

Qualitative modelling of invasive species eradication on subantarctic Macquarie Island

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Summary

1. Invaded ecosystems present complex management issues. This problem is exacerbated in many situations by a lack of knowledge about the ecosystem. However, delaying conservation action to collect further data and so reduce such uncertainty is often either impractical or inadvisable.

2. The Macquarie Island Pest Eradication Project, currently underway, is attempting to eradicate rabbits, rats, and mice from the island. We undertook qualitative modelling of this project, examining a range of likely outcomes and their possible ecological consequences. The results were aggregated across a large number of possible models, in order to account for uncertainty concerning interactions within the ecosystem.

3. The results strongly support the current actions of simultaneous eradication of all three pest species, as simulated eradications of only one or two generally led to continued impacts on the island's native biota. The results also provided support for the anticipated positive outcomes of the project, with predicted recoveries of tall tussock vegetation, and burrow- and surface-nesting seabirds.

4. However, the model predictions also highlighted potential risks: the eradication of mice from the island may not succeed, due in part to the structural position of this species within the ecosystem. Successful eradication of all three target species could potentially release the self-introduced, non-native redpolls and starlings, allowing expansion of their populations, with possible impacts on macro-invertebrates and vegetation.

5. *Synthesis and applications.* These results demonstrate that qualitative modelling approaches can in some cases deliver consistent results, despite high levels of uncertainty regarding interactions within the underlying ecosystem. Such outcomes can provide assistance in the development of strategic contingency plans and ongoing future management action.

Key-words: cats, conservation, invasive species, mice, rabbits, rats, starlings, subantarctic island, uncertainty

Introduction

Invaded ecosystems present complex management issues, with multiple interacting elements and indirect effects, giving sometimes unexpected effects of management action. Even in relatively simple island ecosystems, the dynamics can be poorly understood and outcomes counter-intuitive (e.g. Rayner *et al.* 2009). There is a need for applied research in order to provide

decision support for management actions (Buckley 2008; Bergstrom *et al.* 2009), but uncertainty about outcomes can be a difficult issue to overcome (Maguire 2004). Delaying conservation action in order to collect additional data can reduce such uncertainty, but this may not always be the best strategy (Grantham *et al.* 2009).

Subantarctic Macquarie Island is currently being subjected to one of the largest island eradication actions attempted (Parks & Wildlife Service 2008) with the aim to eradicate European rabbits *Oryctolagus cuniculus* L., ship rats *Rattus rattus* L., and house mice *Mus musculus* L. Brodifacoum-laced cereal

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bait is being aerially spread, to be followed up by hunting teams and rabbit detector dogs. Action to eradicate rabbits and rodents was long planned as part of the island's integrated pest management framework (Copson 2002). Before this action could be implemented, however, the island suffered substantial destruction of vegetation because of an increase in the rabbit population, which followed the eradication of cats and cessation of Myxoma virus releases (see Scott & Kirkpatrick 2008; Bergstrom *et al.* 2009; Dowding *et al.* 2009).

Significant gaps exist in our knowledge of the Macquarie Island ecosystem, and the ecological outcomes, should one or more of the target species survive the eradication attempt, are acknowledged as being largely unknown (Parks & Wildlife Service 2009b). However, the immediate priority of removing the pests from the island (particularly the rabbits, because of the extensive vegetation damage and onward impacts) far outweighed the advantages of further research.

The island's ecosystem involves a large number of potential interactions between species. Not only are the functional forms of these interactions often poorly understood, in some cases it is not even apparent whether or not an interaction between a pair of species is of sufficient importance to warrant inclusion in an ecosystem model. Such structural uncertainty can be an important source of indeterminacy in ecological predictions and associated decision making (Punt & Hilborn 1997; Hosack, Hayes & Dambacher 2008). Qualitative modelling (Levins 1974; Puccia & Levins 1985), which focuses on model structure rather than the quantitative details of a model's

components, can be a valuable tool in such circumstances. Such modelling is also well suited to the exploration of the relative balance of direct and indirect effects in an ecosystem. Indirect effects (that is, an effect from one member of the community upon another, mediated by one or more intervening members) can in some cases oppose and outweigh direct effects, causing counter-intuitive outcomes such as a population increasing despite reduced food availability (Sih *et al.* 1985; Yodzis 1988). Qualitative modelling has previously been applied to the analyses and simulation of pest management actions (e.g. Ramsay & Veltman 2005; Ramsay & Norbury 2009).

This study explores the possible consequences of eradication activities under various success scenarios, and investigates whether informative results can be obtained, despite the relatively high levels of uncertainty.

Materials and methods

STUDY SITE AND HISTORY

Subantarctic Macquarie Island (54°30'S, 158°57'E) is a tundra-covered, World Heritage listed sliver of land in the Southern Ocean. Oiling gangs plundered the seal and penguin populations on the island throughout the 19th and early 20th centuries. This activity was accompanied by a litany of non-native species arrivals at various times (Fig. 1): dogs *Canis lupus familiaris* (~1815), cats (1820), wekas *Gallirallus australis scotti* (1870s), rabbits (1879), mice (1890), and rats (1900) (see Cumpston 1968; Copson & Whinam 2001). Several non-native bird species also arrived, probably through self-introduction

