probabilistic approach to qualitative modelling. The approach circumvents the philosophical problems with Monte Carlo simulation whilst still enabling decisions with limited data. The approach uses Boolean analysis, which stems from sociology research to analyze binary-response (yes/no) questionnaire data (Theuns, 1994), and uncovers the logical relationships between species responses that occur in the model regardless of the parameter values (e.g. if species A responds positively to pest control then species B will respond negatively). Initial work has tested the approach in a theoretical setting but its potential in a real-world setting is yet to be explored. In particular, it remains a question whether deterministic species-response rules, as derived by Boolean analysis, can provide useful information to conservation decision-makers.

Here we seek to perform the first real-world test of the Boolean method, applied to pest eradication on an isolated Australian territorial island, Christmas Island. In 2015, to ameliorate the impact of invasive species on biodiversity (Martin et al., 2012; Misso and West, 2014; Woinarski et al., 2017), an island-wide eradication of introduced feral cats (*Felis catus*) was initiated. However, management decisions are further complicated by the potential regulatory role of cats on invasive black rats (*Rattus rattus*), which are both predator and prey of endangered endemic native species (Hill, 2004). In this study, we compare

the predictions of both the probabilistic and Boolean qualitative modelling approaches regarding the effects of cat and rat management on native species. We found that the predictions from the probabilistic approach were ambiguous, limiting their utility for decision-making. In contrast, the Boolean approach identified a key determinant of outcomes – how rats respond to cat management – and provided guidance for monitoring and adaptive management.

2. Material and methods

2.1. Modelling overview

Two different approaches for predicting the outcomes of invasive species management on Christmas island were applied: (1) Boolean analysis, which is the focus of this study and (2) probabilistic modelling, as a contrast. The two approaches share in common the Christmas Island ecological networks (section '2.2 Ecological networks of Christmas Island and structural uncertainty'), and the method of predicting species responses using community matrix analysis (section '2.3 Obtaining species responses from the community matrix'). The methods differ by the way in which they deal with interaction-strength uncertainty (section '2.4 Two approaches for dealing with interaction-strength uncertainty').

2.2. Ecological networks of Christmas Island and the structural uncertainty

Expert elicitation and existing literature were used to construct ecological networks for Christmas Island. A link between two nodes indicated either a predator-prey relationship or interference competition, while exploitative competition between species occurred when species shared the same prey species or resource nodes. Self-limitations were imposed to all model components representing self-regulated effects.

All interactions (links) between species were categorized as certain or uncertain based on existing literature and expert beliefs: certain links indicating the relationship was considered influential enough to be included in the network, while uncertain links indicating there is uncertainty about whether to model them as present or absent. The inclusion or otherwise of the uncertain links led to multiple representations of the network structure. For the Boolean analysis, each possible network structure was analyzed separately, while for the probabilistic analysis, network structures were sampled at random and the results were pooled.

Two distinct ecological networks were constructed – the Forest and Town networks – to reflect not only the spatial separation of the two areas, but also the difference in the ecological communities represented (Fig. 1, see detailed information of species and species interactions in Table A.1 – A.3). Each network and its variations contained: cats and rats as the focal species for management; key native species that were of conservation concern and under threat from cat and rat predation; species that connect with the above species to form the ecosystem structure; and finally food resource nodes used to capture exploitative competition interactions between species. Where species shared the exact same set of links, they were lumped together into one node and each full network had two uncertain links, and thus we explored all four possible network variations (see details in Table A.4).

2.3. Obtaining species responses from the community matrix

Species responses to pest control were simulated with the commonly used sensitivity matrix approach (e.g. Raymond et al. (2011)). The population dynamics were described by a linearized approximation around the steady state, which was summarized by the community matrix (Levins, 1968). This is a common way to simplify the analysis, which means that transient population dynamics are not taken into account. Pest management was simulated as a press perturbation, which is the continual removal of members of the pest species from the Y. Han, et al.



