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Reconstructing lost ecosystems: A risk analysis framework for planning multispecies reintroductions under severe uncertainty

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Title: Reconstructing lost ecosystems: a risk analysis framework for planning multispecies reintroductions under severe uncertainty

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ABSTRACT

1. Reintroduction projects, which are an important tool in threatened species conservation, are becoming more complex, often involving the translocation of multiple species. Ecological theory predicts that the sequence and timing of reintroductions will play an important role in their success or failure. Following the removal of sheep, goats and feral cats, the Western Australian government is sequentially reintroducing 13 native fauna species to restore the globally important natural and cultural values of Dirk Hartog Island.

2. We use ensembles of ecosystem models to compare 23 alternative reintroduction strategies on Dirk Hartog Island, in Western Australia. The reintroduction strategies differ in the order, timing, and location of releases on the island. Expert elicitation informed the model structure, allowing for use of different presumed species interaction networks which explicitly incorporated uncertainty in ecosystem dynamics.

3. Our model ensembles predict that almost all of the species (~12.5 out of 13, on average) will successfully establish in the ecosystem studied, regardless of which reintroduction strategy is undertaken. The project can therefore proceed with greater confidence and flexibility regarding the reintroduction strategy. However, the identity of the at-risk species varies between strategies, and depends on the structure of the species interaction network, which is quite uncertain. The model ensembles also offer insights into why some species fail to establish on Dirk Hartog Island, predicting that most unsuccessful reintroductions will be the result of competitive interactions with extant species.

4. *Synthesis and applications:* Our model ensembles allow for the comparison of outcomes between reintroduction strategies and between different species interaction networks. This

framework allows for inclusion of high uncertainty in dynamics. Finally, an ensemble modelling approach also creates a foundation for formal adaptive management as reintroduction projects proceed.

Keywords: ecological modelling, fauna reconstruction; island conservation; reintroduction ecology; species interaction networks; threatened species; translocation.

INTRODUCTION

As global biodiversity loss continues apace (Diaz et al. 2019), conservation efforts have turned to not just managing threatening processes contributing to these losses, but actively restoring individual populations through conservation reintroductions (Corlett 2016). While most reintroductions (defined here as the re-establishment of a population in an area following local extinction; IUCN 2013), have focused on single species (Seddon et al. 2005, 2014), multispecies approaches are increasingly common (Ostendorf et al. 2016; Zamboni et al. 2017; Robinson et al. 2020). “Rewilding” campaigns have commenced across the world, with each emphasising the role of multispecies reintroductions in restoring ecosystems (e.g., Africa, Johns 2019; Europe, Jones and Comfort 2020; Britain, Wynne-Jones et al. 2020; North America, Root-Bernstein et al. 2018; South America, Zamboni et al. 2017). In Australia, multispecies reintroductions of mammal species within predator-free fenced enclosures and islands have become an important conservation management tool (Legge et al. 2018). The core objectives of multispecies reintroductions are to prevent the extinction of threatened species (Armstrong and Seddon 2008; Seddon et al. 2014), reconstruct historical faunal assemblages, and restore ecosystem functioning (Seddon et al. 2014; Palmer et al. 2020).

Whatever their objectives, these reintroductions have generally focused on maximising the success of individual species in isolation and have rarely considered the potential interactions between them (e.g., competition, predation, or mutualism) or their differing population dynamics (Godefroid et al. 2011; Plein et al. 2016). While many past translocations have failed due to basic autecology, i.e. failure to predict when a site is suitable for a species (Berger-Tal et al. 2020), interspecific interactions are likely to influence the success of multispecies reintroductions, adding complexity above and beyond single species programs (Plein et al. 2016;

Hunter-Ayad et al. 2020), and critical reviews of reintroduction biology have identified the need for ecosystem-focused approaches (Armstrong & Seddon, 2008; Taylor et al. 2017). Individuals of reintroduced species interact with each other, and with species already present at the reintroduction site, which can complicate reintroductions (Baker et al. 2019). Predation can be a notorious driver of translocation failure, accounting for 80% of failed translocations in one review of mammals (Short 2009). Competition has compromised the success of reintroduced herbivorous species (Moseby et al. 2018), and had negative consequences for endemic herbivores and extant plants (Lovari et al. 2014). The absence of extant mutualist species – generally mycorrhiza and pollinators – is also considered a key factor in the failure of plant translocations (Reiter et al. 2016).

The sequence and timing of reintroductions may be as important as the identity of reintroduced species in determining translocation success (Armstrong and Seddon 2008; Commander et al. 2018). Pollinators, for example, may require host plants to be established (Reiter 2016). Predator reintroduction may only be possible after appropriate prey species have been reintroduced and their populations have reached sustainable levels (Hayward and Somers 2009). However, if predator reintroductions are delayed for too long, reintroduced herbivore populations may exhibit deleterious boom-bust cycles and intense competition (Moseby et al. 2018; Duncan et al. 2020). For species that compete, priority effects (where early establishment allows one species to exclude another) may result in reduced success of later reintroductions (Plein et al. 2016; Moseby et al. 2018). Species with small founder sizes or low dispersal rates might benefit from being reintroduced before competitors or predators. Finally, ecosystem engineers (e.g., digging animals; James and Eldridge 2007, or pioneer plant species that increase soil quality; Sun et al. 2018) might offer benefits to subsequent reintroductions if they are established or released early enough to improve habitat complexity and quality.

Accurate predictions of ecosystem dynamics would therefore help to guide multispecies reintroductions. However, ecosystems are complex, heterogeneous, stochastic, nonlinear and dynamic systems, and are therefore inherently challenging to predict (Geary et al. 2020). The responses of ecosystems to conservation interventions have regularly surprised ecologists and modellers in the past (Buckley et al. 2014; Bode et al. 2017). Even in ecosystems with few species, parametric and structural uncertainty put accurate predictions out of reach (Raymond et

al. 2011; Adams et al. 2020; Geary et al. 2020). Unpredictability is heightened in reintroduction ecology since species may have been absent from the ecosystem for extended periods. Moreover, the multiple species intended for reintroduction are often rare and threatened and may therefore never have been observed co-occurring. This combination of complexity and uncertainty makes multispecies reintroduction planning an exercise in risk analysis (Baker et al. 2019). Ideally, the underlying models should be able to predict the full range of potential outcomes and be designed to allow for adaptive management (McCarthy et al. 2012), so that uncertainty can be reduced as the results of the initial releases are observed.

