

Applying ecological coexistence theory to improve management

Thesis submitted by

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March 2020

For the degree of Doctor of Philosophy

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ACKNOWLEDGEMENTS

First, thank you to my supervisors. This thesis would not exist if it were not for Terry seeing my potential and inviting me to pursue a PhD. Thank you, Terry, for also giving me freedom to develop my own project even though that meant jumping down a rabbit hole of quantitative ecology. Sean, thank you for pushing me to challenge myself intellectually. Our discussions early in my candidature helped me to see that it is actually feasible to ask big picture questions, and then scale them down appropriately. I would not have the confidence in myself as a scientist if it had not been for your guidance. Mike, thank you so much for providing a safe space at QUT in Brisbane for me to finish my thesis. I am also so grateful that you let me be a part of a collaborative work atmosphere, your encouragement during the many times I felt overwhelmed by imposter syndrome, and for your always positive but realistic attitude.

Thank you to all of the administrators and staff at JCU and QUT. I am especially thankful, however, for Alana Grech's help. Thank you for your guidance and empathy while I navigated some hardships during my PhD.

Thank you to the Ecological Modelling Group at JCU, who have been helpful not only in discussing ideas with and troubleshooting code, but also in maintaining morale. Thank you to the Mathematical Ecology Group at QUT, who have shown me what a community of scientists should look like and helped to restore my faith in academia.

I am extraordinarily lucky to have a stellar network of friends within Australia and abroad, who have been instrumental in helping me to stay afloat during the lows of my PhD and celebrating the highs with me. I could probably write a dissertation in of itself on the extent of my gratitude for the incredible friends I have in my life. Thank you for your unwavering support, encouragement, and mentorship.

Finally, thank you to my family, particularly my parents. From day one you have raised me to aim high and never give up. This stubbornness was crucial in getting through the past few years. Most of all, thank you for your unconditional love and support, all the way across the Pacific.

Statement of contribution of others

All research presented in this thesis was conducted under the supervision of Sean Connolly, Michael Bode, and Terry Hughes. Contributions to each chapter can be found in Table I. Financial support was provided by the Australian Research Council (ARC) and James Cook University (JCU).

Table I. Statement of contribution to individual chapters. Initials: KAP = Katie A. Peterson; MQB = Michael Q. Bode; SRC = Sean R. Connolly; CMB = Christopher M. Baker; CJS= Cailan Jeynes Smith; MDB = Megan D. Barnes; CS = Colleen Sims; LG = Lesley Gibbons; SC = Saul Cowen

<i>Chapter</i>	<i>Statement of Contribution</i>
<i>Chapter 1: General introduction</i>	KAP wrote the chapter with feedback from MQB.
<i>Chapter 2: Signature of coexistence mechanisms on stability components</i>	KAP and SRC conceived the research. KAP developed the models under the supervision of SRC. KAP wrote the chapter with feedback from MQB and SRC.
<i>Chapter 3: Using ensemble modelling to predict the impacts of assisted migration on recipient ecosystems</i>	KAP and MQB conceived the research. KAP and MQB developed the models. KAP wrote the chapter with feedback from MQB. Additional comments on the chapter were from CMB.
<i>Chapter 4: Risk analysis of faunal reconstruction decisions on Dirk Hartog Island</i>	KAP, MQB, conceived the research. KAP, CJS, and MQB developed the models. KAP wrote the chapter with feedback from MQB. Additional comments on the chapter were from CMB, CJS, MDB, CS, LG, and SC.
<i>Chapter 5: General discussion</i>	KAP wrote the chapter.

Abstract

To manage ecosystems effectively, it is critical to understand as much as possible about how species interact to predict how they will respond to changes in the environment. Interactions between species, combined with habitat type and quality, shape which and how many species can coexist within a community. However, since researchers seldom have perfect information on the ecology and biology of each species and their interactions, there is often a great amount of uncertainty in models of ecological systems. Constraints of funding and time make it impossible to perfectly understand a system. Models that explicitly include uncertainty are a cost-efficient way to evaluate possible outcomes and inform management decisions, prior to implementing a management action. In this thesis, I use community models that explicitly incorporate uncertainty to demonstrate how community outcomes change when the parameter strengths and model structure is modified using different ecological assumptions. These chapters explore the repercussions of species' interactions for ecological stability and species richness, which are key community attributes that practitioners measure. These chapters evolve from a classical theoretical ecology framework (Chapter 2), followed by a theoretical examination of a conservation intervention (Chapter 3) towards an applied conservation management problem (Chapter 4).

Chapter 2 utilises numerical simulations of communities based on two mechanisms of coexistence and five community sizes to identify how coexistence mechanisms affect aggregate community attributes. The two coexistence mechanisms in this study are niche partitioning and the storage effect. Niche partitioning is based on imperfect overlap of competition, and the storage effect is dictated by how species respond to environmental fluctuations. Community stability was calculated from the simulated time series as the coefficient of variation of abundance, as well as indices that can be statistically derived from stability. My findings indicate that the community statistics have unique signatures based on the coexistence mechanism in place. For example, low synchrony in abundances is associated with communities generated by storage effect based coexistence. However, the coefficient of variation is indistinguishable between mechanisms. This indicates that while mechanisms may affect secondary attributes of community stability, on the whole, community stability is unaffected by the type of coexistence mechanism operating.