Fig. 1. Ecological networks (a) Forest network (b) Town network. Each network comprises focal species for management (black), species of conservation concern (grey), the species that are not under concern but form the ecosystem structure (grid), and food resources nodes representing exploitative competition between species (white). A line terminated with an arrow indicates a positive influence while a line terminated with a dot indicates a negative influence. All species are self-limiting (negative self-loop not shown). Dashed lines represent uncertain links, i.e. experts were not certain whether potential interactions between these species were important enough to be modelled as present or absent.

ecosystem at a constant rate (Yodzis, 1988). The sign-structure of the community matrix corresponded to the sign-structure of the ecological network, with zero entries between pairs of species with no direct link. Once the non-zero entries representing interaction-strengths were specified, both the local stability properties of the system and each species' response to press perturbations could be quantified (Yodzis, 1988). Local stability of the population dynamics is established when all eigenvalues of the community matrix have negative real parts (note this excludes communities with stable limit cycles). The response of each species' population steady state to press perturbation (cat or rat management) can be determined from the sensitivity matrix, which is the negative inverse of the community matrix (Nakajima, 1992). If the entry of the sensitivity matrix corresponding to the managed species (i.e. cats or rats, column) and response species (row) was positive, the response-species' population steady state is predicted to decrease with management of the managed species, and vice versa.

This analysis simulates pest management as a small press

perturbation on the target population, however pest control usually involves an effort at eradication, i.e. a sudden population decrease to very low abundance. Given that this simulation approach cannot precisely reflect the effects of real-world eradication practice, we used the term 'management' throughout this study.

2.4. Two approaches for dealing with interaction-strength uncertainty

Two methods were used to obtain model predictions and analyze their results (Fig. 2). In both approaches, the same validation criteria were used to filter parameterized matrices: (1) local stability, assuming the system would return to equilibrium after small perturbations; and (2) a negative response of the managed-species to the perturbation on itself, assuming each management action had led to a population reduction of the species targeted.



Fig. 2. A summary of different sources of model uncertainties and a comparison between the probabilistic approach and the Boolean analysis approach. The focus of this study is interaction-strength uncertainty. Interaction-strengths are needed to parameterise the population dynamic model. After expert elicitation there often remains some structural uncertainty about whether certain interaction is present or absent. In our Boolean analysis, the alternative network structures were analysed separately.

2.4.1. Approach 1: Probabilistic

Following Raymond et al. (2011), for a given network structure, the non-zero entries representing interaction-strengths in the community matrix were randomly sampled from a uniform distribution. Over many community matrices that passed the validation criteria, signs of responses (positive/negative) of each species to each pest management (cats and rats) were pooled. The proportion of each species' response that was positive/negative was interpreted probabilistically, as being indicative of the support for that response occurring in the real system.

The way we aggregated these response outcomes differed from Raymond et al. (2011). Raymond et al. (2011) assumed that the effect of perturbations of multiple species upon a single species can be obtained by simply taking the sum of the corresponding elements of the sensitivity matrix (this remains a common practice, see Marzloff et al. (2016) for a recent example). However, this summation practice only holds when each pest-management effect is weighted by the relative magnitude of the perturbation for that pest (Eqn 15, Nakajima (1992)) (see Appendix B for a detailed explanation). The relative magnitudes of cat versus rat management was not known a priori, and hence these weightings were not known. Therefore, when considering the effect of press perturbations upon two or more species, if the signs of responses for all perturbed species was the same, then the sign of the effect for combined perturbations can be determined (i.e. all positive responses give a combined positive response and all negative responses give a combined negative response); however, if the signs of two or more responses differed, then the sign of the response to combined perturbations was not known.

We summarized simulation outcomes as follows: for the management of cats alone, species respond positively or negatively to the perturbation of cats; while for the combined management of cats and rats, species' responses were categorized as positive (positive to both managements), negative (negative to both managements), or uncertain (positive to cat management and negative rat management or vice versa). The simulation and was implemented in R (R Core Team, 2019). 10^6 stable, valid matrices were generated, and the responses were then aggregated (code can be found in Appendix C).