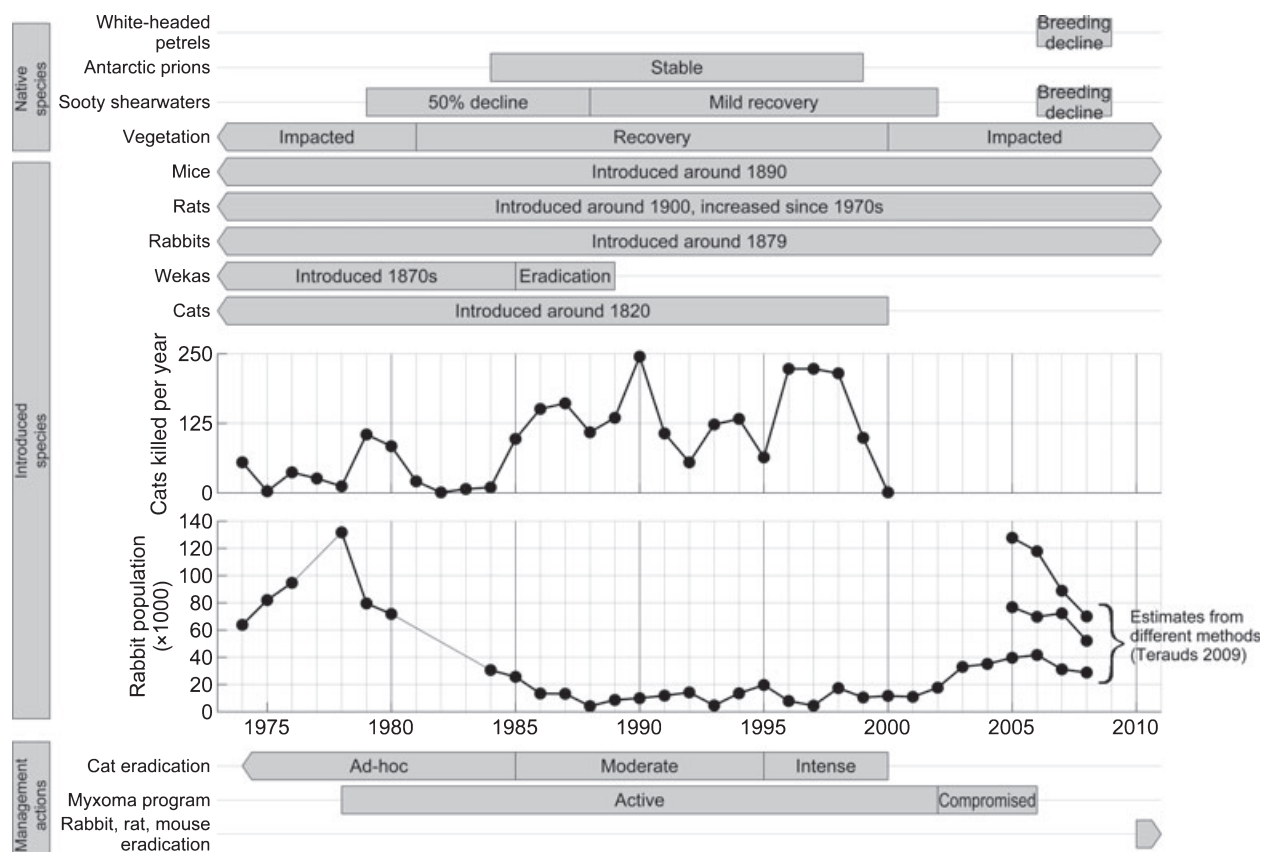


Fig. 1. Timeline of pest species introductions, management actions, and other events on Macquarie Island.

from New Zealand and Australia (Copson & Brothers 2008): starlings *Sturnus vulgaris* L. in 1930 (Falla 1937), common redpolls *Carduelis flammea* L. in 1912 (Falla 1937) and mallards *Anas platyrhynchos* L. in the 1950s (Cumpston 1968).

Dogs died out after 1820, but the other species established and began to impact native biota. Two native ground-dwelling bird species, the Macquarie Island parakeet *Cyanoramphus erythrotis* Wagler and the buff-banded rail *Gallirallus philippensis macquariensis* Hutton, became extinct by the 1890s, probably through a hyperpredation interaction with cats and rabbits (see Vestjens 1963; Taylor 1979). Extensive rabbit grazing of the native vegetation was noted in the early 1900s (Taylor 1955; Costin & Moore 1960). Rabbit control efforts began in 1968 with the release of the European rabbit flea *Spilopsyllus cuniculi* Dale followed by successful introduction of the Myxoma virus in 1978 (Brothers *et al.* 1982), resulting in substantial reductions in the rabbit population. The Myxoma virus was spread until 2006, but efficacy was possibly compromised after about 2002 (Copson 2002; Dowding *et al.* 2009).

The reduction in rabbit numbers probably resulted in increased cat predation on burrow-nesting seabirds (Brothers 1984; Copson & Whinam 2001) and the cat management programme was refocused in 1985, intensified in 1998, and the last cat was shot in 2000 (Copson & Whinam 2001; Copson 2002). From 2002, rabbit numbers on the island increased to 40 000–130 000 in 2005 (Fig. 1; Terauds 2009), with the upper estimate close to the estimated maxima of 150 000 prior to Myxoma release (Sobey *et al.* 1973; Copson, Brothers & Skira 1981).

The recent increase in rabbits has again caused substantial vegetation destruction, with particular impact on coastal slopes (Scott & Kirkpatrick 2008; Bergstrom *et al.* 2009), and the impacts to some areas of seabird breeding habitat are reaching critical levels (McInnes & Way 2010). The Macquarie Island Pest Eradication Project (Parks & Wildlife Service 2008) began in May 2010, with the objectives of the recoveries of vegetation, burrowing seabird habitat, and populations of invertebrates and burrowing seabirds (Parks & Wildlife Service 2009b).