Chapter 3 demonstrates that conservation interventions can have negative effects on recipient ecosystems. This chapter explores hypothetical outcomes of assisted migration, in which

ensemble modelling is applied to quantify the impacts to recipient communities when a new species is introduced. Assisted migration is a highly controversial conservation intervention methodology in which a population of a threatened species is moved beyond their natural ranges in an effort to conserve the species. While this could save species from extinction, it also introduces a range of risks. The magnitude of the threat to recipient ecosystems has not been investigated quantitatively, despite being the most common criticism levelled at the action. The magnitude of the threat to recipient ecosystems has not been investigated quantitatively, despite being the most common criticism levelled at the management action. The modelling approach used in this chapter predicts both the probability of successful assisted migration, and the impact it will have on richness within recipient ecosystems. Using an ensemble of 10,000 simulated 15-species recipient ecosystems, the results indicate that translocated species can cause multiple extinctions within the recipient ecosystem. Quantifying the impacts to species within recipient ecosystems is critical to help managers weigh the benefits and negative consequences of assisted migration.

Extending the ensemble model, Chapter 4 identified how a conservation initiative may be affected by three factors: i) assumptions on the direction of interspecific interactions occurring; ii) the order in which species are introduced; and iii) the spatial dynamics of the system (i.e. dispersal rates of species and the location of introduction). Dirk Hartog Island is undergoing a faunal reconstruction; non-native species were removed from the island to allow for the translocation of 13 native vertebrates. Translocation of such a large number of species to an insular ecosystem will be challenging, and multi-species translocation theory is relatively undeveloped in reintroduction ecology. Using the ensemble modelling framework, I incorporated the expert-elicited information to evaluate potential translocation outcomes. In 50% of models in the ensemble, one species translocation will fail as a result of species interactions and stochastic population fluctuations. Multiple local extinctions are possible but unlikely. The translocation alternatives I modelled result in similar aggregate outcomes, but affect each species differently, depending on the interaction matrix. The findings from this study indicates that assumptions regarding interactions between species has a greater impact on community structure and species persistence than other factors such as timing or order of introduction.

Interspecific interactions influence community dynamics in complex and unexpected ways. The type of interaction affects secondary community properties (Chapter 2) and which species are vulnerable (Chapter 4), while changes to existing interaction networks can have

significant impacts such as leading to extinctions (Chapter 3). Minimising parameter uncertainty may be attempted through increasing and improving sampling or minimising human error. However, minimising uncertainty limited by time and resources, and conservation initiatives are time sensitive. Parameter values are also subject to various forms of variability, further increasing uncertainty. Ensuring an accurate overall representation of the system is difficult, as this is dependent on knowledge of the system and interpretation of that knowledge. Additionally, ecological systems are marked by complexity such as nonlinearity, feedbacks, and second-order interactions, which are difficult to capture in models. Therefore, in almost all instances, practitioners are underestimating the uncertainty within a system. The implications for managing natural systems are considerable. This research highlights the importance of incorporating a framework with realistic estimates of uncertainty within the decision-making process for environmental management and conservation.

Glossary of Terms

This glossary provides a brief definition for terms used in the context of this thesis, some of which differ from the official or broadest definition of the term.

Assisted migration – the intentional movement of a subset of a population outside of that population’s native range or historic distribution.

Coexistence – the phenomena where at least two species within the same community that compete for resources do not fully outcompete each other and drive the other to extinction.

Community – any group of interacting populations of multiple species within a defined spatial area.

Ecosystem – a community and its abiotic environment or habitat.

Extinction – when the abundance of a population is low enough so that the species makes no discernible impact within the ecosystem.

Expert elicitation – working with multiple experts to determine the ecology of an ecosystem and the objectives and alternatives of a conservation project.

Refaunation – the intentional movement of a subset of a population to a new location after the ecological alteration of that location (such as through vegetation restoration or eradication of pest species).

Translocation – the intentional movement of a subset of a population for the purposes of conservation.

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CHAPTER 1: General introduction

1.1 Thesis overview

In this thesis, my central goal is to use community models and coexistence theory to demonstrate how conservation outcomes depend on the characteristics of species interactions one assumes to be true in a system. This statement may seem self-evident, but by careful analysis of three separate problems, I demonstrate that it is true to an unexpected degree. At the same time, I demonstrate that critical conservation problems can nevertheless be answered usefully in the face of this uncertainty.

