DR. CHRISTOPHER BAKER (Orcid ID : 0000-0001-9449-3632)
PROF. DAVID B. LINDENMAYER (Orcid ID : 0000-0002-4766-4088)

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A novel approach to assessing the ecosystem-wide impacts of reintroductions.

Christopher M. Baker[1,2,3*], Michael Bode[4], Nick Dexter[5], David B. Lindenmayer[6,7], Claire Foster[6,] Christopher MacGregor[6] , Michaela Plein[8] and Eve McDonald-Madden[8]

[1] *School of Biosciences, The University of Melbourne, Parkville, VIC 3010, Australia*
[2] *Centre for Biodiversity and Conservation Science, School of Biological Sciences University of Queensland, St Lucia, QLD 4072, Australia*
[3] *CSIRO EcosystemSciences,41 Boggo Road Dutton Park QLD 4102, Australia*
[4] *School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD, 4000, Australia*
[5] *Booderee National Park, Parks Australia, Jervis Bay, Jervis Bay Territory 2540, Australia*
[6] *Fenner School of Environment and Society, Australian National University, Canberra, ACT 2601, Australia*
[7] *Long Term Ecological Research Network, Australian National University, Canberra, ACT 2601, Australia*
[8] *Centre for Biodiversity and Conservation Science, School of Earth and Environmental Science, University of Queensland, St Lucia, Australia, 4072*

*c.baker7@uq.edu.au

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Abstract

Reintroducing a species to an ecosystem can have significant impacts on the recipient ecological community. Although reintroductions can have striking and positive outcomes, they also carry risks; many well intentioned conservation actions have had surprising and unsatisfactory outcomes. A range of network-based mathematical methods have been developed to make quantitative predictions of how communities will respond to management interventions. These methods are based on the limited knowledge of which species interact with each other and in what way. However, expert knowledge isn't perfect and can only take models so far. Fortunately, other types of data, such as abundance time-series, is often available, but, to date, no quantitative method exists to integrate these various data types into these models, allowing more precise ecosystem-wide predictions. In this paper, we develop mathematical methods that combine time-series data of multiple species with knowledge of species interactions and we apply it to proposed reintroductions at Booderee National Park in Australia. There have been large fluctuations in species abundances at Booderee National Park in recent history, following intense feral fox (*Vulpes vulpes*) control – including the local extinction of the greater glider (*Petauroides volans*). These fluctuations can provide information about the system isn't readily obtained from a stable system, and we use them to inform models that we then use to predict potential outcomes of eastern quoll (*Dasyurus viverrinus*) and long-nosed potoroo (*Potorous tridactylus*) reintroductions. One of the key species of conservation concern in the park is the eastern bristlebird (*Dasyornis brachypterus*), and we find that long-nosed potoroo introduction would have very little impact on the eastern bristlebird population, while the eastern quoll introduction increased the likelihood of eastern bristlebird decline, although that depends on the strength and form of any possible interaction.

Keywords: Interaction network; Decision science; Population dynamics; Ensemble forecasting; Trophic cascade; Conservation; Ecological Modelling

Introduction

Biodiversity across the globe are threatened by numerous and pervasive threats (Butchart *et al.* 2010; Hooper *et al.* 2012; Steffen *et al.* 2015). For highly threatened species suffering dramatic range declines, one of the key conservation actions is to translocate species – to either introduce species to new areas, or to reintroduce them into areas where they previously occurred (Ripple *et al.* 2014; Seddon *et al.* 2014). While the literature on translocations rapidly expands (reviewed by Griffith *et al.* 1989; Fischer & Lindenmayer 2000; Armstrong

& Seddon 2008; Perez *et al.* 2012), management is primarily focused on the species being translocated rather than on how such an action impacts the recipient ecosystem. Recent articles have urged for more research in understanding ecosystem implications of introductions (Armstrong & Seddon 2008; Perez *et al.* 2012), and particularly for more predictive modelling, which is only in its early stages (Taylor *et al.* 2017). A rich history of food web theory (e.g. Cohen 1978) highlights the potential catastrophic cascading impacts of ecosystem modification (Estes *et al.* 2011; Saterberg *et al.* 2013), and such collateral impacts have been well-documented following the introduction of invasive species (see Zavaleta *et al.* 2001). A single-species perspective to translocations ignores potential collateral impacts on other species in the recipient ecosystem, and it is important to take an ecosystem management perspective to environmental management (Simberloff 1998). While these issues have been recognised in the translocation literature, they have mainly focussed on "assisted colonisation": the release of species outside their natural range (sensu McLachlan *et al.* 2007; Ricciardi & Simberloff 2009; Rout *et al.* 2013). Yet, a growing number of translocations within a species' former range (i.e., reintroductions) have produced unanticipated outcomes, both positive and negative, at an ecosystem level (e.g. Hughes *et al.* 2013). A well-documented case of cascading ecosystem change from reintroductions comes from the re-establishment of wolves (*Canis lupis*) to Yellowstone National Park which was followed by dramatic vegetation changes because wolves predated on elks (*Cervus elaphus*), the dominant herbivore in that ecosystem (Estes *et al.* 2011). Examples like this clearly show that even translocation of species into their former range can lead to substantial ecosystem changes; sometimes this may be positive, but others may lead to negative implications on a system.