MODEL CONSTRUCTION

The dynamics of n interacting species is often represented as a Lotka-Volterra system of differential equations of the form:

$$\frac{1}{N_i} \frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_n, c_1, c_2, \dots, c_m) \quad \text{eqn 1}$$

where N_i is the density of population i , f_i is a function describing the per-capita growth rate of that population, and c_h represents growth parameters that account for processes of birth, death and migration. The interaction coefficient a_{ij} measures the effect of a change in the density of species j on the per-capita growth rate of species i , and is defined as the partial derivative of f_i with respect to N_j (Levins 1968; Berlow *et al.* 2004):

$$a_{ij} = \partial f_i / \partial N_j. \quad \text{eqn 2}$$

At equilibrium, the negative inverse of the matrix **A** (which has elements a_{ij}) can be used to estimate the long-term effects of a press perturbation (Bender, Case & Gilpin 1984; Nakajima 1992), which is defined as a sustained shift in the magnitude of a growth parameter c_h of a species (Puccia & Levins 1985). Precise quantitative specification

of **A** is rarely practicable (Levins 1998), and not possible for the Macquarie Island ecosystem. One solution is to instead specify **A** only in terms of the signs of its interaction coefficients (Levins 1974). This qualitative approach permits inclusion of important variables and interactions in a model, despite an inability to precisely measure them, and can give qualitative predictions of press perturbation impacts (Levins 1974; Puccia & Levins 1985). However, for even moderately complex models, there can be multiple interaction pathways that connect species, and the qualitative predictions from the inverse matrix can be ambiguous because of the propagation of both negative and positive effects between species (Dambacher, Li & Rossignol 2002). Our particular situation is further complicated by another form of ambiguity: model structure uncertainty (there are a number of interactions that could potentially be included or excluded from the model). These issues, and previously described approaches to the problem, are discussed further in the Appendix S1 (Supporting information).

In this work, we adopt a hybrid solution, which simultaneously addresses uncertainty within and between qualitative models. For a given model structure (that is, a set of community members and their signed interactions), a realisation of this structure was obtained by assigning randomly selected interaction strengths for the non-zero elements of **A**. Strengths between 0.01 and 1.0 were used, with the sign of each interaction remaining unchanged. Self-effects (a_{ii}) were assigned a magnitude between -1 and -0.25 . The Lyapunov stability of this realisation was checked, and an unstable realisation discarded. Predictions were obtained from the negative inverse of **A**, and compared against validation information. If the signs of the predictions matched the signs of the known (validation) responses, then this realisation was considered plausible and added to the pool of accepted realisations. This process was repeated for each model structure until 1000 stable, valid realisations were obtained. Structural uncertainty was addressed by considering a large number of model structures, encompassing all possible combinations of unknown interactions (sensu Montañó-Moctezuma, Li & Rossignol 2007). Results were aggregated across this set of model structures. A summary of the method is shown in flowchart form in Fig. 2.

The use of random interaction strengths (a similar approach to that used by e.g. Yodzis 1988; Dambacher *et al.* 2003; Hosack, Hayes & Dambacher 2008) shares the advantage of purely qualitative methods, in that it requires knowledge only of the signs of the species interactions. Our method provides an additional advantage by constraining the allowable parameter values to those which are consistent with both system stability and the validation data. Increasing constraints can potentially be achieved by increasing the number of responses in the validation set through experiments or expert knowledge.

Example R code is available in the Supporting information, or from <http://data.aad.gov.au/analysis/qualitative/>.

THE MACQUARIE ISLAND MODEL

The model comprised three categories of vegetation, macro-invertebrates, seven categories of native seabird, rabbits, and their control agent the Myxoma virus, the introduced meso- and apex predators cats, rats, mice, and redpolls and starlings. A description of these elements, including the species within each group and their Latin names, is given in Table 1, and their interactions are shown in Fig. 3 (details of the interactions can be found in Table S1, Supporting information). All community members in the model are self-limited, although these self-interactions are not shown on Fig. 3 for clarity of presentation. Self-limitation represents processes such as competition

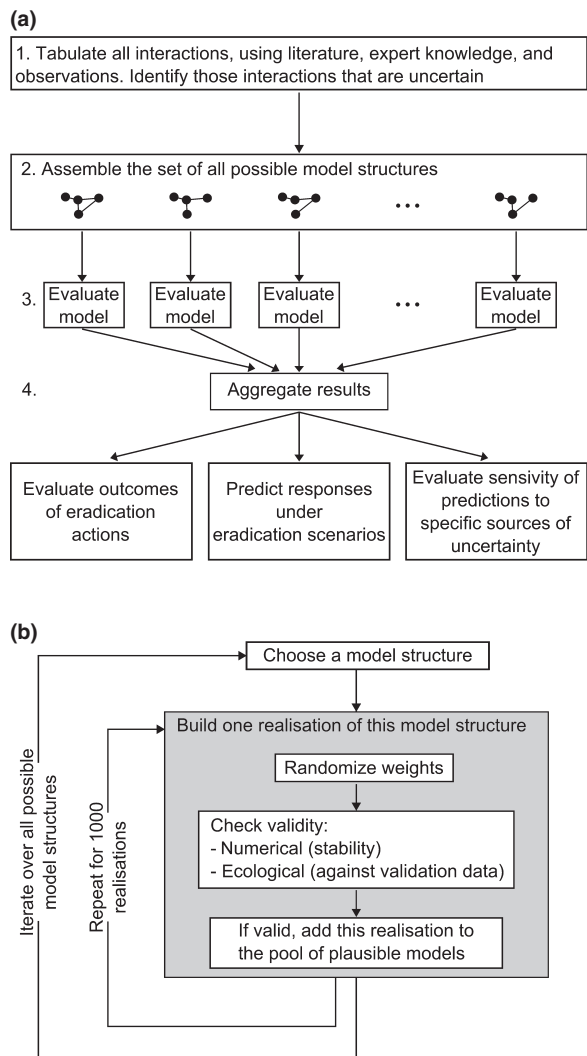


Fig. 2. (a) Summary flowchart of the modelling method used. (b) Details of step 3 (evaluation of each of the possible model structures).