2.4.2. Approach 2: Boolean analysis – identifying the rules of species' responses

We followed Kristensen et al. (2019) to perform the Boolean analysis approach and described the way of applying the approach under a multi-species management scenario. For a given network structure, the Boolean analysis approach first performed a parameter-value sweep and used the validation criteria to obtain many community matrices. For each possible matrix, the signs of responses of each species to management of each of the controlled species (cats and rats) was determined, to give a particular species-response combination. Over many community matrices, a long list of observed species-response combinations was obtained. Then a Boolean analysis involving a Boolean minimisation (Theuns, 1994) was performed on the species response combinations that were never observed, to find simple implication rules describing relationships between species' responses in the model.



Fig. 3. Species responses in the Forest network predicted by the probabilistic approach to cat management alone (a), and to combined cat and rat management (b). For cat management alone, several species (e.g. Brown Booby) were predicted to have a positive response in more than 75% of the Monte Carlo ensemble. In contrast, when cat and rat management was combined, mixed responses (striped regions) were common across all species; in these cases the sign of the species response cannot be predicted.

The parameter sweep involved randomly choosing the magnitudes of non-zero entries of the community matrix from a uniform distribution until a total of 10^8 valid matrices were obtained. In contrast to the probabilistic approach, this method of sampling from a uniform distribution is not an expression of neutrality of belief about the interaction-strength values. Rather, the uniform distribution was chosen for convenience only, to obtain reasonable coverage of all the possible species response combinations that the interaction network can produce. While there is no guarantee that all possible response combinations were found in this ensemble, the short rules (up to approximately five species) that were obtained in the following Boolean minimisation did not change very much across the different network structures.

A Boolean minimisation was then performed on the species-response combinations that were never observed in the 10⁸ community matrices obtained from the parameter sweep. Boolean minimisation is a method for finding the shortest statement describing relationships. and it is widely used to design digital circuits that are small and cost efficient (e.g. Mano and Kime (1997)). In this application, Boolean minimization was used to find simple implication rules describing relationships between the species' responses to different management scenarios. For n species, each can have two possible population-size responses to a given management action ('positive' or 'negative'). Theoretically, there is a set U of maximum of 2^n combinations of responses possible. However, due to the structure of the network imposed and the validation constraints, not all of these 2^n response patterns can be produced by the model. Then there is a subset U^* of possible responses and a subset U^0 of impossible responses, where $U = U^* \cup U^0$ and $U^* \cap U^0 = \emptyset$. This implies that certain rules exist constraining the outcomes of the model. Finding these rules is equivalent to performing a Boolean minimization upon the response patterns (see Appendix D for a detailed method description). Specifically, performing Boolean minimization upon the subset U^0 of impossible response patterns produces the ultimate canonical projections (UCPs), which are the minimal descriptions of these impossible responses, which can then be converted into implication rules that are always true for the simulation outcome. These implications can describe the relationships between species' responses (Degenne and Lebeaux, 1996; Theuns, 1994).

For our case on Christmas Island, the Boolean minimisation was first performed on the set of possible responses that were never observed ('never-observed responses') to individual cat management, and response rules were determined. This step described the species' responses to cat management alone. Next, we investigated the effects of combined cat and rat management. We performed Boolean minimisation on the never-observed responses to rat management alone. Based on the never-observed responses to the cat management alone and rat management alone together, we were able to explore response rules for combined cat and rat management. The Boolean analysis was performed using the software accompanying Kristensen et al. (2019). We also provide an equivalent R code derived from the original Python code using *Espresso algorithm* in Package *LogicOpt* (Stiehl, 2016), which produced the same results (code can be found in Appendix C).

Only the shorter implication rules obtained were presented in the logic implication networks. In general, a rule with length two produces the most straightforward implications and is easy to interpret; while a rule with a length longer than five produces implications that are often too complex to have clear, meaningful interpretations. Shorter rules (longer than two but less than six) were all evaluated, and meaningful implications can be drawn from these rules to provide insights into understanding the system, and in our case, inform management. However, not all these rules are informative. For a complicated network such as these Christmas Island networks, rules can be too contingent to base management decisions on, and the underlying ecological explanations for some rules are not always clear as they may simply reflect behaviours of the network itself.