In recognition of the potential unexpected consequences of translocations on the wider ecosystem, the "IUCN guidelines for re-introductions and other conservation translocations" (IUCN/SSC 2013), explicitly called for formal decision-making methods to evaluate ecosystem-wide risks before a reintroduction or translocation takes place (IUCN/SSC 2013). The ecosystem consequences of introductions has previously been the purview of invasion ecology (e.g. Kumschick & Nentwig 2010; Wardle *et al.* 2011), which has developed risk assessment methods (Sikder *et al.* 2006; Hayes & Barry 2008) that can, in theory, evaluate the potential impacts of reintroductions. However, the utility of these risk assessment methods has recently been questioned (Hulme 2012), in part because they lack consideration of the complex and indirect nature of interactions between species in an ecosystem (Sih *et al.*

2010; Jones & Gomulkiewicz 2012). While the dynamics of ecosystem responses to reintroductions can be investigated retrospectively, they have proven difficult to anticipate because they often involve a cascading series of indirect effects through extensive species interaction networks (Raymond *et al.* 2011). To improve the rigor and acceptability of decisions for reintroductions, we must look beyond invasion ecology and develop novel methods that explicitly incorporate the complex interactions between species and allow for cascading changes to propogate through the system to give a quantitative assessment of the ecosystem-wide outcomes associated with species translocation.

A thorough ecosystem-based risk assessment for a proposed translocation would identify the range of possible ecosystem consequences (i.e., the effects of the translocation on all species in the ecosystem), and provide a quantitative estimate of their relative magnitudes and likelihoods. Such predictions require an understanding of both the direction and relative strength of the interactions between species, including predator-prey, mutualism and competition (Herr *et al.* 2016). Estimates of strength and direction of species relationships requires focused experiments and/or analysis on small suites of species such as small-scale field experiments (e.g. Foster *et al.* 2015) and, controlled microcosm experiments (e.g. Fronhofer *et al.* 2015). Importantly, the number and diversity of interactions scale nonlinearly with ecosystem size (Bender *et al.* 1984; Dambacher 2003), giving little chance of completing empirical measurements of all interaction strengths within an ecosystems (but see (Hone *et al.* 2015) for some small case studies).

Time-series data of species' abundances is much more readily available compared to comprehensive interaction strength information. These data can therefore provide indirect information about the strength of species interactions (Raymond *et al.* 2011; Baker *et al.* 2017; Bode *et al. 2017*). With the reality of limited information and a pressing need to make decisions about reintroductions at an ecosystem level, it is crucial that methods are developed that can use all available forms of information to inform ecosystem-wide decisions. A variety of methods have been developed that use interaction networks to predict how perturbations will flow through an ecosystem (Dambacher 2003; Raymond *et al.* 2011; Dexter *et al.* 2012; Baker *et al.* 2017). However, using time-series data to inform an interaction network is challenging, and although methods to estimate shifts in interaction strengths from time series have recently emerged (Ushio *et al.* 2018), these have not been employed in conservation management. To ensure that predictions are as accurate as possible, we urgently require methods that can use this data to further constrain and improve ecosystem predictions.

In this paper, we develop a new method that can incorporate time-series data when predicting ecosystem-wide responses to translocations. Our approach extends previous modelling approaches (e.g. Raymond *et al.* 2011; Dexter *et al.* 2012; Baker *et al.* 2017), allowing us to predict future dynamics, rather than being limited to equilibrium changes, in a system with time-series data and connected to an ongoing conservation management project. We apply this technique to a planned translocation of two species of regionally extinct marsupials to Booderee National Park (BNP), Australia: a fungivore (long-nosed potoroo, *Potorous tridactylus*) and a carnivore (eastern quoll, *Dasyurus viverrinus*). Extensive monitoring in the park has generated time series of species abundances (Lindenmayer *et al.* 2008; Lindenmayer *et al.* 2016), which we use to inform our qualitative ecosystem models for more accurate estimates of reintroduction risk. We use this case study to illustrate two important benefits of our new method: first, that ecosystem models can be generated that can recreate a suite of complex ecosystem dynamics observed over 6 years at BNP. Second, that the resulting parameterised models allow us to undertake quantitative risk assessments for some key aspects of the BNP ecosystem in response to the staged reintroduction of two species, which we do in collaboration with park management. In doing so, we provide a template for undertaking quantitative modelling of the ecosystem-wide risks of specific reintroductions on the basis of limited quantitative information.

METHODS

Case study

Our study area was BNP which is located in the Jervis Bay Territory, 200 km south of Sydney, south-eastern Australia. BNP supports more than 725 species of native plants and provides habitat for more than 260 species of terrestrial vertebrates. These include populations of many species of conservation concern, and it contains an important remaining population of the endangered eastern bristlebird (*Dasyornis brachypterus*) (Lindenmayer *et al.* 2016). The reserve is also subject to one of the highest intensity exotic predator baiting programs in Australia (Lindenmayer *et al.* 2014). Since 2003, intensive baiting of foxes has taken place throughout BNP, in concert with a multi-species monitoring program that annually surveys 134 sites to quantify population changes in response to management interventions of vascular plants, reptiles, mammals and birds, giving us time-series data from 2003 to 2009 (Lindenmayer *et al.* 2013; Lindenmayer *et al.* 2014; Lindenmayer *et al.* 2016).

The long-nosed potoroo has recently been reintroduced to Booderee National Park, and there are plans to reintroduce the eastern quoll. The eastern quoll has been extinct on mainland Australia since the 1960s, and long-nosed potoroo populations are generally small and isolated, having significantly contracted since European settlement (Maxwell *et al.* 1996). Re-establishing their populations within Booderee National Park will reduce the risk of species extinction. The long-nosed Potoroo is a medium sized marsupial with males (740–1640g) being typically heavier than females (660–1350g) (Van Dyck & Strahan 2008). Like all potoroos they are largely fungivorous and experiments from a study in East Gippsland confirmed that spores carried in the faeces were viable and that potoroos are probably an important agent in maintaining the fungal-plant symbiosis (Claridge *et al.* 1992; Claridge *et al.* 1993). The eastern quoll is a medium sized carnivorous marsupial with males (900-2000g) typically bigger than females (700-1100g) (Godsell 1995). Its diet is mainly comprised of invertebrates, small terrestrial mammals and birds. Re-establishing eastern quolls could be a first step in the re-establishment of the largely extinct native carnivore guild (Dexter 2016).