for food and breeding territory, as well as dependence on elements not explicitly included in model, such as marine resources for seabirds. The dashed lines in Fig. 3 represent interactions that are poorly understood, and the importances of such interactions (to either of the interacting elements, or to other elements in the system) are unknown. We consider that such interactions are of a known type (e.g. predator–prey) and that their signs are therefore known, but which of those interactions should be included in the model is not clear.

Simulations were run in two broad phases. First, the suppression of cats and the Myxoma virus within the island ecosystem was simulated. A pool of candidate model structures was assembled, using all possible combinations of presence or absence of the unknown interactions. For each combination, 1000 stable, valid realisations were generated, each with random interaction weights, as described above. Following the eradication of cats and cessation of Myxoma virus releases, the rabbit population increased and the extent of tall tussock vegetation was reduced (Bergstrom *et al.* 2009; Dowding *et al.* 2009). These two responses were used as validation data for the first phase of simulations.

The eradication project was then simulated. Cats and Myxoma were completely removed from the models. We used only those

models that passed the stability and validation criteria in the previous simulations, and also passed a further stability test (i.e. with the cats and Myxoma removed). The eradication of various species from this system were then simulated.

Results

CAT AND MYXOMA VIRUS SUPPRESSION SIMULATIONS

The model has 17 unknown interactions, giving 2^{17} (c. 131 000) possible model structures. We thus obtained a pool of 131 million (1000×2^{17}) model realisations that passed the stability and validation tests. Figure 4 summarizes the predicted responses of the community members to the suppression of cats and the Myxoma virus. Rabbits increased and tall tussock vegetation decreased in all cases by definition, because these were the validation criteria.

The results provided moderate support for decreases in albatrosses (79% of cases) and burrow-nesting seabirds (70%), stronger support for decreases in redpolls and starlings (91%) and giant petrels (94%), and moderate support for an increase in skuas (76%) and Antarctic prions (70%). Grassland showed no change, as the model included no interactions that affected it (other than its own self-limitation). The predictions for the remaining community members did not give clear indication of increases or decreases, with majorities of 52–65%.

COMBINED ERADICATION SIMULATIONS

The target species in a given scenario did not necessarily decrease in response to simulated suppression (Table 2), with non-negative responses of target species generally more prevalent in simulations where multiple species were being targeted simultaneously. For example, simulations suppressing mice alone were almost always successful. In contrast, mice decreased in 65% of cases with simultaneous suppression of mice and rats, and in only 51% of cases with simultaneous suppression of rabbits, rats, and mice. Indeed, for the simultaneous suppression of rabbits, rats, and mice (i.e. the target species of the eradication project), the most common outcome was decreases in rabbits and rats, but not in mice (occurring in 45% of cases). The successful suppression of all three target species occurred in 33% of cases (Table 3).

Figure 5 shows the predicted responses for the suppression of rabbits, rats, and mice. These results are presented using only those cases in which the target species actually decreased (that is, effectively assuming that the eradication actions were successful in causing a sustained decline in the target species). Successful suppression of all three target species predicted increases in all native biota except skuas and penguins, with levels of support ranging from 72% to 99% (Fig. 5). Redpolls and starling were universally predicted to increase. The response of skuas was ambiguous, and there was moderate support (80%) for decreases in penguins.

The results of other simulated eradication scenarios (i.e. targeting only one of the three target species, as well as combinations of those species and also with redpolls and starlings) are

Table 1. Model community members. Indicators of abundance (abundant, common, uncommon, rare) from Copson (2002)