Thematically, my thesis is therefore organised around two fields of scientific research: community ecology (and specifically species interactions), and uncertainty analysis (specifically, decision-making in uncertain systems). Chapter 2 examines how two different coexistence mechanisms, can result in different aggregate community attributes. Chapter 3 evaluates the repercussions of an increasingly common conservation initiative, assisted migration, on recipient communities through the disruption of the network of interactions. Finally, Chapter 4 determines how which conservation alternative has the greatest probability of success depends on assumptions of how species interact.

1.2 Managing ecological systems in the face of uncertainty

Unexpected outcomes due to uncertainty are common throughout scientific disciplines. While this is a given, it is a less than ideal consequence when uncertainty is ignored in ecological decision making (Regan et al., 2005; Doak et al., 2008; Bevin, 2010). Uncertainty can be defined as the circumstance where there is more than one outcome consistent with my expectations (Pielke, 2001). Adequately taking uncertainty into account allows for informed and cautious decision making given the limited knowledge of all of the many processes and interactions that operate within natural systems (Bevin, 2010; Addison et al., 2013). Reducing uncertainty may be unrealistic, but accurately quantifying it can help to reduce unexpected outcomes (Pielke, 2003).

Novel and unanticipated impacts to communities have caused the restructuring of ecological communities through the addition of new interactions and weakening of existing interactions (Doak et al., 2008; Lindenmayer et al., 2010). One classic example is the kelp forest trophic cascade due to changes in sea urchin and sea otter populations (Paine 2002; Estes et al., 2004). These unexpected outcomes could theoretically have been foreseen and avoided if the uncertainty had first been resolved, but it is not feasible to perfectly understand a system due to constraints of funding and time (Pielke, 2001). Conservation management is generally an urgent affair (Getz et al., 2018; Schuwirth et al., 2019); this constrains the types of quantitative approaches practitioners can use; computationally and mathematically complex methods that require significant amounts of data simply may not be feasible (Jackson et al., 2000; Pielke 2003; Schuwirth et al., 2019). Simplified models that focus on

key species can reduce measurement effort and may allow practitioners to make sufficiently accurate predictions (Pielke, 2003; Aufderheide et al., 2019).

Ecological models can serve as a representation of the current understanding of a system (Jackson et al., 2000; Pielke, 2001; Getz et al., 2018; Schuwirth et al., 2019). This can contribute to the overall theory regarding a natural system, and can highlight current knowledge gaps (Jackson et al., 2000). In this thesis, Chapter 2 seeks to understand how different mechanisms affect ecological community, by using ecological models with differing functional forms. Ecological models can also be used to make predictions about the future state of a system, which is most often the case when models are applied to conservation and ecological management problems (Pielke, 2003; Getz et al., 2018; Schuwirth et al., 2019). Despite the potential for increased uncertainty associated with forward projections, ecological models can result in better conservation outcomes than management that relies solely on non-quantitative expertise (García-Díaz et al., 2019). Therefore, Chapter 3 quantifies the probability of a range of possible futures following assisted migration. Then, Chapter 4 predicts the likelihood of persistence and community assemblage of different conservation alternatives.

1.3 Types of Uncertainty

Models are simplified representations of complex natural systems and are subject to different kinds of uncertainty (Refsgaard et al., 2006; Lek, 2007; Schuwirth et al., 2019). Because unacknowledged uncertainty can lead to unexpected outcomes, it is imperative that the predictions gleaned from ecological models must be accompanied with forthright explanations of their uncertainty (Regan et al., 2005; Doak et al., 2008; Milner-Gulland & Shea, 2017). Unfortunately, the full scope of uncertainty is not always represented when outputs from models reach the decision-making phase in conservation (Regan et al., 2005; Milner-Gulland & Shea, 2017). The types of uncertainty that affect predictions made from ecological models are categorised as epistemic uncertainty, and linguistic uncertainty (Regan et al., 2002; Milner-Gulland & Shea, 2017). Epistemic uncertainty is uncertainty in the knowledge of the state of a system (Regan et al., 2002; Milner-Gulland & Shea, 2017). Linguistic uncertainty is uncertainty in conclusions and interpretations due to the way information is communicated (Regan et al., 2002; Milner-Gulland & Shea, 2017). Here I focus on epistemic uncertainty, focusing on parameter uncertainty and structural uncertainty. This thesis addresses both of these types of uncertainty using different, but complementary ecological contexts.

Parameter uncertainty arises from a variety of sources: measurement error, variability, and stochasticity (Regan et al., 2002; Pielke, 2003). Measurement error is often the most commonly addressed, though difficult to reduce, as the data used to inform parameters are typically not sufficient to provide exact estimates of parameter values (Pielke, 2003). Data are expensive to collect, and there

are often errors in sampling design and measurement (Lek, 2007). This thesis uses numerical simulations which eliminates the need to consider measurement error. This allows me to instead focus on two other sources of parameter uncertainty: natural variability and inherent randomness. Natural variability a source of uncertainty where the value of a parameter changes due to changes in a different independent variable (Regan et al., 2002). Metabolic rates depend on body size; competition between species depends on the amount of resource available. Natural variability is a fundamental quality of ecological systems, which is why it is recommended to collect data over a range of conditions (Regan et al., 2002; Godoy, 2019). Stochasticity is due to random processes, and well-known statistical techniques are useful in studying and quantifying this form of uncertainty (Pielke, 2003). However, stochasticity is inherent in natural systems and is an irreducible source of uncertainty, which must be taken into account when making predictions (Regan et al., 2002; Pielke, 2003).