Ecosystem modelling

We use an ecosystem network model by Dexter *et al.* (2012) to represent the structure of interactions between extant species and functional groups in the BNP ecosystem (Figure 1) – specifically the existence and direction of the pairwise interactions between species (positive/negative interactions are beneficial/detrimental to the abundance of the recipient). We extended a previous interaction network for this system (Dexter *et al.* 2012) to include the species considered here for reintroduction, the long-nosed potoroo and the eastern quoll. Interactions for these species were included based on their ecology as well as the authors' collective knowledge of the system from long-term monitoring of vertebrates at Booderee National Park (Lindenmayer *et al.* 2018). Since the network model contains individual species (e.g. eastern bristlebird) and functional species groups together (e.g. lizards), we refer to these as *ecosystem elements*. The BNP interaction network contains a total of twenty ecosystem elements resulting in hundreds of possible interspecific interaction terms, even in the simplest model of the system. In relation to the available data, the parameter space of such an ecosystem model is large and complex – which is typical of natural ecosystems.

Hence, we propose an ensemble modelling approach, where we construct a large number of models that attempt to replicate the observed dynamics (Battogtokh *et al.* 2002; Raymond *et al.* 2011; Baker *et al.* 2017) and thus are a feasible representation of the system. Our method therefore contrasts with other ecosystem modelling methods which seek to find the best-fitting model (Battogtokh *et al.* 2002). Apart from the network structure, we also have data on the relative change in the populations of nine species, post-fox control. Like all estimates of species abundance in ecosystems, uncertainty is associated with these data due to both the monitoring process and underlying stochasticity in the ecosystem dynamics. We therefore use information from time-series data to define *dynamic constraints*, that we place on particular features in each ensemble member (defined during a workshop with park managers). Information on population change in nine ecosystem elements (see Table 1) in six years following the instigation of fox control at BNP, distilled into dynamic constraints, form the constraints through which generated population trajectories must pass to be considered plausible realisations of the system. The dynamic constraints are deliberately kept wide as we seek models that qualitatively recreate the observed dynamics at BNP.

We used a set of generalised Lotka Volterra equations to model the rate of change of the ecosystem elements through time (Murray 2002):

$$\frac{dn_i}{dt} = r_i n_i + n_i \sum_{j=1}^{N} \alpha_{i,j} n_j, \qquad \textbf{(1)}$$

where n_i and r_i are the abundance and growth rate respectively of the i^{th} ecosystem element, and N is the number of number of ecosystem elements being modelled. The $\alpha_{i,j}$ terms describe the per-capita interaction strengths between ecosystem element i and j. We aim to obtain an ensemble of parameter sets (i.e., a set of both r_i and $\alpha_{i,j}$), that are both “viable” pre-fox control and that can replicate the system dynamics following fox control. Viability means that there exists a stable equilibrium with every ecosystem element present. This is done by first solving for the steady state of Eq. (1) and ensuring that each $n_i > 0$, and then checking stability of that equilibrium point. The equilibrium point is stable if the real part of every eigenvalue of the community matrix is negative (Baker *et al.* 2017).

We generated the magnitude of each parameter randomly. Estimates of growth rates are prevalent in the literature (Duncan *et al.* 2007; Hone *et al.* 2010), and we use these estimates to constrain possible growth rates, while the magnitude of each of the interaction strengths $\alpha_{i,j}$ are drawn from a log-normal distribution (see *Appendix S1* for details). Uniformed choices for these distributions provided no parameter sets that passed the dynamic constraints. Hence, we implemented an iterative process: first, we widened the dynamic constraints to find 100 parameter sets that are both viable and that pass the dynamic constraints. This yields an initial set of parameters that forms the basis of log-normal distributions, which are then further used to generate the parameters in the next iteration. We continue this process of tightening the dynamic constraints until a set of 100 parameter sets that satisfies the original dynamic constraints. To ensure that the parameter sets and dynamics are varied, we added some “random noise” to the distributions at each iteration (see *Appendix S1*). We do this because we wanted many different models that all satisfy our constraints, rather than a single model (or many very similar models). Finally, once we attained parameter sets that passed all original constraints, we draw a further 10,000 parameter sets to use for making future projections. See *Supporting Information* for full details of the fitting process. We fit the ensemble using six years of data from 2003 to 2009, but, since the reintroductions only started in 2015, we need to simulate a further six years. To recreate realistic processes, we suppress glider abundance to zero over this final six year time period (as gliders went extinct (Lindenmayer *et al.* 2008; Lindenmayer *et al.* 2011).

Once we generated the ensemble, we simulated the reintroductions of long-nosed potoroos and eastern quolls. The first step was to estimate their growth rates, which we did in the same way as every other ecosystem element, along with their interactions with other species. To draw the magnitude of interaction strengths, we fitted a lognormal distribution to all $\alpha_{i,j}$’s in ensemble, and used that distribution to draw $\alpha_{i,j}$’s for the new species. To simulate a reintroduction, we started with the system (without the species to be reintroduced) and project forward using Eq. (1) for six years with foxes suppressed to 5% of their 2003 abundance. We then simulated it for a further six years with foxes suppressed and also suppressing greater gliders to zero. The final state of this simulation gives us the initial condition for the reintroduction. We reintroduced the target species to the system, starting with a very low abundance (10% of the smallest abundance of the other ecosystem elements). We required the initial change in the reintroduced species to be positive, as we are interested in how a successful introduction will affect other ecosystem elements and then solve the system for a further ten years. We also simulated this ten year period without reintroducing the species, which provides the counterfactual – what would have occurred if there was no reintroduction. We repeated this simulation 10,000 times for each ensemble member and each reintroduction.