Community member	Description
Penguins	King penguin <i>Aptenodytes patagonicus</i> (abundant) Gentoo penguin <i>Pygoscelis papua</i> (common) Royal penguin <i>Eudyptes schlegeli</i> (abundant) Rockhopper penguin <i>E. chrysocome filholi</i> (abundant)
Skuas	Subantarctic skua <i>Catharacta lonnbergi</i> (common)
Giant petrels	Southern giant petrel <i>Macronectes giganteus</i> (common) Northern giant petrel <i>M. halli</i> (common)
Burrow-nesting seabirds	White-headed petrel <i>Pterodroma lessonii</i> (uncommon) Sooty shearwater <i>Puffinus griseus</i> (uncommon) Blue petrel <i>Halobaena caerulea</i> (uncommon) Grey petrel <i>Procellaria cinerea</i> (uncommon) Fairy prion <i>Pachyptila turtur</i> (rare) Soft-plumaged petrel <i>Pterodroma mollis</i> (rare) Diving petrels <i>Pelecanoides georgicus</i> and <i>Pelecanoides urinatrix</i> (rare)
Antarctic prions	Antarctic prion <i>Pachyptila desolata</i> (abundant)
Albatrosses	Light-mantled sooty albatross <i>Phoebastria palpebrata</i> (common) Black-browed albatross <i>Thalassarche melanophrys</i> (uncommon) Grey-headed albatross <i>Thalassarche chrysostoma</i> (uncommon) Wandering albatross <i>Diomedea exulans</i> (rare)
Small surface-nesting seabirds	Macquarie Island shag <i>Phalacrocorax purpurascens</i> Antarctic tern <i>Sterna vittata bethunei</i> Cape petrel <i>Daption capense</i> Pacific black duck <i>Anas superciliosa</i> Grey teal <i>Anas gracilis</i> Mallard* <i>Anas platyrhynchos</i> Kelp gull <i>Larus dominicanus</i>
Macro-invertebrates	Terrestrial and aquatic macro-invertebrates, including moths and moth larvae, spiders, worms, and flies
Tall tussock vegetation system	The tall tussock vegetation class (Selkirk <i>et al.</i> 1990). Dominated by the tall tussock grass <i>Poa foliosa</i> and the megaherb <i>Stilbocarpa polaris</i> , with other tall species including <i>Polystichum vestitum</i>
Herbfield vegetation system	The herbfield vegetation class (Selkirk <i>et al.</i> 1990). Dominated by <i>Pleurophyllum hookeri</i> and/or <i>S. polaris</i> , with <i>Blechnum penna-marina</i> and <i>Acaena</i> spp.
Grassland vegetation system	The short grassland vegetation class (Selkirk <i>et al.</i> 1990). Meadow-like vegetation dominated by species of <i>Agrostis</i> , <i>Luzula</i> , <i>Uncinia</i> , <i>Deschampsia</i> , or <i>Festuca</i>
Cats	Feral cat* <i>Felis catus</i>
Rabbits	European rabbit* <i>Oryctolagus cuniculus</i>
Rats	Ship rat* <i>Rattus rattus</i>
Mice	House mouse* <i>Mus musculus</i>
Redpolls and starlings	Redpoll* <i>Acanthis flammea</i> (common) Starling* <i>Sturnus vulgaris</i> (common)

Asterisk denotes introduced species. Naming authorities can be found in Selkirk, Seppelt & Selkirk (1990).

presented in Fig. S1 (Supporting information). Successful suppression of rabbits and rats, but not targeting mice, yielded broadly similar but much less definitive results compared with the successful suppression of all three species. Burrow-nesting seabirds, tall tussock vegetation, redpolls and starlings, and giant petrels were all predicted to increase, albeit with lower support (76–86%). However, the responses of albatrosses, macro-invertebrates, small surface-nesting seabirds, skuas, and Antarctic prions were ambiguous. Interestingly, simulations targeting all three pest species, but only successfully suppressing rabbits and rats, gave intermediate results, that is, predictions lying between those obtained with the successful suppression of all three, and those targeting only rabbits and rats (results not shown).

The sensitivities of the predictions to structural uncertainties are presented in Fig. 6. These results apply to the simultaneous suppression of rabbits, rats, and mice. The values indicate the dissimilarities between predicted responses with the link present, and with the link absent, aggregated over all model realisations. The predictions were most sensitive to those structural uncertainties involving small surface-nesting seabirds, and redpolls and starlings. The uncertainties involving small surface-nesting seabirds generally had little effect beyond the seabirds themselves. However, the redpoll and starling uncertainties had implications for the majority of the community members, including members without direct interactions with redpolls and starlings. The community members with the

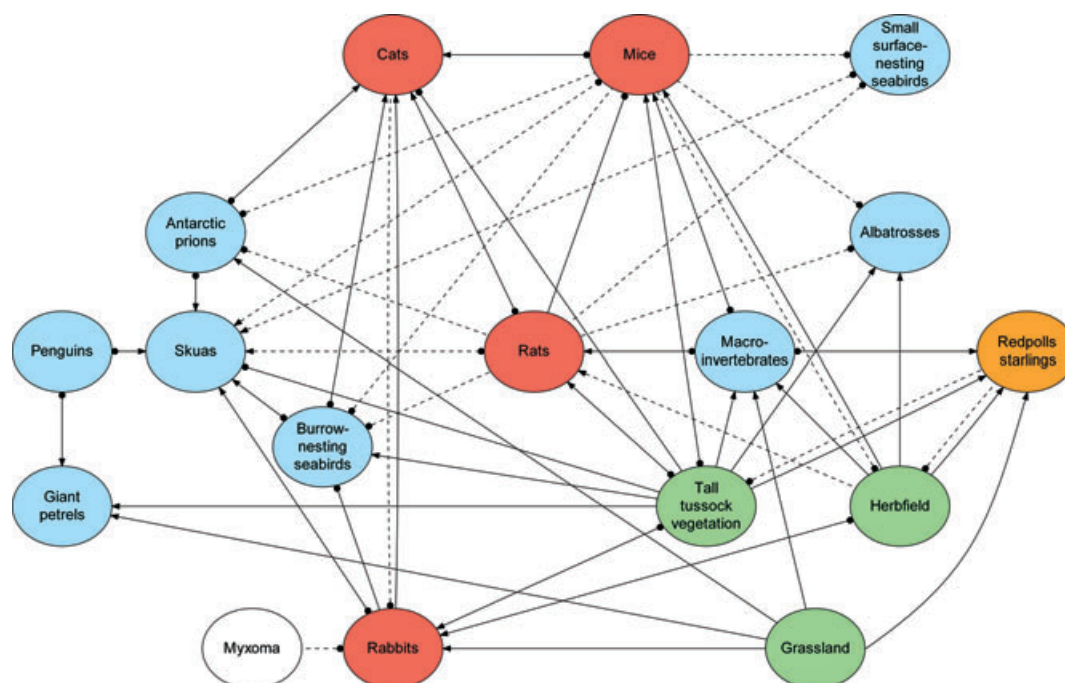


Fig. 3. Interaction network of subantarctic Macquarie Island. A line terminated with an arrowhead indicates a positive influence; one terminated with a dot indicates a negative influence; a link with both an arrow and a dot therefore indicates a predator–prey relationship. Dashed lines indicate interactions that are not well understood. All members have a limiting (negative) self-interaction, but for clarity these are not shown. Red indicates introduced pest species; blue indicates native species; orange indicates self-introduced alien species; green is vegetation.