Here, we design a risk analysis framework to support multispecies reintroductions, which recognises both the complexity and uncertainty of the problem. Our approach allows decision-makers to compare alternative reintroduction strategies, while also identifying at-risk species and suggesting mechanistic ecological explanations for failures. Our approach is founded on ensemble ecosystem modelling (e.g., Baker et al. 2017), as it provides a quantitative framework for modelling different system structures and incorporating parameter uncertainty. We demonstrate the application and value of this framework by applying it to an ambitious multispecies reintroduction program on Dirk Hartog Island (DHI), in Western Australia, to help inform the order, timing, and location of releases on the island.

MATERIALS AND METHODS

Dirk Hartog Island case study

Dirk Hartog Island (DHI) is the largest island in Western Australia (Figure 1a). It is 80 km long, up to 12 km wide, and covers an area of 63,300 hectares within the Shark Bay UNESCO World Heritage Area. The island is managed by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA), which is currently undertaking the Dirk Hartog Island National Park Ecological Restoration Project, or “Return to 1616” (Morris et al. 2017). The fauna reconstruction phase of the project (the release of 13 native species; Figure 2) commenced in 2017, following the removal of sheep, goats, and feral cats from the island (Cowen et al. 2019; Algar et al. 2020a). The 13 selected species includes eight marsupials, four rodents and one bird (Table 1). Rufous hare-wallabies *Lagorchestes hirsutus bernieri* and banded hare-wallabies *Lagostrophus fasciatus* were released on the island between 2017–18, followed by the Shark Bay bandicoot *Perameles bougainville* and dibbler *Parantechinus apicalis* in 2019–20 (Cowen et al.

2019). DBCA aims to reintroduce nine additional native vertebrates to the island by 2025 (Figure 2 and Table 1). Based on evidence from the subfossil record (Baynes 1990) and historical specimens, 11 of these species occurred on the island (Morris et al. 2017). The remaining two hare-wallaby species were not recorded by Baynes (1990), but anecdotal evidence suggests at least one species was present, and possibly both (Morris et al. 2017; Algar et al. 2020b). As such, translocations of the two hare-wallaby species are considered conservation introductions, although we use “reintroduction” for all taxa throughout for simplicity. The objectives of the DHI fauna reconstruction project are diverse and holistic, ranging from threatened species conservation, to the restoration of ecosystem processes and social, cultural and economic services. However, the primary objective is to maximize the number of persisting, secure populations of the reintroduced species, across the timeline 2020–2060.

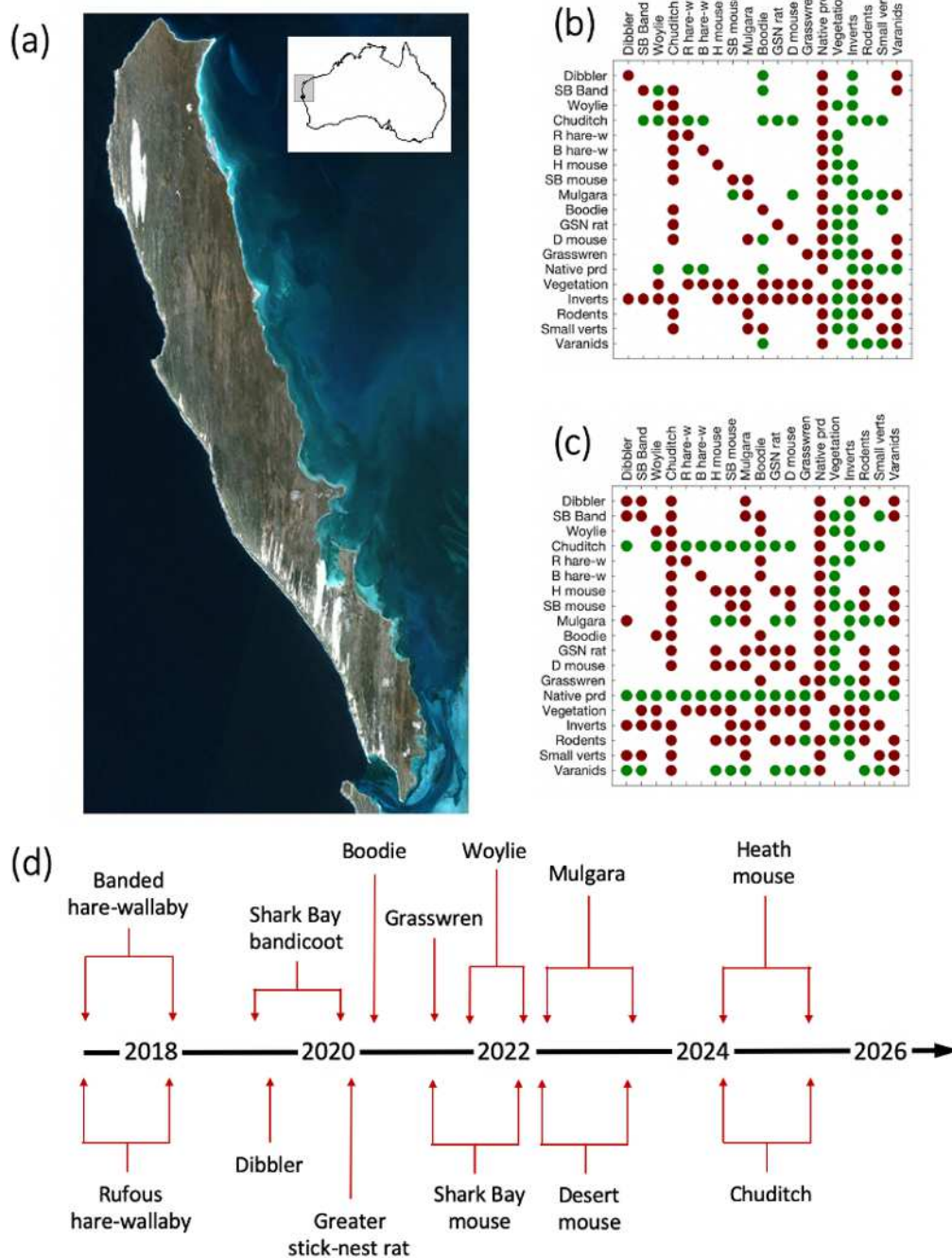


Figure 1: (a) Satellite map of Dirk Hartog Island. (b-c) Two of the expert-elicited ecosystem interaction matrix. Red circles show positive interactions, green circles show negative interactions. (d) Timeline of an example reintroduction strategy; red arrows indicate the approximate dates that species (see Table 1 and Figure 2) will be translocated.