For each simulation, we then checked whether there were any *adverse* outcomes for any ecosystem elements. We then consider the frequency that adverse outcomes occur for every ecosystem element under three scenarios; a long-nosed potoroo reintroduction, a long-nosed potoroo and eastern quoll reintroduction and no reintroductions (the counterfactual). We do not consider an eastern quoll-only reintroduction scenario because the potoroo reintroduction was already approved at the beginning of this project making a quoll-only scenario very unlikely. An adverse outcome was defined as an unacceptable decline in a species or ecosystem element after ten years (defined during a workshop with park managers, Table 1). The values represent the relative proportional change in the abundance of each ecosystem element that is considered unacceptable, and are informed by the importance of the ecosystem element to the national park (e.g., the endangered eastern bristlebird has a smaller threshold for adverse outcomes than the widely distributed brushtail possum; and the species' starting (equilibrium) abundance. Generally, highly abundant species are allowed large declines (such as unpalatable plants), while for species with lower abundance, we only allowed small declines. For example, a reintroduction that decreased the amount of palatable plants by 5% was considered acceptable, while a decline of 15% would be classified as adverse.

Results

We use a novel approach to model the ecosystem-wide implication of reintroductions. The method finds randomly generated system models that conform to a set of constraints. Using our approach, we were able to generate 10,000 systems that passed all of the constraints and that had a broad range of responses from our constraining nine ecosystem elements while still adhering to our dynamic constraints (Table 1, bolded rows). These trajectories took numerous forms within these bounds (e.g. Figure 2, grey lines).

By forward simulating these 10,000 systems from when intensive fox control began (2003), to beyond our period of observations (the constraints, in 2008), until the recent state of the system (2015), we were able to obtain a picture of the potential changes in species abundances before any further actions are implemented. As our method produces an ensemble of models, we obtain a distribution of change in relative abundance for each species. Numerous species' abundance distributions are centred near one, indicating that these species could have increased or decreased up to 2015. This includes invertebrates, ground-foraging birds, brown antechinus, the flying-fox, brushtail possums, raptors, long-nosed bandicoot and owls (Figure 3). The chestnut mouse shows only decreasing and some stable population trajectories while the trajectories always increase for the endangered eastern bristlebird, as well as for wallabies and pythons. In contrast, lizards, rats and ringtail possums show only decreasing trajectories (Figure 3), including many in which the ringtail possum go locally extinct by 2015, something that is now thought to have occurred (Lindenmayer *et al.* 2018). The greater glider is not shown as it is forced to go extinct after 2008.

Using generated ecosystem models, we can explore potential adverse implications in response to the reintroduction of long-nosed potoroos (Figure 4, green bars) and the planned additional reintroduction of eastern quolls to BNP (Figure 4, yellow bars), both relative to the no-reintroduction scenario (Figure 4, blue bars). We also run these scenarios for the network where the predation of the eastern brislebird and the chestnut mouse from the eastern quoll is removed (Figure 5). The reintroduction of species into BNP changes the frequency of adverse responses we recorded for a number of species. Either reintroduction scenario (i.e., long-nosed potoroo or long-nosed potoroo and eastern quoll) dramatically increases the frequency of adverse responses recorded for the long-nosed bandicoot to above 90%, a doubling of the frequency observed without reintroduction. An increase in adverse responses is also observed for invertebrates, a key food source of long-nosed bandicoots. However, the magnitude increases from below 5% to 40% when both long-nosed potoroos and eastern quolls are reintroduced. Under the no-reintroduction scenario, no adverse outcomes are observed for lizards. Yet, for long-nosed potoroo reintroduction and the addition of eastern quolls, adverse responses dramatically increase, reaching over 40% and 65% of the realisations, respectively. Raptors and the eastern bristlebird both experience a considerable increase in the frequency of adverse outcomes from the reintroduction of eastern quolls. Indeed, no adverse outcomes are observed for the eastern bristlebird in our trajectories until the introduction of eastern quolls when approximately 40% of the realisations result in adverse outcomes for this species (Figure 4). Further, our results show that the eastern bristlebird adverse outcome is driven primarily by potential eastern quoll predation, rather than by a chain of interactions (Figure 5). The bush rat, chestnut mouse and ringtail possum all have a low threshold of population change to be considered an adverse outcome (10%, 10% and 0% respectively) and this is reflected in all scenarios having a high frequency of adverse outcomes (Figure 4).

The level of population decline that managers consider adverse is important for assessing the outcomes of reintroductions. The acceptable levels of population decline used in this exercise were arbitrary and conservative and without reference to the global status of the species. When we explore the relative change in abundance for the reintroductions of long-nosed potoroos (Figure 6, purple bars), and for the combined reintroduction of eastern quolls and long-nosed potoroo (Figure 6, red bars), relative to no introduction we find that species respond in very different ways to reintroductions, with some indicating a tendency toward population increases following reintroductions, some showing a tendency to decline, and others showing little change. Lizards, brushtail possums and long-nosed bandicoots show an increase in the frequency of realisations stable or declining with any reintroduction (Figure 6). Long-nosed bandicoots, in particular, exhibit a large spike in likelihood of extinctions from reintroductions, especially when eastern quolls are reintroduced. The reintroduction of eastern quolls also potentially affects the brown antechinus and the ringtail possum with an increase in realisations with adverse outcomes. Most of the realisations for the bush rats and the chestnut mouse result in a population decline irrespective of whether reintroductions are implemented or not and in many of these realisations the species become locally extinct.