Structural uncertainty is due to incomplete or incorrect knowledge of which components of a system are important and how they interact (Regan et al., 2002; Nuttle et al., 2009). In ecological models, this includes misrepresentation of relationships between variables, incorrect functional forms, and neglecting to include vital components or interactions within the model (Pielke, 2003; Nuttle et al., 2009). In natural systems, it is impossible to account for every interaction and component. Consequently, structural uncertainty will always be an attribute of ecological models (Pielke, 2003; Nuttle et al., 2009). Additionally, uncertainty regarding the appropriate model structure is considered a large source of uncertainty when using ecological models to make predictions (Refsgaard et al., 2006). However, structural uncertainty it is not commonly addressed (Pielke, 2003). Multi-model ensembles are an approach that can be used to incorporate structural uncertainty into model forecasts, because they allow multiple different structural possibilities to inform predictions (Schuwirth et al., 2019). Each chapter in this thesis explicitly address structural uncertainty: through comparison of community attributes generated by models with known dynamics but differing model structure (Chapter 2) or through quantification of predicted outcomes using ensembles of models (Chapters 3 and 4).

1.4 Community models and interspecific interactions

Community models are a means of mathematically representing how multiple populations of interacting species grow, persist, or decline over time (Jackson et al., 2000). Community models offer a more accurate mechanistic representation of an ecological system than population models, because species dynamics are not independent of each other (Jackson et al., 2000; Thrush & Dayton, 2010). Furthermore, Ecosystem-Based Management depends on the maintenance of ecosystem functions, which are shaped by which species are present and how they interact (Mölldmann et al., 2011; Novak

et al., 2011). When conservation is focused on a single endangered species, managers sometimes do not consider possible negative side effects of management decisions on the rest of the ecological community (Krofel & Jerina; 2016). In fisheries management, single species assessments have been the norm, though there is an increasing call for multi-species and Ecosystem-Based Management (Möllmann et al., 2011; Thrush & Dayton, 2010; Masi et al., 2018). Uncertainty of stock sizes is not sufficiently captured in single species stock assessments, particularly when target species have strong interactions (Möllmann et al., 2011; Masi et al., 2018).

Interspecific interactions are the interactions between different species within a community, whereas intraspecific interactions are the interactions between individuals of the same species (Chesson, 2000a). Intraspecific interactions are often summarised as density dependence; crowding of individuals and minimum densities required for successfully finding mates are examples (Chesson, 2000a). There are many different types of interspecific interactions, such as competition, predation, mutualism (Sih et al., 1985; Chesson, 2000a). While intraspecific interactions regulate population growth within a species, interspecific interactions affect the composition of species present in a community, and they regulate the relative abundances of those species (Chesson, 2000a; Dambacher et al., 2002). The recognition that composition and relative abundances have repercussions for ecological function and stability has led to an increase in efforts to quantitatively analyse interspecific interactions (MacArthur, 1960; Tilman, 1999; Novak et al., 2011).

Interactions between species are a significant source of parameter and structural uncertainty. To assess the effects of interaction strengths the structure of interactions in communities, species and their interactions within the community can be represented as a network: nodes and edges that connect them (Novak et al., 2011). This can then be translated into a community matrix to mathematically represent the magnitudes of interaction strength of the linkages, as well as the topology of the linkages (Dambacher et al., 2002; Novak et al., 2011). Topology in ecological networks represents which species interact, and these direct relationships between species' populations define the structure of the community (Dambacher et al., 2002). The strengths of interactions, which are the values of the elements of an interaction matrix, are subsequently subject to parameter uncertainty, and are extremely difficult to reliably estimate (Novak et al., 2011; Aufderheide et al., 2013). The topology, similarly, is subject to structural uncertainty. In complex food webs, for example, predator-prey interactions may not always be known (Aufderheide et al., 2013). The interactions may change from one species to another, as in prey-switching. Uncertainty in the topology of a network has been shown to produce unreliable predictions of how communities will respond to perturbations (Aufderheide et al., 2013).