3. Results

3.1. Probabilistic approach

The outcomes of the probabilistic modelling approach showed that cat management alone led to more than 75% positive responses for the Brown Booby (*Sula leucogaster*), the Christmas Island flying-fox (*Pteropus melanotus natalis*) and the goshawk from the Forest Network, and also led to nearly 75% negative responses for the frugivorous birds (Fig. 3a).

For the combined treatment scenario, the Brown Booby, the giant gecko (*Cyrtodactylus sadleiri*) and the goshawk had the highest proportion of positive responses to both cat management and rat management, around 40%-50%; while the proportions for other species were less than 25% (Fig. 3b). Mixed responses to the combined treatment were common across all species, representing up to 75% of responses (striped grey and striped black, Fig. 3b). Species responses for the Town network can be found in Fig. E.1.

3.2. Boolean analysis - rules governing responses to cat and rat management

Patterns (rules) of species' response were explored by Boolean minimization for all network variations. The full Forest network and the full Town network (hereafter the Forest network and the Town network) with all certain and uncertain links included were used to illustrate the outcomes, while outcomes for other network variations can be found in Fig. F.1 – F.8.



Fig. 4. Under the management of cats alone scenario, for both the Forest (a) and Town (b) networks, the effect that cat management had on rats was the key determinant of the effect of cat management on other species. When cat management decreased rat populations, short rules predicting some positive responses in other species were predicted. However it is more plausible that cat management would increase rat populations through predator release, and under that scenario, no short deterministic rules were found. Grey shade, a negative effect from cat/rat management; unshaded, a positive effect from cat management.

3.2.1. Independent effects of cat management

For both the Forest network and the Town network, the effects of cat management alone were contingent upon the effect that cat management had on the rat population. If cat management had a positive effect on the rat population (e.g. through predator release, a very plausible scenario), then all combinations of species' responses to cat management were possible in the model, making it difficult to predict the outcome. However if cat management had a negative effect on the rat population (e.g. if cats facilitate rats, a less likely scenario), then certain positive outcomes were guaranteed (Fig. 4a & b). This contingency upon negative response of rat to cat management was robust to network structure variations (Fig. F.1).

The implication rules for this less likely scenario showed that the Brown Booby could benefit directly from cat management if cat management had a negative effect upon the rat population (\downarrow Cat Rats⁽⁻⁾ \rightarrow \downarrow **Cat Boobies**⁽⁺⁾) (Fig. 4a). The frugivorous birds and the flying-foxes showed the following pattern: 'if cat management causes a negative response in the rat population, then either frugivorous birds, or the flying-foxes, or both species, will benefit from cat management' (**\Cat** Rats⁽⁻⁾ $\rightarrow \downarrow$ Cat Frugivorous birds⁽⁺⁾ $\vee \downarrow$ Cat Flying-foxes⁽⁺⁾). The 'or' (v) node is a logical OR, not an exclusive OR; in the above example, it is possible that cat management will have a positive effect on either one, or both species. Two other pairs - the White-tailed Tropicbirds (Phaethon lepturus fulvus) and the goshawk, and the gecko and the Christmas Island Hawk-owl (Ninox natalis) - showed the same type of pattern. The longer rule involving goshawks, Christmas Island whiteeyes (Zosterops natalis), Christmas Island thrushes (Turdus poliocephalus erythropleurus) and feral chickens (Gallus gallus domesticus) together also showed a similar pattern (\downarrow Cat Rats⁽⁻⁾ $\rightarrow \downarrow$ Cat Goshawks⁽⁺⁾ $\lor \downarrow$ Cat White-eyes⁽⁺⁾ $\lor \downarrow$ Cat Thrushes⁽⁺⁾ $\lor \downarrow$ Cat Chickens⁽⁺⁾).

3.2.2. Effects of combined cat and rat management

We found that the patterns (rules) of species responses to rat management were contingent upon the effect of rat management on the cat population (see Fig. F.2 for the results of rat management alone). Therefore, we considered two consequences of managing rats in the combined cat and rat management scenario where cat management has a positive effect on rats (predator release scenario): (1) rat management has a negative effect on cats, and (2) rat management has a positive effect on cats. The results of alternative scenarios where cat management does not have a positive effect on rats can be found in Fig. F.7& F.8.