Discussion

Understanding how species reintroductions could affect the recipient ecosystems is a key concern for assessing the risk of implementing introductions (IUCN/SSC 2013), and, although we focus on reintroductions, the same methodology can be used to examine the potential implications of introductions for other reasons, including for assisted colonisation, for ecosystem engineers and for biocontrol agents (e.g. Headrick & Goeden 2001; Lunt *et al.* 2013). Due to the complexity of ecosystems, predicting the likely outcomes of reintroductions requires computational mathematical models that encapsulate both the structure of the interaction networks, and the uncertain constraints of the observed data. We developed methods to generate an ensemble of models that replicated the complex dynamics following fox control in 2003 at Booderee National Park. Using this ensemble, we simulated the reintroduction of long-nosed potoroos and eastern quolls to the park to predict the range of potential impacts on the ecosystem. A species of particular importance is the endangered eastern bristlebird (Lindenmayer *et al.* 2009; Lindenmayer *et al.* 2016), and our model predicts that the population will be relatively stable with the reintroduction of long-nosed potoroos, but, if eastern quolls are reintroduced, there is a chance of an unacceptable decline for the eastern bristlebird, depending on whether eastern quolls predate on it or not. This is of particular interest as the eastern bristlebird listed as an endangered species by the IUCN. Eastern quolls are certainly capable of killing and eating small birds but the only published dietary study shows them to be mainly insectivorous (Blackhall 1980). In our simulations with predation, we find an unacceptable decline in 40% of our simulations, but without predation, there is no decline, indicating this to be a key interaction to better understand. Beyond the impacts on the eastern bristlebird, managers are interested in possible unexpected declines. For example, the model predicts that with the reintroductions, lizards have a reasonably high chance of unacceptable declines. Interestingly, our model predicts with high certainty a drop to nearly zero abundance of common ringtail possums by 2015, despite constraints that forced only a 50% decline during initial fox control. Unfortunately for the ringtail possum it seems our results are reflected in reality as it is now believed that this species has become locally extinct in Booderee National Park.

While the outcome for the ringtail possum indicate some success in our approach for capturing complex dynamics playing out in nature there are some methodological restrictions that warrant further discussion and work to allow unexplainable results to have more ecological support. Computational constraints are often reflected in simplifications in the models of the systems we are trying to predict. The complexity of ecosystems throws up many challenges, in particular the way in which the interactions between species are represented. For simplicity we have represented the interaction strengths as linear relationships, although most inter-specific interactions are likely to be non-linear such as Type II or Type III functional responses of prey to density to prey consumed (May 1981). For example, most mammalian predators are believed to have a type III (sigmoid) functional response so that at low prey densities predation rate decreases (Murdoch 1973). This type of response can be important when reintroducing multiple species: one might need and it can be important to allow a new prey species to build up its population before introducing predators (Plein *et al.* 2015). Thus, the unmodified Lotka-Voltera equations as used in this study, are likely to over-estimate predation rate when prey numbers decline, an outcome that may lead to the prediction of higher rates of extinction. The spatial heterogeneity of habitats may also impact the interactions between species, for example the presence of prey refugia may reduce interaction strength, lowering extinction risk and maintaining overall system stability (Olivares & Jiliberto 2003). At Booderee National Park, for example, eastern quoll and eastern bristlebird largely prefer different habitats, with eastern bristlebird preferring dense vegetation such as heath (Baker 2000) and eastern quolls preferring more open habitat

(Rounsevell et al 1991). Thus the substantial area of dense heathy vegetation at Booderee is likely to provide a refugia for eastern bristlebirds potentially dampening the strength of the interaction between these two species (Taws 1996). Incorporating both these limitations in future would be ideal and our work provides an incremental step towards further advances to capture these limitations whilst allowing for the reality of limited direct information on interactions strengths.

Our method fits into a suite of approaches that analyse the effect of perturbations on an ecosystem. These include qualitative modelling, which has been used widely to model the introduction or removal of species (Dambacher 2003; Raymond *et al.* 2011), and fuzzy cognitive maps (Ramsey & Norbury 2009; Ramsey *et al.* 2012; Baker *et al.* 2018). Our approach is particularly closely related to the computational qualitative modelling approaches of Raymond *et al.* (2011); a method focussing on equilibrium changes. To move from equilibriums to dynamic models (like the one presented here), we have to specify a functional form for the species dynamics. It is important to use non-equilibrium models in this system for two reasons. First, we could not make good use of the time-series data with an equilibrium model. For example, one of our dynamic constraints was that long-nosed bandicoot abundance had to first increase, but then decrease. It is not clear how to translate this information to inform an equilibrium model, because it is unclear whether the new equilibrium is lower or higher than the preceding one. Second, the aim of radical ecosystem interventions like eradication or reintroduction is to drive the system to a new equilibrium – an equilibrium with a new species present. Hence, we believe it important to use dynamic models in these situations.

Incorporating dynamic constraints into ecosystem modelling creates difficult methodological challenges. First and foremost the numerous potential parameters for such a complex system mean that the parameter search space is exceptionally large. Within such a large search space finding parameters that reproduced the complex dynamics observed at Booderee National Park proved difficult. To overcome this, we used a sequential search approach. First starting with broader dynamic constraints, allowing systems that passed these broad constraints to be found. Second we fitted distributions to the parameter sets found to inform future searches and increasing the number of systems found that passed the tightening constraints. Such an approach builds on ensemble modelling approaches (Battogtokh *et al.* 2002; Baker *et al.* 2017) and is related to approximate Bayesian computation (Beaumont 2010). Despite our success in capturing the desired dynamics, there are still some unanswered questions and there is room for further progress. In particular, the complex model means that the underlying reasons for some of our results is unclear. For example, in about 20% of our simulations, a long-nosed potoroo introduction leads to a sharp decline in brushtail possums. While a simple answer is that the whole network causes this decline, there may also be smaller trophic cascades within the network that is the fundamental cause. Further exploration of the mechanisms and pathways of observed dynamics would greatly enhance this work and better inform management. Our model will be a foundation for investigating these type of questions as any future dynamics play out.