Table 1. Species selected for release on Dirk Hartog Island including IUCN status (sp. – species-level), main dietary strategy and weight range. If known, local (WA) names of Aboriginal origin are included (first listed under Common names) as well as European-derived names. More information on the ecological data used to inform the analysis can be found in Appendix S2 of the Supporting Information.

Common names	Latin name	Family	IUCN status	Diet	Weight (g)
Dibbler	<i>Parantechinus apicalis</i>	Dasyuridae	Endangered	Insectivorous	40-125
Chuditch, Western quoll	<i>Dasyurus geoffroii</i>	Dasyuridae	Near Threatened	Carnivorous	615-2185
Brush-tailed mulgara	<i>Dasycercus blythi</i>	Dasyuridae	Least Concern	Carnivorous	60-110
Rufous hare-wallaby	<i>Lagorchestes hirsutus bernieri</i>	Macropodidae	Vulnerable (sp.)	Omnivorous	780-1960
Mernine, Banded hare-wallaby	<i>Lagostrophus fasciatus fasciatus</i>	Macropodidae	Endangered	Herbivorous	1000-2300
Heath mouse	<i>Pseudomys shortridgei</i>	Muridae	Near Threatened	Herbivorous	55-90
Djoongari, Shark Bay mouse	<i>Pseudomys fieldi</i>	Muridae	Vulnerable	Omnivorous	30-61
Wopilkara,	<i>Leporillus</i>	Muridae	Vulnerable	Herbivorous	180-450

Greater stick-nest rat	<i>conditor</i>				
Desert mouse	<i>Pseudomys desertor</i>	Muridae	Least Concern	Herbivorous	11-35
Little Marl, Shark Bay bandicoot	<i>Perameles bougainville</i>	Peramelidae	Endangered	Omnivorous	165-280
Woylie, Brush-tailed bettong	<i>Bettongia penicillata ogilbyi</i>	Potoroidae	Endangered	Herbivorous	750-1850
Boodie, Burrowing bettong	<i>Bettongia lesueur lesueur</i>	Potoroidae	Near Threatened (sp.)	Omnivorous	700-1300
Western grasswren	<i>Amytornis textilis textilis</i>	Maluridae	Least Concern (sp.)	Insectivorous	23-26

Decisions must be made about the order, timing, and location of releases to DHI. The *order* of the release describes the sequence in which the species are released on the island. The *timing* of release refers to the amount of time that is allowed to elapse between each successive release, and determines how long each population is given to increase in size and extent before the next reintroduction occurs. The *release site* of each reintroduction is influenced by accessibility constraints on the island (e.g., airstrips and roads), and in this case, can be one of five different release sites across the island. Each combination of order, timing and release site is referred to as a *reintroduction strategy*. For example, the first proposed reintroduction strategy for DHI, which is the default order and timing of translocations proposed by the experts, is shown in Figure 1d (without the location of the release sites).



Figure 2: Species that the “Return to 1616” project will reintroduce to Dirk Hartog Island.

With releases of four species already complete, there are nine additional species (eight mammals and one bird) to be released, with many possible reintroduction strategies that could be evaluated. The number of options is prohibitively large – even if we only considered the order of their release (not the specific timing or location), there are $9! = 362,880$ unique sequences in which they could be released. To narrow the number of options, we asked expert DBCA ecologists to develop a manageable set of potential reintroduction strategies for the DHI project (see Table 2 for the list of reintroduction strategies and Appendix S3 in *Supporting Information* for details on the proposed locations and years for releases). The three experts consulted all have extensive and varied experience working with multiple vertebrate species in their role as applied ecologists, including planning and implementing fauna translocations. All are familiar with the environment on Dirk Hartog Island, and logistical considerations. The strategies they chose were influenced by a number of issues. The suitability of nearby habitat provided a good rationale for some strategies (i.e., for species with particular habitat requirements). For example, boodies *Bettongia lesueur lesueur* are presumed to need an appropriate substrate to establish warrens (Short and Turner 1999), and so most reintroduction strategies involved the release of boodies at the northern end of DHI, which is predominantly limestone habitat suitable for that purpose.

Logistical considerations helped constrain the strategies too: prescribed funding timelines for the project state that all releases should be completed before 2025. Many of the release sites chosen for the reintroductions are either near the DHI homestead or the DBCA base at Herald Bay, as they are easy to access and close to a diverse range of habitats. Finally, the reintroduction strategies considered species interactions, for example, delaying the release of predators (e.g., chuditch *Dasyurus geoffroii* and brush-tailed mulgara *Dasycercus blythi*) until other species have established populations. A detailed description of the elicitation process, including rationale for the reintroduction strategies can be found in Appendix S1 of the *Supporting Information*.

Table 2. *The potential reintroduction strategies for the release of the 13 species on Dirk Hartog Island. Strategies differ in the order, year, and location of releases, and some strategies include not releasing a species at all. More detail on the strategies can be found in Appendix S3 of the Supporting Information.*

Reintroduction Strategy	Description
1	Status quo - existing plan for the order and location of releases.
2	Move greater stick-nest rats to different zone to reduce interactions with boodies
3	Translocate some species earlier than the status quo, boodies released in single zone
4	Least expensive option if collections from Bernier Island two years in a row are required.
5	Same as RS 4 but translocate the desert mouse later than the status quo.
6	All species are translocated except boodies.
7	All species are translocated except mulgara.
8	Boodies and chuditch are released in the final two years of the translocations.

9	Same as RS 8, but boodies are released equally at all zones.
10	Boodies are released the second to last (2022 and 2023) and chuditch are released last (2024 and 2025).
11	The same as RS 10, but boodies are released equally at all zones.
12	Boodies are released in 2025 and 2026, and chuditch are released in 2023 and 2024.
13	Mulgara are released in 2025 and 2026.
14	Chuditch are released in 2026 and 2027.
15	Desert mouse and boodies are released in 2025 and 2026, and the heath mouse is released in 2023 and 2024.
16	Chuditch and mulgara translocations are delayed.
17	Chuditch and mulgara translocations are delayed.
18	Desert mouse, boodies, mulgara and chuditch are delayed.
19	Shark Bay mouse, desert mouse, boodies, mulgara and chuditch releases are delayed.
20	All species are translocated except the desert mouse.
21	All species are translocated except the desert mouse and mulgara
22	All species are translocated except the desert mouse, and chuditch are translocated after mulgara.
23	Heath mouse is translocated earlier, mulgara and then chuditch are translocated much later.