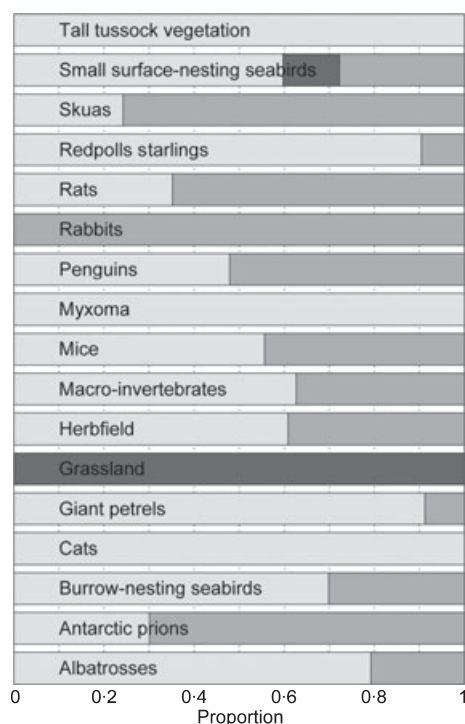


Fig. 4. Responses to simulated suppression of cats and Myxoma virus on Macquarie Island. Bars indicate the proportion of models in which the response was of a given direction. Light grey, negative response; dark grey, no change; mid-grey, positive response.

largest overall sensitivity to structural uncertainties were small surface-nesting seabirds, the herbfield vegetation complex, Antarctic prions, and skuas.

Discussion

MODELLING APPROACH

The approach used here examines outcomes across a large suite of plausible model structures. Results are consistent across all possible model structures are therefore robust, despite the structural uncertainty of the models examined, and are thus potentially informative in a management and planning context.

There are a number of potential issues with the modelling methodology used here. Eradication actions involve high death rates of target species, and modelled perturbations are intended to simulate the depression of target populations to near-zero or zero abundances. **Model predictions are therefore unlikely to be valid if such actions cause the remaining members of the ecosystem to change the way they interact (Dambacher & Ramos-Jiliberto 2007).** This could occur if the target species affects the way two other species interact (Wootton 1994), or if a predator responds to eradication actions by consuming a species it previously did not consume. Such issues did not affect the current study, but may be of concern for more general application to pest eradication modelling.

The qualitative predictions made in these analyses represent long-term responses, as the system arrives at a new equilibrium. Field observations following the eradication of cats, spanning only a decade or so, probably represent responses that can be considered as short-term with respect to the long-lived species, or mid-term with respect to vegetation and shorter-lived species. These observations should therefore be

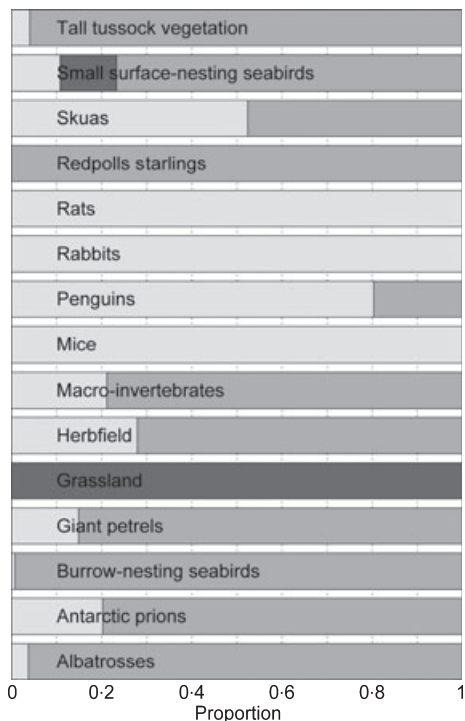
Table 2. The percentage of simulations in which each target species was successfully suppressed, for various eradication scenarios

Species response	Target species in scenario							
	Rabbits	Rats	Mice	Rabbits, mice	Rabbits, rats	Mice, rats	Rabbits, rats, mice	Rabbits, rats, mice, redpolls and starlings
Rabbits	98.6			89.0	96.2		96.2	94.5
Rats		99.4			94.6	91.9	80.2	60.7
Mice			99.5	94.7		65.2	51.4	41.1
Redpolls and starlings								51.9

Table 3. The percentage of simulations by various outcome, for simulated suppression of rabbits, rats, and mice

Outcome: taxa successfully suppressed	Taxa remaining	Percentage of simulations	Predicted ecological consequences
Rabbits Rats	Mice Redpolls and starlings	45%	Highly likely increase in mice and redpolls and starlings Possible impact on macro-invertebrates, small surface-nesting seabirds, albatrosses, Antarctic prions, skuas, and penguins
Rabbits Rats Mice	Redpolls and starlings	33%	Highly likely increase in redpolls and starlings Possible impact on macro-invertebrates and vegetation
Mice	Rabbits Rats Redpolls and starlings	16%	Highly likely increase in rabbits and rats Likely increase in redpolls and starlings Possible impacts to all native biota

Outcomes not listed here (e.g. suppression of rats but not mice or rabbits) occurred in less than 3% of simulations.