Making this type of analysis broadly accessible and widely used is a major aim of work going forward. There is some basic code available (Baker *et al.* 2017) but fitting complex dynamical models to data is challenging (Hudson & Reuman 2013) and the lack of general algorithms to do this is a significant gap in the literature. Such analysis will likely rely on experts to elicit information on ecosystem structure among other components. In these situations it is wise to use expert elicitation techniques to gain insight into the system (MARTIN *et al.* 2012) and indeed there are a range of methods in the fuzzy logic literature for developing interaction networks (Zhang *et al.* 2013; Game *et al.* 2018). The outcomes of this work provide a platform to assess the ecosystem risks from reintroductions, however defining explicit objectives for individual projects was not considered here. For any project it is essential to define all objectives. Imbedding our approach in established process for doing this, such as structured decision making (Martin *et al.* 2009), that aid in objective identification and approaches for dealing with multiple objectives would provide an added layer of rigour to decision-making for reintroductions that we recommend.

Those responsible for the protection of threatened species are increasingly undertaking what some can perceive as radical interventions into ecosystems. Reintroductions are a common and longstanding example of this, but others include assisted migrations, and eradications (Isaac-Renton *et al.* 2014; Jones *et al.* 2016). While such interventions can have important benefits for some target species, it is difficult to forecast the consequences of these actions, especially as we often deal with large and complex novel ecosystems (Hobbs *et al.* 2006) . Decision-makers are willing to take these risks because potential benefits are large, sometimes with extraordinary success. However there is increasing recognition of the potential perverse outcomes that could occur from such actions. With this recognition comes a call for approaches that can identify these potential outcomes and inform proactive, holistic, management of ever increasing list of threatened plants and animals globally. Here we have taken up this challenge and developed methods to better predict the outcomes of conservation interventions (such as translocations and eradications), that can be integrated into existing frameworks for risk assessment. In doing so we hope to add a level of quantitative rigour to a processes which can be, at times, somewhat ad-hoc or qualitative, and to encourage further research to explore novel approaches to model complex ecological systems with limited data and thus to better inform the management of our complex and little understood natural world.

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Table 1: Unacceptable (adverse) changes in abundance after 10 years for each ecosystem element in the Booderee National Park case study, as defined by park managers. Ecosystem elements with dynamic constraints are bolded.

Ecosystem element	**Dynamic Constraints**	**Acceptable change**
Unpalatable plants		-0.7
Brushtail possum	**50% - 200% at year 6**	**-0.6**
Swamp wallaby	**>150% at year 4** **>300% at year 6**	**-0.5**
Brown antechinus	**50% - 200% at year 6**	**-0.2**
Eastern chestnut mouse		-0.1
Eastern bristlebird	**>150% at year 6** **<400% at year 6**	**-0.1**
*Python*s		-0.1
Owls		-0.1
Raptors		-0.1
Flying foxes		-0.1
Ground-foraging birds		-0.1
Lizards	**50% - 200% at year 6**	**-0.1**
Invertebrates		-0.1
Canopy		-0.1
Palatable plants		-0.1
Bush rat	**<90% at year 6**	**-0.05**
Long-nosed bandicoot	**>300% at year 3** **>75% at year 6** **< 200% at year 6**	**-0.05**
Ringtail possum	**<66.67% at year 4**	**-0**

	<50% at year 6	
Greater glider	**<90% at year 4**	**-0**

Figure 1: Network of interacting species at Booderee National Park. The fox (red) has been largely removed from the park since 2003. The long-nosed potoroo and the eastern quoll (yellow nodes) are being reintroduced into the system.

Figure 2: Dynamic constraints and the range of simulation trajectories for the six years following the start of fox control for nine ecosystem elements in BNP. The pink bars depict the dynamic constraints, the solid black line is the average trajectory through time, the light grey lines are a subset of randomly-chosen individual realisations for illustration and the grey shaded region shows the lower and upper bounds for all 10,000 simulated trajectories that satisfied all nine constraints.

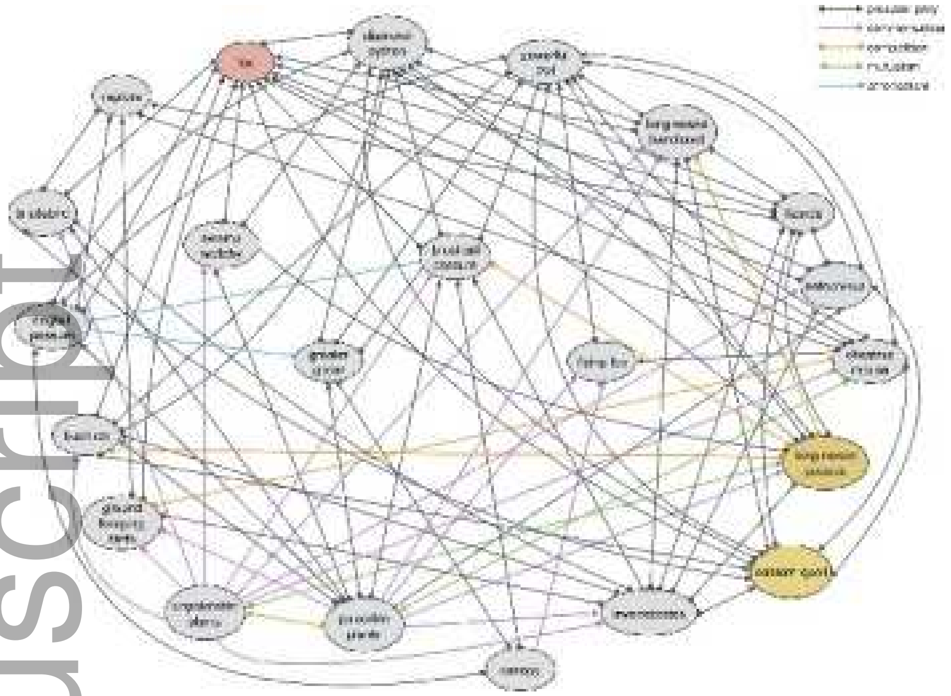
Figure 3: Frequency of relative changes in abundance of a subset of fifteen species in Booderee National Park after fox removal from 2003 to 2015. A value of one represents abundance trajectories without change (dashed line), greater than one means an increase and below one a decrease.