Scenario 1: Cat management has a positive effect on rats (predator release) and rat management has a negative effect on cats (removal of prey)

For both the Forest and the Town network, if rat management had a negative effect upon cats, all rules predicted a positive effect of rat management upon at least one species that was of conservation concern, and this result was robust to all network structure variations (Fig. 5a & b for the full network and Fig. F.4 – F.5 for other structure variations). The only exceptions were the rules involving feral chickens. For example, in the Forest network, the rule **True** (\downarrow **Cat Rats**⁽⁺⁾ $\land \downarrow$ **Rat Cat**⁽⁻⁾) $\rightarrow \downarrow$ **Rat Goshawks**⁽⁺⁾ $\lor \downarrow$ **Rat White-eyes**⁽⁺⁾ $\lor \downarrow$ **Rat Thrushes**⁽⁺⁾ $\lor \downarrow$ **Rat Chickens**⁽⁺⁾, can be read as saying: 'if cat management has a positive effect on rats and rat management has a negative effect on cats, then goshawks, or white-eyes, or thrushes, or chicken, or any two species, or any three species, or all four species will benefit from cat management'. Indeed, one of the possible predictions of this rule was that only the introduced chicken showed a positive response while other species of conservation concerns did not. The '&' node (\land)



Fig. 5. Species response rules for combined cat and rat management in the most plausible scenario: where cat management has a positive effect on rats (predator release) but rat management has a negative effect on cats (removal of prey). In both the Forest (a) and Town (b) networks, a positive response to rat control in at least one species of conservation concern was predicted, and this prediction was robust to network structure uncertainty (see Fig. F.4 for implication rules of different network structures). The 'True' node indicates contingency upon the scenario only (e.g. direct links from the 'True' node indicate that these species responses will always occur in the scenario). The dashed box and lines summarize species-response relationships with conditions that were too complex to draw meaningful ecological and/or management implications, and the full response rules within the dashed box can be found in Fig. F.3.

represents logical AND.

In the Forest network, all rules up to length five predicted a positive effect of rat management upon at least one species of concern, and this result was robust to the full network (Fig. 5a) and other structure variations (Fig. F.4), with the exception of the feral chicken rule mentioned above. Longer rules can also be derived for the Forest network, which revealed more contingencies implying a negative effect of rat management on certain species (Fig. F.5). However, these rules were less robust to structural variation.

In the Town network, complementary rules existed showing that the effect of rat management upon the hawk-owl was contingent upon the effect of cat management upon the hawk-owl, which was robust to all structural variations (Fig. 5b).

Scenario 2: Cat management has a positive effect on rats (predator release) and rat management has a positive effect on cats (e.g. through competitive release)

For both the Forest and the Town networks, under the scenario that rat management had a positive effect on cats, we found symmetric rules: if cat management has positive effects on certain species then the rat management would have a negative effect on the same species, and vice versa (Fig. 6a & b). The rule of the forest network involved the response of Brown Boobies to cat management as a central contingency (Fig. 6a). For example, there is a rule that \downarrow Cat Goshawks⁽⁻⁾ $\land \downarrow$ Cat Tropicbirds (W)⁽⁺⁾ $\land \downarrow$ Cat Brown Boobies⁽⁺⁾ $\rightarrow \downarrow$ Rat Goshawks⁽⁺⁾ $\lor \downarrow$ Rat Tropicbirds (W)⁽⁺⁾ $\lor \downarrow$ Rat Brown Boobies⁽⁺⁾. In the Town network, as discussed above, robust complementary rules existed which showed that the effect of rat management upon the hawk-owl contingent upon the effect of cat management upon the same species (Fig. 6b, Fig. F.6).

4. Discussion

Using a case study of pest management on Christmas Island, we have compared the ability of two qualitative modelling approaches – probabilistic and Boolean – to produce predictions that can inform conservation decisions. The key result was that most of the probabilities of different species responses produced by the probabilistic approach were not large enough to provide a clear prediction, whereas the Boolean approach was able to uncover deterministic predictions for species responses and some of these were clear enough to inform decision making. Below, we discuss how the results can be interpreted and how the management recommendations that can be gleaned from them, and then we discuss the strengths and limitations of the novel Boolean approach from a practical standpoint.