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207 For each reintroduction strategy, certain criteria that accounted for the dynamic nature of the
208 ecosystem needed to be addressed. Given the goals of the reintroduction project, the formulation
209 of this model needed to address certain criteria. First, we were interested in the abundance

trajectories of individual threatened species since we wanted to avoid outcomes where the reintroduced species went extinct on the island. The model therefore had to describe the abundance of each reintroduced species. Second, we also needed to include a network of direct and indirect species interactions that could influence abundance trajectories, which required the model to describe the abundance of species already present on the island. Third, the model needed to be spatially and temporally explicit since reintroduction strategies varied in both the location and timing of the releases. Finally, and most importantly, the model needed to be able to incorporate appropriate uncertainty in both the structure and parameterisation of the ecosystem dynamics.

Ensemble ecosystem modelling (EEM) can satisfy each of these criteria by drawing on Bayesian techniques to generate plausible trajectories given high uncertainty, and so we used this method to simulate the outcome of each reintroduction strategy (Baker et al. 2017; Bode et al. 2017; Peterson and Bode 2020). In this application, ensemble ecosystem modelling uses a coupled system of Lotka-Volterra differential equations to model the abundance $n_{im}(t)$ of “species” i in zone m at time t . Given we cannot model every species in an ecosystem explicitly, the $S = 19$ groups on DHI comprise each of the 13 individual species to be reintroduced to the island, as well as six other biological groups that are already present on the island and are considered important drivers of ecosystem dynamics. These are vegetation, invertebrates, varanids (specifically *Varanus gouldii*, a native reptilian predator), rodents, other small vertebrates, and other native predators including raptors. The model is therefore not suitable for evaluating the impacts of reintroduction on native species on the island. We divided the island into five zones, where dispersal of individuals occurs between adjacent zones. To account for the five zones, we extended the standard EEM equations to allow for dispersal. The change in each species abundance over time was therefore derived as:

$$\frac{dn_{im}}{dt} = r_i n_{im} + \sum_{j=1}^S x_{ij} n_{im} n_{jm} + \sum_{p=1}^5 n_{ip} d_{pm}(t) - n_{im} d_{mp}(t).$$

Equation 1

In Lotka-Volterra dynamics, the abundance n_{im} , for species i , in zone m , changes according to its growth rate, r_i , and its interspecific interactions x_{ij} with species j . The magnitude of the

interaction depends on the abundance of species j in the same zone, given as n_{jm} , for all species S . Our model includes and its immigration into a zone (d_{pm}) and emigration (d_{mp}) from a zone, where m and p are two zones. We assumed that dispersal at the scale of the five DHI zones was primarily driven by a juvenile dispersal phase where a constant proportion left their natal zone. Growth rates and species interactions are assumed to be invariant in space and time. This model allows for antagonistic and beneficial interactions between species using the interaction matrix $\mathbf{X}$ with elements x_{ij} (x_{ii} are assumed negative and represent intraspecific competition).

As outlined above, there is uncertainty about the structure of the species interaction network (e.g., which species interact and how), as well as the values of the model parameters (the specific values of r_i and x_{ij}). To incorporate structural uncertainty about the interaction network, we asked three DBCA experts to independently develop qualitative (i.e., sign-structured) matrices that described which species interacted directly, and how. Negative values of x_{ij} indicated that species i is a predator or competitor of species j , positive values indicate interactions such as mutualism or commensalism. Zero values indicate no direct interaction between species i and j . The experts generated seven interaction matrices (two are illustrated in Figures 1b–c): three by Expert 1, two by Expert 2, one by Expert 3, and one additional “consensus” matrix, which was negotiated among the experts after the individual matrices were completed. There was clear variation within and among expert matrices, reflecting real uncertainty about how the ecosystem might operate.

The values of the model parameters will also influence predictions (Baker et al. 2019; Adams et al. 2020). These can be defined by expert opinion (Martin et al. 2012), experimentation (Roemer et al. 2002), or literature review (Hunter et al. 2016). However, the novelty of the proposed DHI community made these options difficult. Instead, ensemble ecosystem modelling uses a two-step process adopted from computational qualitative modelling (Raymond et al. 2011). First, we generated a large number of ecosystem models that matched the sign structure of the expert matrices, but with randomly generated interaction strengths. We then solved Equation 1 for each model in turn and passed the results through a series of 18 “filters”, which represent known properties of the ecosystem. Models that did not match these filters – that is, which cannot reproduce the observed properties – were discarded. Each filter was based on a piece of evidence about the known behaviour of the DHI ecosystem, or species within it. For example, the fossil

record indicates that most of the species in our model persisted for thousands of years (excluding the two hare-wallaby species which are assumed to have also co-occurred for the purposes of this study). We therefore excluded any ecosystem model which did not exhibit asymptotically stable coexistence. Similarly, the model had to predict that the species currently present on the island can also coexist stably. We repeated these two steps approximately 5 billion times until we had created an ensemble of 1,000 “acceptable” models for each of the expert matrices (see Appendix S1 of the *Supporting Information* for a detailed explanation of this process, and a list and explanation of the filters).

Simulating the reintroduction strategies

For each of these acceptable models, we again solved Equation 1, this time implementing each of the 23 reintroduction strategies. The initial size of each reintroduced population was based on expected founder numbers, and the abundance timeseries were continued until 2060 (i.e., approximately 30 years from the last translocation in 2029). Reintroduced species were considered extinct if their abundance fell below 50% of the initial founder number. While this is a relatively conservative measurement of reintroduction risk, it reflects both the perceptions of the DBCA decision-makers (who would consider such a decrease in abundance unacceptable and requiring remediation), and the extinction risk posed to small populations by demographic stochasticity.

For each model in the ensemble, and for each of the 23 reintroduction strategies, the primary output of these simulations was a timeseries for the abundance of the 13 reintroduced species. These timeseries predicted which of the reintroduced species would persist in the ecosystem, and which would fail. By averaging across the 1,000 models in each ensemble, we were able to estimate the mean number of reintroduction failures each of the seven expert matrices predicted would occur, and which species failed the most frequently (Figure 3).