Figure 4: The frequency of adverse outcomes when there is no reintroduction (blue), long-nosed potoroo reintroduction (green) and eastern quoll and long-nosed potoroo reintroduction (yellow). An adverse outcome occurs when the species declines by more than the percentage specified in Table 1, from 2015 to 2025. The dashed line represents when a quarter, a half, and three-quarters of the realisations are considered adverse. The vertical colour bar shows proportional decrease in the population below which is considered adverse (i.e., ecosystem elements at the top of the figure can change more before adverse events are considered to have occurred).

Figure 5: The frequency of adverse outcomes when there is no reintroduction (blue), long-nosed potoroo reintroduction (green) and eastern quoll and long-nosed potoroo reintroduction (yellow), when the predation of the eastern bristlebird and chestnut mouse from the eastern quoll is removed. An adverse outcome occurs when the species declines by more than the

percentage specified in Table 1, from 2015 to 2025. The dashed line represents when a quarter, a half, and three-quarters of the realisations are considered adverse. The vertical colour bar shows proportional decrease in the population below which is considered adverse (i.e., ecosystem elements at the top of the figure can change more before adverse events are considered to have occurred).

Figure 6: Modelled frequency of relative changes in abundance of a subset of six ecosystem elements in Booderee National Park, ten years after the reintroduction of long-nosed potoroos (purple), or long-nosed potoroos and eastern quolls (red), without eastern quoll predation on the eastern bristlebird. Each realisation is a comparison of the same model with reintroduction and without reintroductions. A relative change of one means no change, greater than one an increase and below one a decrease. Bars at zero indicate realisations where the species went extinct in the simulation.



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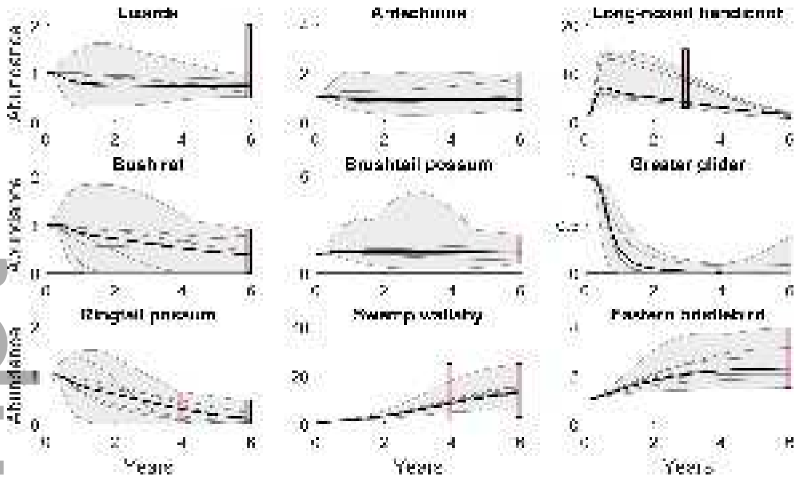

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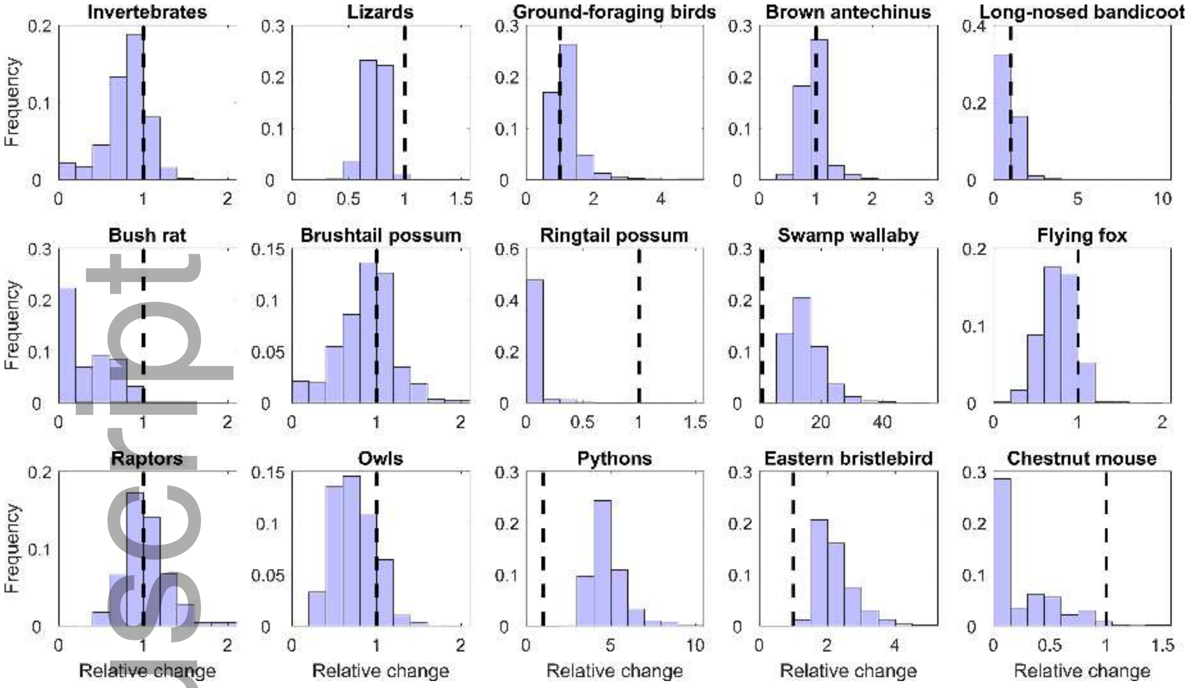