**Fig. 5.** Responses to the simulated suppression of rabbits, rats, and mice on Macquarie Island. Bars indicate the proportion of models in which the response was of a given direction. Light grey, negative response; dark grey, no change; mid-grey, positive response.

compared with model predictions with caution. Short-term responses are known to be poor indicators of long-term responses (Yodzis 1988). In particular, short-term responses are likely to be dominated by direct effects (i.e. those directly related to cat predation in the case of the cat eradication). Rabbit numbers appear to be declining following their initial increase after cat eradication in 2000. The indirect effects of the increased rabbit numbers (e.g. vegetation loss and potential impacts on the integrity of seabird breeding habitat) are still becoming apparent, particularly with albatrosses and other seabird populations that have relatively slow response times.

The simulations do not include impacts on non-target species through primary or secondary poisoning, or human disturbance from eradication activities (e.g. trampling of seabird burrows). These risks, along with the actions being undertaken in order to minimize their impacts, are discussed in detail in the project's environmental impact statement (Parks & Wildlife Service 2009a).

Some additional limitations of the modelling approach are outlined in Appendix S2, Supporting information.

CAT AND MYXOMA VIRUS SUPPRESSION SIMULATIONS

The predictions made by the first phase of simulations were generally in agreement with observations made on the island, and thus provide some confidence in the predictions for the rabbit, rat, and mouse eradication project.

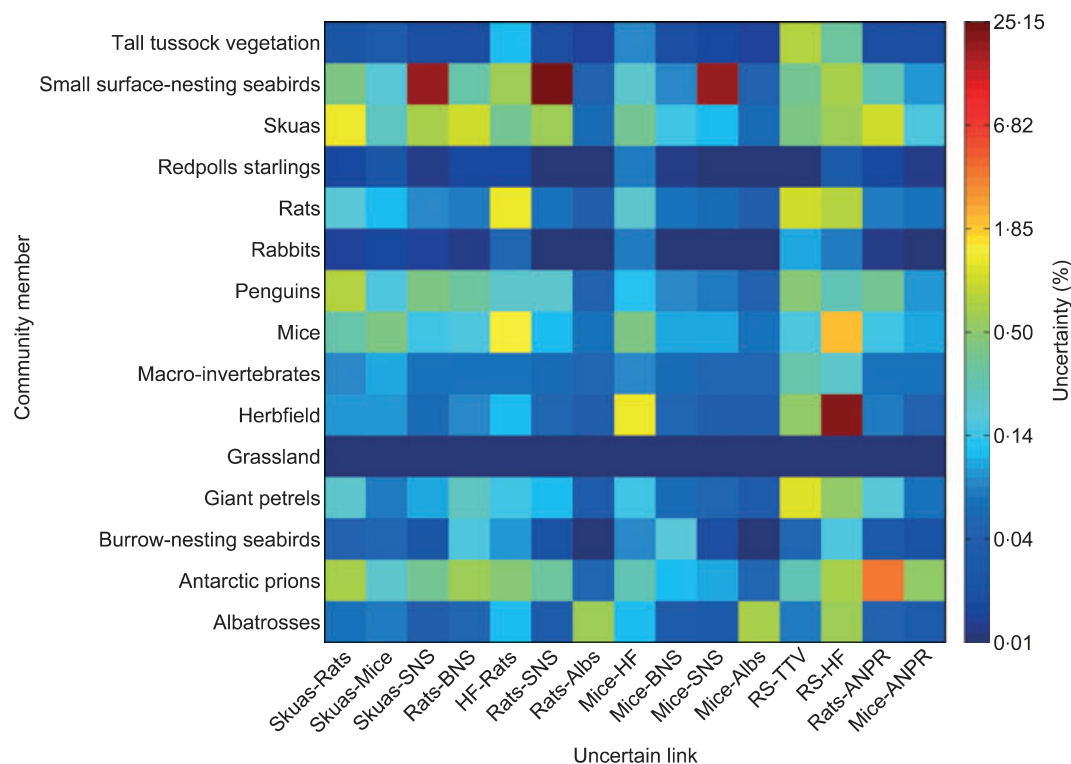


Fig. 6. Sensitivities of the responses of community members to uncertainties in the model structure, for simulated suppression of rabbits, rats, and mice. SNS, small surface-nesting seabirds; BNS, burrow-nesting seabirds; HF, herbfield vegetation; TTV, tall tussock vegetation; Albs, albatrosses; RS, redpolls and starlings; ANPR, Antarctic prions.

The simulations predicted that burrow-nesting seabirds would likely have decreased following cat and *Myxoma* virus suppression. This prediction was due to impacts from increased rabbit numbers, combined with the loss of tall tussock vegetation, that together offset the positive benefit of reduced predation from cats. On the island, the decline in breeding success of white-headed petrels and sooty shearwaters from 2006 to 2009 was thought to be due primarily to rabbit grazing impacts (Way, McInnes & Derry 2009). Some burrow-nesting seabird populations showed favourable responses to the eradication of cats from the island (Schulz, Robinson & Gales 2005; Brothers & Bone 2008; Dowding *et al.* 2009). However, with the decrease in vegetation, these species are now mainly found around the northern tip of the island and on rock stacks, where rabbits are absent or in low numbers. In some cases, these recoveries may have been driven by short-term transient effects: the breeding success of grey petrels peaked in 2005 but then declined again in all sites except the northern tip, again thought to be due primarily to decreases in tall tussock vegetation and associated ground instability and erosion (Way & McInnes 2010).

Model results matched island skua surveys, which showed an increase in the population on the plateau from 1997 to 2004, whereas the coastal population remained constant (Carmichael 2008). Populations remained relatively stable to 2009 (McInnes, Way & Achurch 2010).