The dynamics of Equation 1 can also suggest ecological explanations for why failures occurred. We evaluated the magnitude of the positive and negative interactions experienced by each species in those models where the reintroduction failed. We compared the strengths of these interactions to their magnitude when the reintroductions succeeded, to identify differences in the sign and magnitude of interactions in both cases (Equation 2)

$$\Delta_{ij} = \frac{|\mathbf{S}| \sum_{\mathbf{F}} x_{ij} n_j(t_e)}{|\mathbf{F}| \sum_{\mathbf{S}} x_{ij} n_j(t_E)}$$

Equation 2

where $\mathbf{S}$ and $\mathbf{F}$ are the sets of models where species j was successfully and unsuccessfully reintroduced, respectively. We evaluate Δ_{ij} using the abundance, n , of species j and the value of its interspecific interactions, x_{ij} , one month before species j became extinct (t_e) for unsuccessful simulations, whilst we use the abundance at the end of the simulation (t_E) for successful simulations. The value of Δ_{ij} might tell us, for example, that in the model ensemble for Expert matrix 1, the failed reintroduction of the heath mouse *Pseudomys shortridgei* was associated with consistently stronger negative interactions with varanids. The complex nature of ecosystem interactions means that Δ_{ij} must be interpreted with care, but it does provide useful ideas about what factors might increase the risk of reintroduction failure.

RESULTS

Figure 3 shows an example timeseries output from the ecosystem ensemble modelling process for all 1,000 models created for the consensus matrix and first reintroduction strategy. For most of these species, and most of the models, the analysis predicts that the reintroduced species can establish, increase in abundance, and persist until 2060 on DHI (timeseries for all strategies and matrices are in Appendix S4 of the *Supporting Information*).

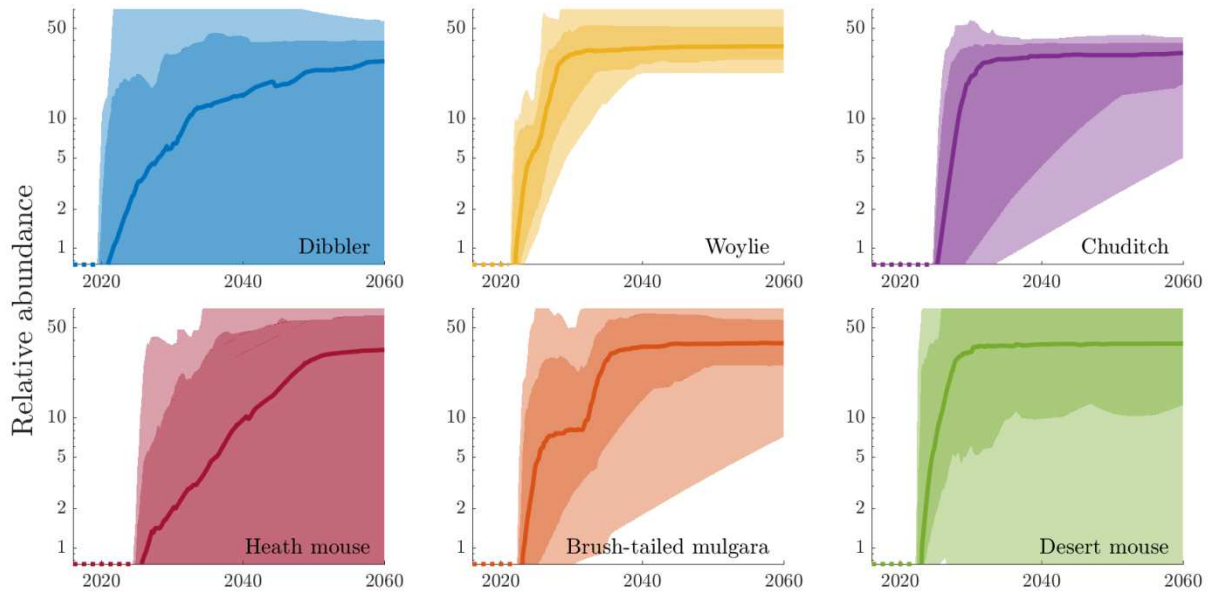


Figure 3: Example timeseries outputs for the “status quo” reintroduction strategy and the consensus interaction matrix model ensemble. Solid line indicates the median result. Shaded areas enclose 95% and 80% of the ensemble predictions at each time.

Measured by the average number of failed reintroductions, the 23 different reintroduction strategies performed similarly with an average of 0.5 failed reintroductions, although strategy 6 performed worse (Figure 4a). The distributions all have long tails, indicating a small subset of models where two or more species failed to establish. Figure 4a shows the results for the consensus matrix, but all the expert matrices produced similar outcomes (Appendices S5 and S6 of the *Supporting Information*).