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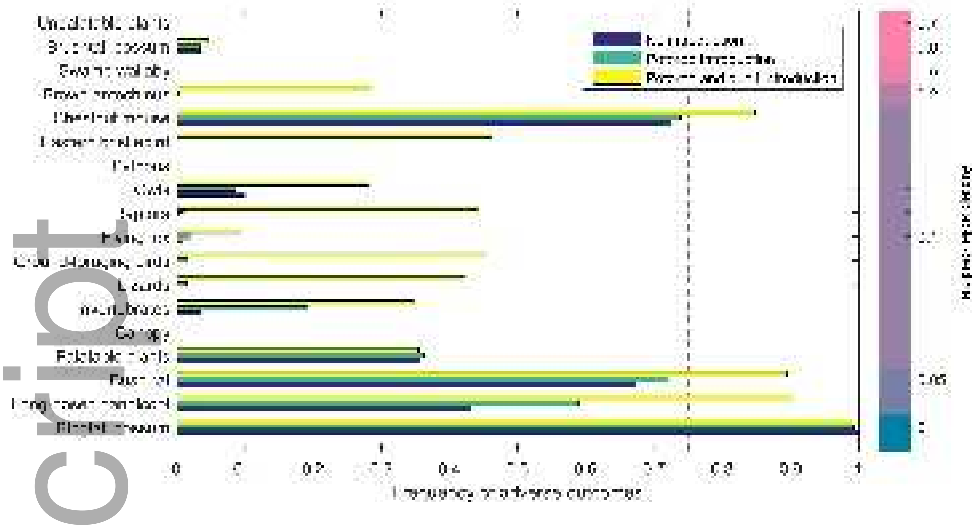

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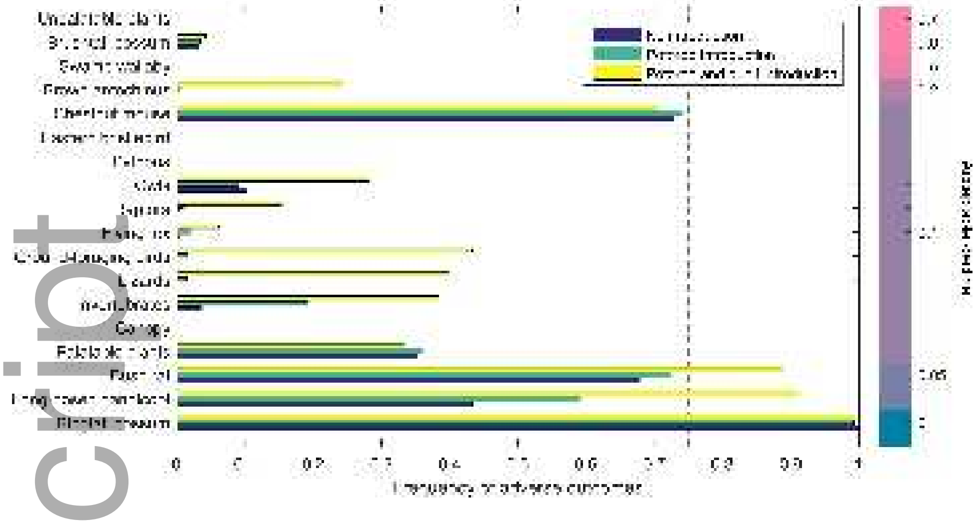

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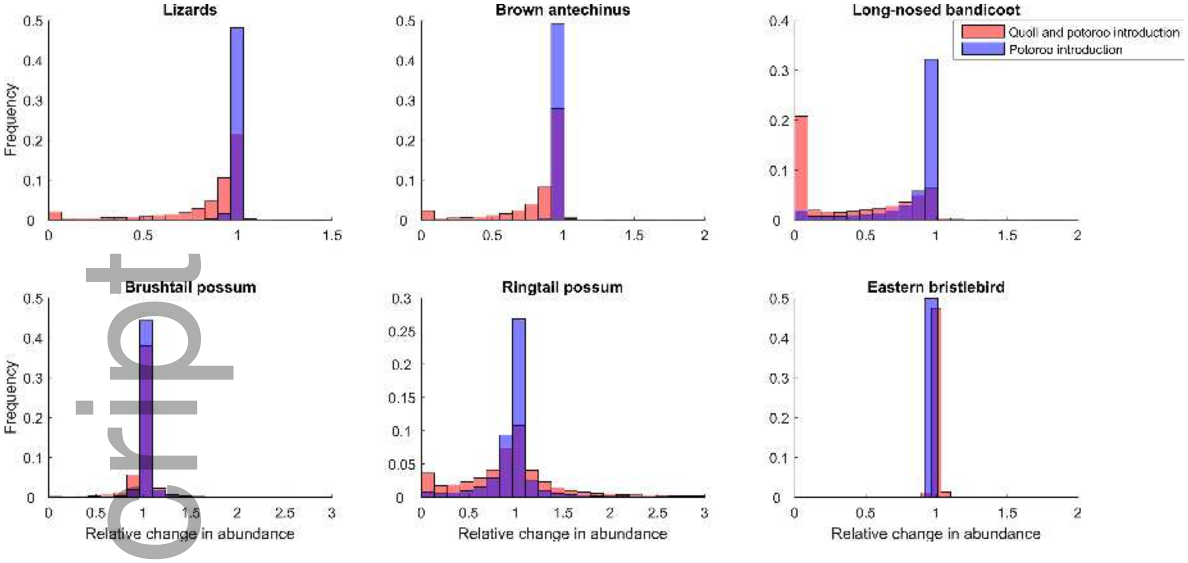

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