A consequence of incorporating species interactions in ecological models, however, is uncertainty. Determining the magnitude of interspecific interactions is difficult, as the strength of interactions can change spatially or temporally (Novak et al., 2011). Some interactions are also context dependent; some interactions have been shown to have a greater influence on species at particular life history stages. Ideally, data on interspecific interaction strengths would be obtained from distributions of various biological characteristics such as body size or age (Godoy, 2019). Interspecific interactions also increase uncertainty by generally increasing model complexity (Aufderheide et al., 2013). It is more likely the model structure or topology of interactions may be incorrect, as complexity of a system increases (Aufderheide et al., 2013). Complexity often means more parameters are incorporated in the model, which further add to overall uncertainty (Aufderheide et al., 2013). This, in part, is why parsimony is an important consideration in model development; practitioners should strive for a sufficiently simple model that is still useful to address management objectives (Getz et al., 2018; García-Díaz et al., 2019).

1.5 Modern coexistence theory

Interspecific interactions are most commonly examined through the framework of modern coexistence theory (Barabás et al., 2018; Ellner et al., 2019). Modern coexistence theory was formalised to explain how interactions between species allow for the maintenance of high diversity in multispecies communities, despite the presence of antagonistic interactions such as competition and predation (Chesson, 2000a). Coexistence is the state in which species that occupy the same spatial region and have similar ecology do not outcompete each other to extinction (Gause, 1934; Chesson, 2000a). This is usually in an ecological community, and often it is within a “guild”, where species occupy the same trophic level and compete for the same resources (Chesson, 2000a). Mathematically, coexistence requires that species can increase from low density in the presence of the other species (Chesson, 2000a). Mechanisms of coexistence explain how incomplete competition between species, either in space or time, facilitate coexistence (Chesson, 2000a; Levine & HilleRisLambers, 2009; Chase & Myers, 2011).

Resource partitioning (via ecological niches) is the most commonly-studied coexistence mechanism, because it is both conceptually and mathematically straightforward (Chase & Leibold, 2003; Levine & HilleRisLambers, 2009). A classic example of ecological niches is MacArthur’s 1958 observation that five species of warblers, though seemingly occupying the same space, utilised zones within trees differently (MacArthur, 1958). In Lotka-Volterra models of competition, niche separation can be represented by an interaction matrix where off-diagonal elements have smaller values than diagonal elements (Chesson, 2000a; Chase & Leibold, 2003). This mathematically represents the fact that intraspecific competition is greater than interspecific competition, because species are competing

more with members of their own species than members of other species, and hence niche overlap is reduced (Chesson, 2000a; McGill et al., 2006). Similarly, a mechanistic derivation of niches is based on a principle called R^* , which represents the minimum amount of resource needed by a species to maintain a positive growth rate (Tilman, 1982). The smaller a species' R^* , the more efficient it is in its consumption of that resource and therefore a superior competitor (Tilman, 1982). This concept confers coexistence because natural systems have multiple resources and species within a community use the resources in slightly different ways, so no one species is superior competitor to all others (Tilman, 1982).

Fluctuation mediated coexistence are another important mechanism that allows species to coexist (Chesson, 1983; Chesson, 2000b; Tredennick et al., 2017). These mechanisms rely on changes in environmental conditions to confer coexistence, and so they cannot be used in deterministic models and depend on stochasticity (Chesson, 1994; Tredennick et al., 2017). Stochasticity, as mentioned earlier, is a source of increased uncertainty in parameters (Pielke, 2003). Mathematically, these mechanisms also cannot be represented in models by simply manipulating the matrix of interactions between species like niche-based coexistence (Tredennick et al., 2017). A key attribute of the storage effect is species' different responses to fluctuations in the environment (Chesson 1983; Warner & Chesson 1985; Chesson, 1994; Chesson 2000). This can be represented using the covariance matrix, to model how species differ in their responses to fluctuations in the environment (Chesson, 2000a). Specifically, the covariance matrix quantifies how demographic parameters respond to stochasticity (Chesson, 2000a). Changes in demographic parameters in turn affect the relationships between species, as the magnitude of interactions between and within species are density dependent (Chesson, 2000a; Chesson, 2000b). Fluctuation mediated mechanisms of coexistence are less researched as they involve two sources ecological sources of uncertainty, stochasticity and indirect species interactions, to allow species to persist within a community. Chapter 2 in this thesis directly compares the outcomes of the storage effect with niches, to see how community outcomes differ between a coexistence mechanism that depends on environmental stochasticity to a coexistence mechanism that does not.

A common criticism of modern coexistence theory is that, while straightforward in theory, it is too mathematically complex for use in empirical applications (Ellner et al., 2019). Because the underlying ideas in modern coexistence theory are useful in explaining ecological consequences, Ellner et al. (2019) recommend that the concepts can be generalized for empirical work by separating the conceptual framework from the mathematics in Chesson (2000). To provide a quantitative measure of coexistence, Ellner et al., (2019) derive two kinds of functional decompositions for use in empirical studies. The E-decomposition is analogous to measuring the storage effect or temporal niche

partitioning, as it quantifies how species respond to environmental variability using variances and covariances of variables that contribute to species-specific growth rates (Ellner et al., 2019). The T-decomposition is more similar to general niche partitioning, as it quantifies differences in traits among species (Ellner et al., 2019). While the decompositions developed by Ellner et al. (2019) aim to quantify coexistence, I use the statistical decomposition of stability developed by Thibaut and Connolly (2017) to determine if coexistence mechanisms are identifiable based on their impacts on aggregate community attributes. The decompositions by both Ellner et al. (2019) and Thibaut and Connolly (2017) allow ecologists to use calculations on timeseries data to reveal underlying dynamics that affect the coexistence of multiple community.