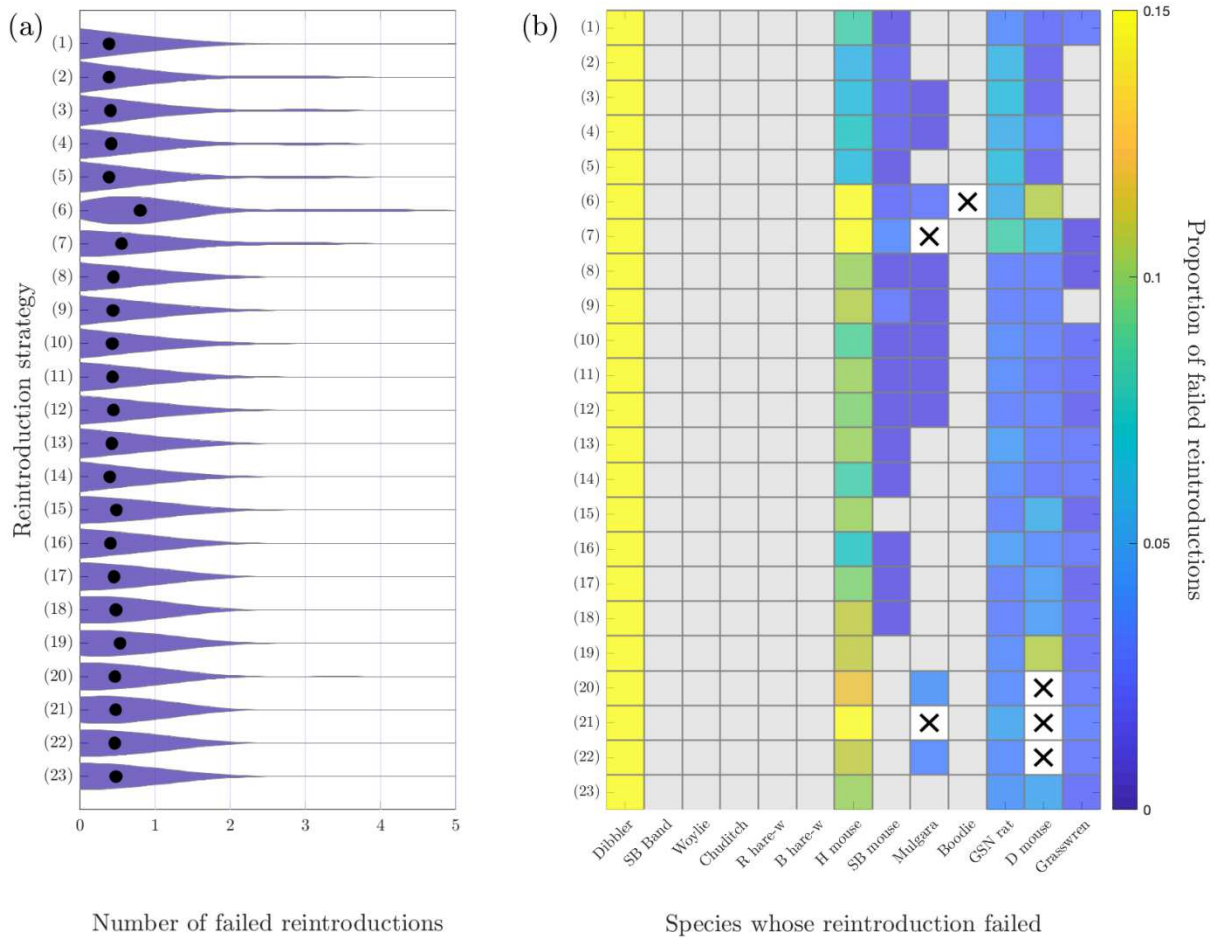


Figure 4: Failed reintroductions for the consensus matrix ensemble. (a) Frequency distributions of the number of failed reintroductions, for each reintroduction strategy. Black dot indicates the average across all models. (b) Proportion of models where the reintroduction of each species failed, for each strategy. Grey squares indicate proportions lower than 1%; crosses indicate that a given species was not reintroduced in a strategy.

While the number of failed reintroductions is relatively unaffected by reintroduction strategy, the identity of the at-risk species varies between strategies (Figure 4b). Using the consensus matrix as an exemplar, we can see that some species are consistently prone to failure (e.g., dibbler) or success (e.g., chuditch) regardless of reintroduction strategy. Others (e.g., heath mouse) are more likely to fail under some strategies than others.

Our final analyses offered possible explanations for why particular species failed to be reintroduced. Figure 5 shows the strength of different interspecific interactions on dibblers in

models where reintroduction failed, relative to models where dibbler reintroduction succeeded. These results are aggregated across all expert matrices and reintroduction strategies. They show that negative interactions with Shark Bay bandicoots, rodents, and varanids were uncommonly strong when dibbler reintroductions failed. However, negative interactions with mulgara and chuditch were relatively weaker in those models. The full set of these figures are shown in Appendix S7 of the *Supporting Information*.

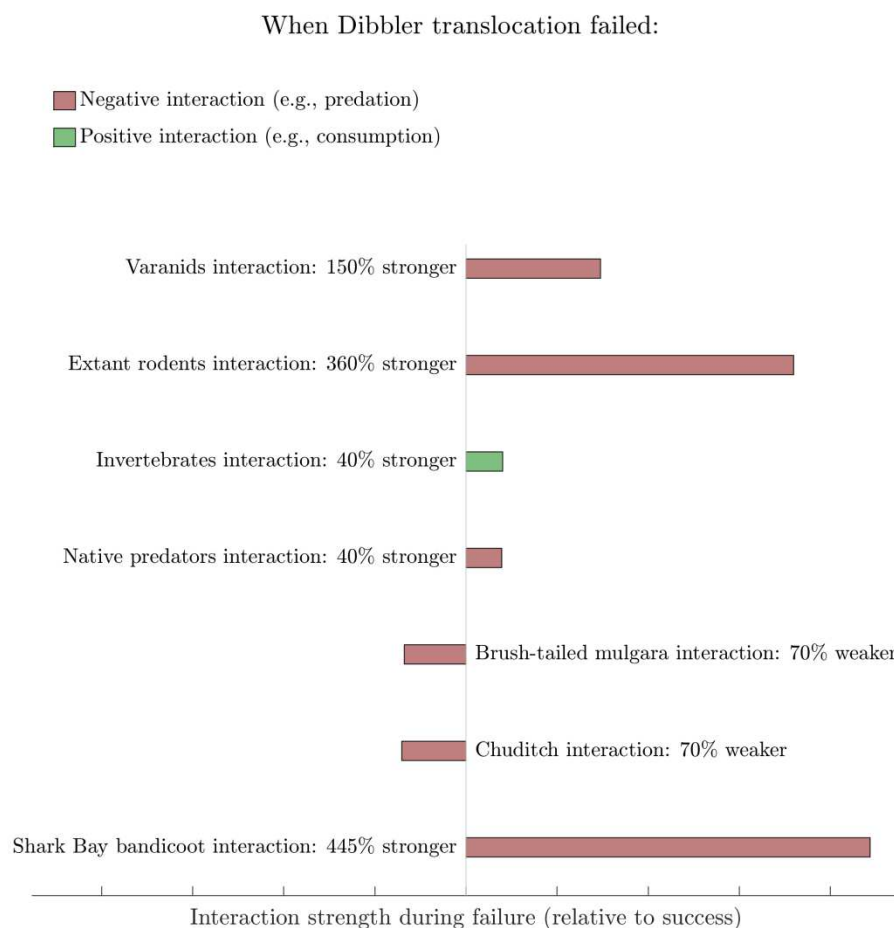


Figure 5: Strengths of positive and negative interspecific interactions in models where dibbler reintroduction failed, relative to models where it succeeded (for the consensus matrix). Bar colour indicates whether the interaction was positive (e.g. consumption) or negative (e.g. competition) for dibbler. Interactions with Shark Bay bandicoots, varanids, and rodents were unusually strong in the models where dibbler translocation failed.

349 The relative strengths of these interactions may be cautiously interpreted as explanations for why
350 particular reintroductions fail. The most common association with reintroduction failure is a
351 strong negative interaction with species extant on DHI. Sixty percent of the species experienced
352 a strong negative interaction with varanids at the point of extinction. Strong negative interactions
353 with other native predators, such as birds of prey, were also associated with reintroduction failure
354 for half of the species. Extant DHI species have higher abundances (and therefore stronger
355 negative impacts) than newly established populations, which contributes to higher interaction
356 strengths. Unusually strong negative interactions with other reintroduced species were rarely
357 associated with reintroduction failure, perhaps because the reintroduction strategies were
358 designed to avoid this outcome, although negative interactions among the reintroduced rodents
359 were evident when reintroductions failed (e.g., heath mouse).