4.1. Management recommendations

The probabilistic predictions were highly uncertain, which meant that it was difficult to draw any management recommendations from their results. When cat and rat management were combined, the outcome predicted with the highest probability was that species responses could be either positive (+) or negative (-), depending upon the relative magnitudes of cat versus rat suppression (hatched region in Fig. 3b). Even in the simplified scenario, where cat management was considered alone, only four out of the total nine species had a positive or negative response to cat management in more than 70% of the models generated, where a value greater than 70% -80% is often arbitrarily interpreted as 'moderate' or 'strong/high' support for that outcome occurring in the real system modeling (e.g. Raymond et al. (2011); Reum et al. (2015); Sobocinski et al. (2017)); while the results for the other five species gave no clear indication with positive responses in 50% - 60% of all cases.

In contrast, the Boolean approach revealed more interpretable



Fig. 6. Species response rules for combined cat and rat management in the second most plausible scenario: where cat management has a positive effect on rats (predator release) and also rat management has a positive effect on cats (competitor release). For both the Forest (a) and Town (b) networks, the species response rules were symmetric: if cat management has a positive effect on certain species then the rat management has a negative effect on the same species, and vice versa.

model predictions. First, analysis of cat management revealed that the key predictor of native species' responses was the response of rats to cat management, which could be positive or negative, leading to separate analyses. The model informs us that cat management alone is a risk prone strategy, since Boolean analysis found no short rules under the more likely scenario that suppressing cat will lead to a positive response of rat population. However, under the less likely scenario, that cat management leads to a negative response of rats, certain species will respond positively. This key role of rat population response in determining native species' responses hints that exploring simultaneous rat management may be a fruitful next step.

Cat eradication has started on Christmas Island, so a key question is whether supplementary rat management will lead to better outcomes for the native species. Based on the evidence that rats account for a significant proportion of cats' diet on Christmas Island (Tidemann et al., 1994), it is likely that cat management would have a positive effect on rats through predator release, and that rat management would have a negative effect on cats through removal of prey. Given this, we focus our conclusions upon this *a priori* scenario. The addition of rat management to a cat eradication programme is expected to ameliorate at least some of the potential negative impacts of cat management alone (Fig. 5). However, the Boolean analysis also revealed that rat management is predicted to have negative impacts in certain situations, for example, leading to a negative effect on hawk-owls when cat management has a positive effect on hawk-owls (Fig. 5).

The Boolean analysis also gives guidance on how monitoring can be used to predict these adverse effects. For example, in the Town network model (Fig. 5b and Fig. 6b), the species-response rules indicate that if an increase of the hawk-owl population to cat control alone is observed during monitoring then rat control effort should be carefully considered due to its potential negative impacts on the hawk-owl.

By identifying groups of species that repeatedly appeared in rules together, the Boolean analysis may provide us with some insights into the ecological drivers of species-response associations. Species groups that appeared together often shared the same food resources within the network. For example, frugivorous birds and flying-foxes respond together and also share the fruit resource, and hawk-owls and geckos respond together and also share the nocturnal insect resource as well as a predator-prey relationship. In contrast, the Brown Booby as a seabird species is less connected to the rest of the native species, and its response to rat and cat control is independent of the responses of all the other species. While these species-response associations appear interpretable in terms of the structure of the original web, this understanding could only be achieved retrospectively; the response associations could not have been predicted from examining the network structure alone, and therefore the Boolean analysis adds to our understanding of the system.