Building on work by Shea and Chesson (2002), who frame invasion ecology through the lens of coexistence and community ecology, Godoy (2019) employs modern coexistence theory to evaluate community vulnerability to invasions and the invasibility of new species. Shea and Chesson (2002) reviewed how coexistence mechanisms, specifically “niche opportunities”, can be used to examine the likelihood of biological invasions. They define niche opportunities as the ability to capitalise on a resource that is not being monopolised by other species (Shea & Chesson, 2002). Godoy (2019) extended the concept of framing invasions using coexistence theory to networks of multispecies interactions. Rather than incorporating niche opportunities through R^* , niche partitioning is implied through the interaction network (Godoy, 2019). To analyse the invasibility of new species and the likelihood of invasion within a community, Godoy (2019) proposes a structural approach, where the strength of interactions defines a geometric space where all species may coexist. This approach aims to differentiate the cause of invasion from differences in demographic properties or the structure of the network of interactions (Godoy 2019). This is a complimentary approach to the framework established by Shea and Chesson (2002); and demonstrates how coexistence theory can be useful to study introductions in communities, without using Chesson’s formal invasibility analysis.

These studies underscore the broad utility of coexistence theory as a conceptual framework, and the flexibility in its quantitative interpretations. Coexistence theory has been invoked in an emerging suite of literature to predict changes to communities in contexts relevant to conservation and management, without using the mathematical frameworks established by Chesson (2000a) and Ellner et al. (2019). This includes but is not limited to predicting changes to species composition and relative abundances (Paine et al., 2018), determining repercussions for fisheries management (Masi et al., 2018), and evaluating the effects of invasive species (Godoy, 2019). Similarly, in this thesis, I use modern coexistence theory explicitly in Chapter 2 by contrasting the effects of niche based and storage effect based coexistence. I also draw on the concepts of modern coexistence theory in Chapters 3 and 4, which evaluate the introduction of one species and the sequential introduction of multiple species.

Conservation has begun to favour approaches focused on communities and ecosystems, because persistence of one species is almost always influenced by other species (Thrush & Dayton, 2010). Interspecific interactions shape and define community attributes, some of which are directly measurable management objectives, such as maximizing species richness (Chesson, 2000a; Paine et al., 2018). Interspecific interactions also determine how individual species and communities as a whole will respond to changes (Novak et al., 2011; Aufderheide et al., 2013). Therefore, coexistence is important in conservation even when it is not formally applied. However, there is a growing class of literature that explicitly invokes coexistence theory in scenarios that are of interest to conservation and management (Shea & Chesson, 2002; Paine et al., 2018; Godoy, 2019). This thesis seeks to contribute to that growing body of literature, while also evaluating how uncertainty propagates from species interactions through to community outcomes.

CHAPTER 2: Signatures of coexistence mechanisms on stability components

2.1 Introduction

One of the primary objectives of conservation programs is the preservation of intact habitats to maintain species richness in the face of anthropogenic threats (Cardinale et al., 2012; Hooper et al., 2012). As rationale, conservation organisations argue that not only is high biodiversity important for its intrinsic value, but that biodiversity is a critical component in sustaining stably functioning ecosystems (Hooper et al., 2005). The relationship between biodiversity and ecological attributes such as stability and productivity was initially based on observations of natural systems and was generally considered to be positive: stability and productivity was higher in communities with high species richness (Odum 1953; MacArthur, 1955; Elton, 1958). However, there is a lack of consistency in the relationship between diversity and ecological attributes in experimental and theoretical research, and many studies indicate the diversity-stability relationship is sensitive to other properties that shape communities (Doak et al., 1998; Tilman et al., 1998; McCann, 2000; Ives & Carpenter, 2007; Anderson et al., 2013). May (1972) mathematically demonstrated that stable and complex communities are statistically unlikely. Conversely, Yodzis (1981) showed that complex communities can be stable if the interactions reflect natural dynamics in structured food webs, but randomly assembled communities are less stable. However, Doak et al. (1998) revealed that stability in diverse systems does not always rely on the interactions between species, but it is instead an outcome of the statistical averaging of species' biomasses. Tilman et al. (1998) found that statistical averaging due to sufficient species richness alone does not necessarily stabilize communities; other properties of the ecological system are important as well. Further, the relationship between community stability and species diversity may depend in part on the type and magnitude of mechanisms allowing for the coexistence of species in diverse communities (Mouquet et al., 2002; Loureau & de Mazancourt, 2013; Tredennick et al., 2017).