360 Different reintroduction strategies tended to deliver similar aggregate outcomes (fewer than one
361 reintroduction failure on average), across all expert matrices. However, the different
362 reintroduction strategies, and particularly the different expert matrices, disagreed on which
363 species reintroductions were most likely to fail. Each panel in Figure 6 shows the proportion of
364 models where reintroduction failed for a particular species. Some species (e.g., chuditch and
365 boodie) appear robust to failure, no matter what reintroduction strategy or expert matrix is used.
366 However, the results vary most frequently across the expert matrices. The heath mouse, for
367 example, is considered a moderate-to-high failure risk by all matrices except E1-3, which
368 considers it low risk. The dibbler is considered a high risk by matrix C a low risk by matrices E1-
369 1, E1-2, E2-1 and E2-2, and a moderate risk by matrices E1-3 and E3-1.

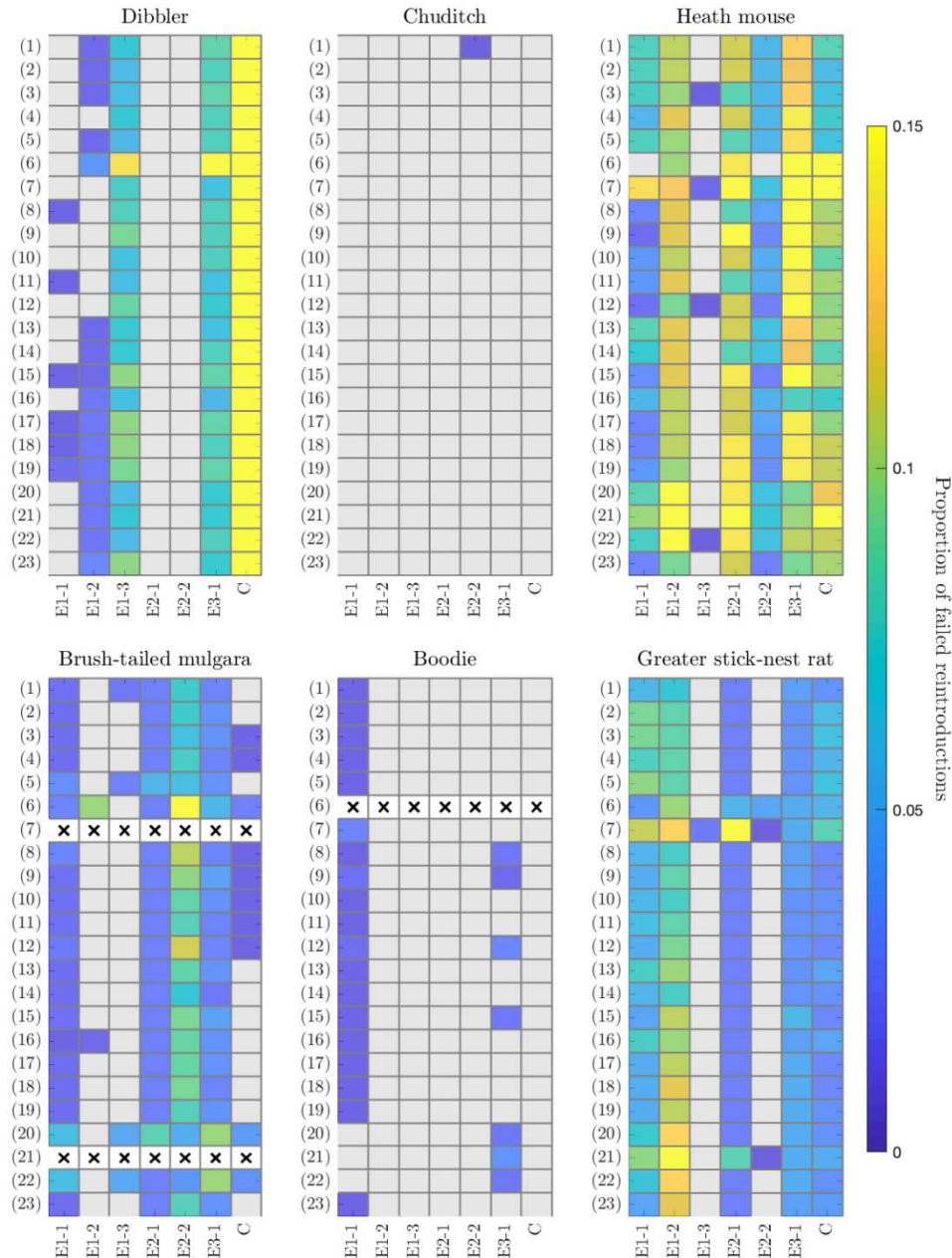


Figure 6: Proportion of ensemble models where reintroduction failed for six species across different reintroduction strategies (rows) and expert matrices (columns). Grey squares indicate proportions lower than 1%; crosses indicate species that were not reintroduced in that strategy.

DISCUSSION

Multispecies reintroductions pose dual challenges of complexity and uncertainty, and ‘Return to 1616’ is one of the largest, most complex and challenging ecological restoration projects ever

undertaken. There are literally billions of potential combinations of order, timing, and location to choose from, and hundreds of pairwise interspecific interactions that could affect the outcome. The latter are very poorly understood - the co-occurrence of the 13 candidates for reintroduction on Dirk Hartog is mostly based on sub-fossil evidence, so a contemporary reference site to help inform reintroduction decisions does not exist. Fortunately, mathematical risk analyses were developed for precisely these types of complexity. Armed with the power of modern computing, these methods can rapidly sort through millions of alternative actions and propagate uncertainties through to produce distributions of predictions (Geary et al. 2020).

Even with the high level of uncertainty seen throughout these analyses, our results provide some reassurance. While reintroduction failures may occur, their number is likely to be small – fewer than one on average. The result was robust to both parameter uncertainty (i.e., the different models in each ensemble), and structural uncertainty (i.e., the different ensembles created for each interaction matrix). There are two qualifications here. First, while the average number of failed reintroductions was consistently low, the distributions in Figure 4a show the potential for multiple failures (in some cases, as many as four). For risk-averse decision-makers, these rare but catastrophic outcomes could play a disproportionate role. The second qualification is that the consistency in the average number of failures masks a large amount of variation in which species are at risk. If species' values vary (for instance, based on their threat status), this will influence the choice of reintroduction strategy, and may lead to conflicting preferences if there is no consensus. For example, the conservation status of the heath mouse in Western Australia is currently unclear, with few records in recent years (K. Morris pers. comm.). Consequently, their reintroduction to DHI may be considered a conservation priority. In Figure 6, expert E1-3 indicates low risk for this species, while E2-2 (and most others) indicates otherwise; would we choose a low-risk strategy that maximises success of the heath mouse that potentially compromises other species? Either way, the value of this analysis is that it can support greater clarity to decision makers, by highlighting potential trade-offs under particular strategies.