4.2. Strengths and limitations of Boolean analysis

Kristensen et al. (2019) developed the Boolean approach in order to address a philosophical problem, however the question remained as to whether the new approach has practical value to inform conservation decision-making. In this study, the Boolean approach identified rat

population response to cat management as a key determinant of whether positive outcomes could be expected for species. Subsequent analysis led to the recommendation that cat management be supplemented by rat control because of its predicted positive effects on some native species. This recommendation is not entirely surprising; it concurs with information from other ecosystems and with the decision makers' intuition that including rat control would be prudent given the ecology of this interaction (Oppel et al., 2014; Rayner et al., 2007). The agreement between the model and expert knowledge is promising and bolstering for decisions on the Christmas Island. However, while the importance of rats could have been predicted from knowledge of the system, the Boolean analysis also revealed information that was not obvious a *priori*. Species that co-occurred in the same rule often shared a resource. but co-occurrences could not be predicted from examining the original network structure alone as these resource-sharing relationships are entangled with other components via multiple prey-predator and/or competition relationships. This result is typical of dynamical systems, where complex feedback relationships make it difficult to discern how the system will respond. Therefore, Boolean analysis appears to be one way to uncover hidden relationships with limited data.

With cat management already implemented, we can in principle predict the effects of subsequent rat management, by monitoring species responses to the current programme and comparing that to the response rules obtained. In this case study, prediction is hampered by a lack of knowledge about which rat-cat relationship scenario (e.g. Fig. 5 versus 6) the system is in, and the contingent nature of long rules produced, but nevertheless one clear recommendation regarding the response of hawk-owls was obtained. Thus, Boolean analysis holds some promise for informing monitoring for adaptative management in a multi-species management context.

Using species-response rules for decision-making has three key limitations. First, the rules are for the species' qualitative responses (positive/negative) regardless of their magnitude. However the rules are only meaningful if the magnitude of the real-world response is large enough, including our key conclusion, that rat control be used to ameliorate potential negative effects of cat control.

Second, the longer a species response rule is, the less informative and useful it is. A single species' response in an *k*-species-length rule is only guaranteed contingent upon the responses of the other *k*-1 species satisfying the rule. A noteworthy example is the rule involving the response of the feral chicken. Under the *a priori* likely scenario, all other rules predict that rat control will have a positive effect on at least one native species. However, for the rule involving goshawks, white-eyes, thrushes and feral chickens, it is possible for this rule to be satisfied by a positive response of feral chickens alone. Thus, there was a potential risk that none of the three native species in this rule would benefit from rat control.

Third, the contingent nature of the rules obtained can reduce their usefulness for guiding decision making. In the Christmas Island application, the rules were highly contingent upon rat response to cat control and cat response to rat control. On one hand, this informs us that the response of the two predators to the control of the other is a key determinant of the overall response of the system. On the other hand, it means that, if we do not know *a priori* which of these scenarios is most likely, then it is difficult to give general advice on the best management strategy to pursue.

5. Conclusions

Given its ability to model systems without extensive parameterization, probabilistic qualitative modeling has received increased attention and has been applied to a wide range of environmental and conservational problems (e.g. Goedegebuure et al. (2017); Marzloff et al. (2016); Reum et al. (2015); Sobocinski et al. (2017); Zador et al. (2017)), but the philosophical grounds of this approach has been criticized (Kristensen et al., 2019). In this study, we found that this probabilistic approach was also impractical, because it produced predictions that were too ambiguous for management recommendations to be drawn. An alternative non-probabilistic Boolean analysis approach using the same limited data, as exemplified by our case study, was able to provide predictions that were interpretable from a decision-making perspective in real-world setting. Although the Boolean approach has its assumptions and limitations, it could be the only viable option in data-limited scenarios, where it is preferable to have some information from a model than none at all. With the pressing conservation need for a method of understanding system dynamics, despite limited information, in response to environmental stressors or management interventions (Hodgson and Halpern, 2018), the Boolean analysis approach has considerable potential. Future work may expand its application to help add our understanding of the system, predict consequences of anthropogenic stressors, and evaluate management alternatives and support programme initiation.

CRediT authorship contribution statement

Yi Han: Investigation, Data curation, Methodology, Software, Writing - original draft. Nadiah P. Kristensen: Methodology, Software, Writing - original draft. Yvonne M. Buckley: Conceptualization, Supervision, Writing - review & editing. Dion J. Maple: Investigation, Writing - review & editing. Judith West: Investigation, Writing - review & editing. Eve McDonald-Madden: Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109122.

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