The inconsistencies in results across empirical and theoretical examinations of the relationship between diversity and stability underscore the importance of carefully examining how different ecological dynamics contribute to community outcomes. In particular, the nature of the interactions between species has important implications for community stability (Doak et al., 1998; Yodzis, 1981; Mouquet et al., 2002; Loureau & de Mazancourt, 2013; Tredennick et al., 2017). Therefore, coexistence mechanisms are a useful framework for evaluating the nuanced and complicated relationship between diversity and stability. Coexistence mechanisms are likely to influence ecological stability because they influence both levels of diversity and species composition in a community (Chesson, 2000a).

Community stability through the lens of coexistence mechanisms has been studied from two distinct approaches: applying and analysing process-based models, and decomposing time-series species abundance data into statistical components. These studies have focused on either niche-based coexistence or fluctuation-mediated coexistence mechanisms, but few have considered these classes of mechanisms together. Resource partitioning (via ecological niches) is the most commonly studied coexistence mechanism, because it is both conceptually and mathematically straightforward (Chase & Leibold, 2003; Levine & HilleRisLambers, 2009). However, the shift towards including fluctuation-mediated coexistence mechanisms has been crucial because stochasticity in natural communities are ubiquitous (Chesson, 2000a; Loreau and de Mazancourt, 2013; Loreau, 2010). Obviously, fluctuations can be disadvantageous in that they directly affect populations and the resources they rely on, but there are some mechanisms that depend on fluctuation in the environment to allow communities to persist. Improved computational tools have enabled a growth in studies examining fluctuation mediated coexistence mechanisms (Tredennick et al., 2017).

This study focuses on two coexistence mechanisms, to compare and contrast their effects on community stability: classical fluctuation-independent niche partitioning, and the fluctuation-dependent storage effect. Niches are a coexistence mechanism that describes how different species utilise the same resources in different ways, or different resources within the same space (Chesson, 2000a; Chase & Leibold, 2003). In order for communities of multiple species to coexist, intraspecific competition must be higher than interspecific competition; that is, members of the same species must compete with each other more than they compete with other species (Chesson, 2000a). This manifests in nature through niche partitioning, where different species rely on different resources or use the same resources in different ways, which minimises their competition (Chesson, 2000a). The storage effect can be considered a type of temporal niche differentiation, as temporal variation in the environment and resources are necessary for this mechanism to allow species to coexist (Chesson & Warner, 1981; Chesson, 1985). More specifically, the storage effect is the coupling of environmental processes with competition, and is measured as the covariance between changes in the environment and per capita demographic rates (Chesson, 1985; Chesson, 2000b). Additionally, species must differ in their responses to the environment and have buffered population growth (Chesson, 1985; Chesson, 2000b). Therefore, the positive or negative effects of temporal variability of the environment affects species differently, thereby reducing interspecific competition relative to intraspecific competition, and species may “store” the positive impacts of environmental change through buffered population growth (Chesson and Warner 1981; Chesson, 1985; Chesson 2000a; Chesson, 2000b).

Although most natural ecosystems are influenced by a combination of coexistence mechanisms, these were chosen because they have both been found to allow communities to coexist through the

individual mechanisms alone, and they provide a good contrast of static and fluctuation-mediated coexistence mechanisms (Chesson, 2000a; Hughes and Roughgarden, 2000; Tredennick et al., 2017). Furthermore, the mode of operation for these mechanisms will likely produce different outcomes in statistical descriptors of communities. For example, in a community governed by a strong storage effect where species are responding very differently to environmental fluctuations, the synchrony of species' abundances through time is likely to be low.

The overarching aim of this chapter is to investigate how community stability is affected by the ecological coexistence mechanisms that support species diversity. This chapter develops a comprehensive evaluation of community stability by merging two of the primary tools used to characterise and explain variation in ecological communities. By combining the use of numerical simulations and statistical decomposition, I aim to determine if the difference in the operation of niche and storage effect-based coexistence translate into noticeable signatures on statistical quantities decomposed from my calculation of community stability. That is, do the values of a community's stability components (the community coefficient of variation, synchrony, evenness, and overyielding) differ if a community is characterised by niche partitioning or the storage effect?

2.2 Methods

2.2.1 Statistical decomposition of stability

By decomposing stability, I am able to reveal a more nuanced relationship between community dynamics and stability. While stability is mathematically defined in various ways, the definition of stability as the coefficient of variability, CV_n^c , is straightforward to calculate from abundances in time series data of communities. Here, the superscript c distinguishes the statistic as the community coefficient of variation rather than species' coefficient of variation. The subscript n indicates the community size. Furthermore, it can be decomposed into statistical components, which I employ to determine if there are distinct signatures of coexistence mechanisms in the overall magnitude of these quantities.

The calculations for stability and its components were adapted from Thibaut and Connolly (2013).