Multispecies reintroduction projects pose an unusual challenge for risk analyses. At a fundamental level, risk analyses require a list of all possible outcomes under different interventions, each with a probability of occurrence. This is impossible to provide for multispecies reintroductions for two reasons. First, because many interventions are available to

managers, and many outcomes could result from each. From a computational perspective, it is therefore impossible to enumerate all possible risks. Second, each outcome is determined by complex ecosystem dynamics with highly uncertain structure and parameters. Consequently, it is not possible to unambiguously associate a probability with each outcome. However, our approach using ensemble ecosystem modelling addresses these challenges by creating a very large number of plausible models with a variety of parameters and structures to estimate the relative frequency of a range of possible outcomes.

Despite the ability of the ensemble ecosystem modelling approach to include an enormous range of plausible outcomes, this technique has some limitations. Even after searching through billions of candidates to identify plausible ecosystem models, we have only sampled a tiny fraction of the possible models (i.e., $\ll 1\%$). The colours shown in Figures 4b and 6 are therefore the relative frequency of particular outcomes in our model ensemble, they are not probabilities. The spatial Lotka-Volterra models at the centre of our ensemble approach are widely used and mathematically tractable, but they do omit important dynamics. They do not represent environmental variation, age-structure, or Allee effects (*inter alia*), and they do not include the critical effects of demographic or environmental stochasticity, which play a large role in the extinction of small populations (Ovaskainen & Meerson 2010). Our methods are also limited in their treatment of stochasticity, to more effectively focus on the role of species interactions in extinctions. They could therefore be effectively complemented by single-species population viability analyses (PVA; Lacy 2019), which are principally concerned with the role of demographic and environmental stochasticity and Allee effects. Where sufficient data exists, PVA models are being constructed for the species being released on DHI, and are being used to support decisions that cannot be addressed by ensemble modelling, such as founder population size and structure, influence of environmental stochasticity and post-release monitoring required to address translocation success criteria (e.g. White et al. 2020). When modelling such a wide range of alternatives for a very complex system, trade-offs and simplifications must be made. All options involve compromise along important dimensions of the problem.

Our set of filters was able to exclude a large number ($>95\%$) of models from the ensemble, but involved a series of assumptions that have the potential to affect our conclusions. For example, we applied a filter that required all 13 reintroduced species to be able to coexist on DHI. This

filter was based on subfossil evidence from the island, and co-occurrences elsewhere, but the island's ecosystem has changed a great deal since Dirk Hartog first landed in 1616. Similarly, we applied a filter that required subsets of species which coexist on other islands, and within fenced enclosures on the mainland, to be able to coexist on DHI. However, coexistence in one location does not guarantee coexistence in other locations (Chamberlain et al. 2014). For example, DHI is significantly larger than these other islands and fenced enclosures (Legge et al. 2018). The filtering process may therefore have excluded some models that should have remained in the ensemble. We used expert elicitation to qualitatively parameterise (i.e., identify the sign-structure) of the species interaction matrix. Because experts often disagree about food web structure (Stier et al. 2017), we elicited separate networks from each of our experts rather than assuming a single network structure (e.g., Hunter et al. 2016). We also assumed that the expert elicitation process resulted in a reasonable parameterisation of the system, although the environment is novel and expert estimates are therefore based on fundamental ecology, behaviour, and information from other locations. Doing so allowed us to make assumptions regarding the dynamics on DHI in an ecologically-realistic way. Finally, the assumptions that we made about the ecosystem dynamics will also have implications for the specifics of post-release monitoring.

Return to 1616 fauna reintroductions are planned to continue until at least 2025, and data will continue to be collected for many years beyond that date. An important benefit of ecosystem ensemble modelling is its ready integration with the process of formal adaptive management (McCarthy et al. 2012). Each model in our ensembles makes a prediction about the outcomes of previous and current reintroduction actions, which can be qualified through ongoing data collection. Indeed, our model filtering step already excluded models that cannot explain the dynamics observed following the 2017/18 reintroductions of banded and rufous hare-wallabies to the island. As the project continues, models that do not agree with new data can also be excluded, refining the model ensemble and reducing uncertainty. Further, using this approach, monitoring can be targeted towards species and interactions that will most rapidly improve our understanding of ecosystem dynamics, and or help choose between future reintroduction alternatives. For example, the current analysis suggested that negative interactions (i.e., predation) with extant species (notably varanids and birds of prey) on the island could pose a risk to reintroduction success for many species, and so monitoring of those extant species is

important. Similarly, the influence of competition among the reintroduced rodents needs to be tracked closely. Finally, as new ecosystem dynamics are observed, the interaction matrices could be updated as data are collected.

This study was a collaboration between mathematical and applied ecologists. The approach was iterative, with model components and reintroduction strategies being revised according to feedback from experts. The amount of variation in the outputs was the greatest surprise to all participants, primarily due to the unexpected differences between the ecosystem interaction matrices. While the process of expert elicitation exposed differences in opinion between experienced colleagues, it also identified reasonable alternative hypotheses about how the system operates. Once this uncertainty had been captured during the model formulation, the link between different interaction matrices and resulting predictions helped to better interpret the variation in the results. This was why, even when a consensus interaction matrix had been retrospectively constructed and analysed, we retained the predictions of all matrices.

The primary benefit of this analysis is to clarify and simplify a very complex problem. For example, as variation in reintroduction order had limited influence on outcomes, the project can proceed with greater confidence and flexibility regarding the strategy used. To give another example, Figure 6 identifies robust species that appear unlikely to fail under any reintroduction strategy or ecosystem model (e.g., chuditch). This allows closer scrutiny of those species that appear to be positively or negatively influenced by specific strategies and interactions, facilitating more rapid intervention. This may be one of the most important roles of decision-support tools in very complex ecological management problems: to identify elements of the problem that, while they are not themselves important, can distract decision-makers from the most important issues.

CONFLICT OF INTEREST

MDB, SC, LG, and CS are involved in carrying out the ‘Return to 1616’ project on Dirk Hartog Island.

AUTHORS’ CONTRIBUTIONS

All authors contributed to the initial conceptualization of this project, and to model development. KP wrote the first draft of the manuscript with all authors making a substantial contribution to subsequent drafts.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.t1gljw2p> (Peterson et al., 2021).

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