Albatrosses were predicted to decrease due to the reduction in tall tussock vegetation. Albatross breeding success remained roughly constant from 2001 to 2007. However, the majority of

albatross breeding areas have now lost substantial areas of tall tussock vegetation. The breeding successes of black-browed, grey-headed, and light-mantled sooty albatrosses have declined over the last two seasons. For black-browed and grey-headed albatrosses, the breeding successes recorded in the 2009/10 season were the lowest for 16 years (McInnes & Way 2010). It is difficult to quantify the extent to which this habitat degradation contributed to these declines, as other influences (e.g. prey availability) also have significant effects on breeding success.

The model prediction of decreases in giant petrels was not matched by observations on the island: both giant petrel populations are increasing. These increases are thought to be due to increased adult survival through improved mitigation of fisheries impacts and increased breeding success through reduced disturbance around colonies following the introduction of special management areas and expeditioner education (R. Alderman, unpublished data). These factors were not included in the model.

SUCCESSFUL SUPPRESSION OF RABBITS, RATS, AND MICE

The simulations provided good support for the anticipated positive outcomes of the eradication project, with predicted recoveries of tall tussock vegetation, burrow- and small surface-nesting seabirds, and albatrosses.

Redpolls and starlings were, however, also predicted to increase. The eradication project anticipates this as a possible

outcome, with unknown consequences (Parks & Wildlife Service 2009a). Our results suggest that an increase in redpolls and starlings might inhibit the recovery of macro-invertebrates and herbfield vegetation: support for their recoveries with the suppression of rabbits, rats, and mice were moderate (79% and 72%). The additional simulated suppression of redpolls and starlings raised these levels of support to 100%. While starlings have been shown to be capable of exerting significant pressures on soil invertebrates and vegetation in other parts of the world (Whitehead, Wright & Cotton 1996; Linz *et al.* 2007), an improved understanding of the pressures that redpolls and starlings might bring to bear on a post-eradication Macquarie Island ecosystem would allow more rigorous assessment of the risk that these species might present. Redpolls, for example, are known to feed on seed heads of *Pleurophyllum hookeri* and *Leptinella plumosa* (Warham 1969; Parks & Wildlife Service 2009a), but it is not known whether they will forage in recovering and increasingly dense tussock and herbfield. The eradication project monitoring plan does not explicitly include any ongoing action regarding redpolls or starlings. Our results suggest that such monitoring and/or additional action is warranted.

Giant petrels were predicted to increase with the recovery of tall tussock vegetation, which could provide expanded northern giant petrel breeding habitat. However, we note that vegetation changes have rarely been implicated in investigations of giant petrel population changes (e.g. Patterson *et al.* 2008; but see also McInnes & Way 2010), and that the model does not take into account at-sea factors that might be affecting giant petrel populations. This prediction should be therefore be assessed with caution, and similarly the predicted decrease in penguins, which was driven by increased giant petrel predation.

OTHER ERADICATION SCENARIOS

The results support the current actions of simultaneous eradication of all three pest species, with generally sub-optimal outcomes with suppression of only one or two pest species. Brothers & Bone (2008) suggested that if the eradication of all three species was not possible, the eradication of rabbits (but not rodents) would be adequate for the recovery and increased breeding success of the majority of burrow-nesting petrels. Our results showed high support (89%) for this prediction; however, rabbit-only suppression had unsatisfactory outcomes for other taxa, particularly macro-invertebrates.

A common outcome of the simulations was the failure to suppress mice. This has been identified as a risk for the eradication project (Parks & Wildlife Service 2009a). Indeed, in other island eradications, failure to eradicate mice has been more common than failure to eradicate rats (Howald *et al.* 2007). Mouse eradication is increasingly problematic when other pest species are present (Caut *et al.* 2007; Harper & Cabrera 2009). This is, at least in part, a result of the structural position of mice within the ecosystem. The simultaneous control of rats and mice can, on balance, be beneficial to mice, if the indirect positive effect to mice (i.e. the suppression or removal of rats) outweighs the direct negative effect of the control programme

on the mice (Caut *et al.* 2007). This phenomenon, whereby the decline of a top predator can allow smaller predators to increase, is known as mesopredator release (Rayner *et al.* 2009). Here, the effect may be exacerbated by the difficulty in targeting all individuals of the mouse population (thus reducing the magnitude of the direct negative impact of control actions on the mouse population). Consistent with these previous analyses, our results showed increased failure to suppress mice when targeted as part of a multi-species eradication scenario (Table 2). While mice on Macquarie Island have not yet been observed to have major impacts on seabird or other native species, recent publications have provided graphic documentation of the potential impacts that mice may have if left as the only introduced mammals on the island (e.g. Jones & Ryan 2009).

Even relatively simple island ecosystems can have poorly understood ecosystem dynamics, and the eradication of multiple invasive species from such ecosystems is complex because of interdependencies and indirect effects. Our study has shown that quite robust conclusions can be derived about some management actions by using qualitative analyses, without requiring detailed knowledge of the interaction strengths. Our results not only raise the prospect of many successful outcomes for the current eradication actions but also highlight the risks of failure to eradicate mice and the competitive release of redpolls and starlings. Refinements to this model could be made as new data is collected and as the eradication project unfolds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Model construction: further details.

Appendix S2. Additional limitations of the model.

Appendix S3. Example R code.

Figure S1. Responses to simulated eradication scenarios of rabbits, rats, mice, and redpolls and starlings on Macquarie Island.

Table S1. Details of the interactions within the Macquarie Island ecosystem.

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