Community stability was measured as coefficient of community variation, $CV_n^c = \sqrt{\varphi} \widehat{CV}_n^s$, where the root of synchrony, φ , is multiplied by the average species coefficient of variation, weighed by species' respective mean abundance. The weighted-average species coefficient of variation is $\widehat{CV}_n^s =$

$\sum_i \frac{m_n^s(i) \sqrt{v_n^s(i,i)}}{m_n^c}$ where $m_n^s(i)$ is mean species biomass, m_n^c is mean community biomass, and $v_n^s(i, i)$

is species variance. Synchrony is $\varphi = \frac{\sum_{ij} v_n^s(i,j)}{(\sum_i \sqrt{v_n^s(i,i)})^2}$. The numerator is the summed variances and

covariances between species, $v_n^s(i, j)$, which is the total community variance, v_n^c . The denominator represents the variance of community biomass if all the species' fluctuations were perfectly positively correlated. The evenness index used here is the mean of the variances of logged biomass among species at a certain time, averaged over time. The calculation is $E = \frac{\sum_{ij} v_n^s(i, j)}{time}$. Overyielding is the phenomenon where community biomass increases with increased species richness. Overyielding is often calculated from $m_n^c = \sum_i \frac{m_1(i)}{n^x}$, where m_n^c is mean community biomass, $m_1(i)$ is the mean biomass of species i in monoculture, and n is the number of species in the community (Thibaut and Connolly, 2013). This equation can be solved for the value of x to determine if overyielding is occurring. If x is between 0 and 1, then community biomass increases with diversity, but mean species' abundances (or biomass) decrease with diversity, indicating the overyielding is occurring (Tilman 1999; Thibaut and Connolly, 2013). However, if x is greater than one, then community (and thus mean species' abundances) both decrease with species richness and therefore underyielding, rather than overyielding, is occurring (Tilman 1999; Thibaut and Connolly, 2013). If x less than 0, then mean species abundance would increase with diversity, implying some sort of facilitation.

Typically, community dynamics are not readily observable from time series data for multiple species. Figure 1 shows the time series of abundances for generated communities governed by one of two mechanisms. From visual inspection, it is not clear which coexistence mechanism is driving the dynamics. Dynamics are even less obvious in natural communities, as they have more mechanisms and abiotic factors impacting their dynamics than what is practical in a general model. In order to discern if the community statistics correspond with any coexistence mechanisms, they need to be analysed from data with known dynamics. Therefore, I use numerical simulations to generate time series data, to limit the likelihood of making a Type I Error. A Type I Error is the detection of an effect where there is none, and this can be avoided by limiting the number of variables that are changing in the system. Additionally, by generating my own data, I was able to analyse potential relationships without measurement error.

2.2.2 Community model

I considered a guild of n species, with densities N_1, N_2, \dots, N_n and i representing any one species, in a variable environment. Growth through time t in years was modelled using an exponential fitness model, where per capita recruitment is a function of the strength of intra- and interspecific competition and the magnitude of environmental stochasticity.

$$N_i(t + 1) = (1 - M_i(t))N_i(t) + R_i(t)N_i(t),$$

$$\text{where } R_i(t) = \exp [r_i(t) - \lambda_{ii}e^{r_i(t)}N_i(t) - \sum_{j \neq i} \lambda_{ij}e^{r_j(t)}N_j(t)],$$

$$\text{and } \overline{r_i(t)} \sim N(\vec{0}, \mathbf{V})$$

Equation 2.1

In the community model, M_i is mortality, and varies with time. R_i is the recruitment rate which takes into account competition through the λ matrix. Specifically, the λ matrix defines the strength of intra- and interspecific competition. The covariance-variance matrix represents how much species' abundances covary in response to environmental fluctuations. The growth rate, r_i , is randomly chosen from normal distribution with a mean of 0, defined by the variance-covariance matrix \mathbf{V} . The values for each parameter that were used in the simulations are detailed in Table 1, along with the rationale for why those values were used. This functional form allows for the implementation of either the storage effect or niche partitioning in a stochastic environment, through the exponential recruitment function. A simpler functional form such as the basic Lotka-Volterra model of competition would allow for niche partitioning, but not the storage effect. Similarly, simple models of the storage effect do not facilitate inclusion of niche partitioning.

To evaluate fluctuation-independent coexistence via niche partitioning, the λ matrix, which defines the strength of intra- and interspecific competition, the off diagonal elements and diagonal elements were chosen at discrete values to represent increasing niche separation, with the diagonal elements always at greater values than the off diagonal elements. See Table 2.1 for parameter values.

To model the storage effect, the growth rates of species were defined by a covariance matrix, \mathbf{V} . This allowed me to modify the magnitude in which intrinsic growth rates responded to fluctuations in the environment as well as modify the magnitude in which species' responses to environmental fluctuations differed. The overall storage effect was manipulated by changing the values of the off-diagonal elements, $\text{cov}(\mathbf{X})$, and the diagonal elements, $\text{var}(\mathbf{X})$. Environmental fluctuations were generated by sampling intrinsic growth rates from a multivariate lognormal distribution, according to the specified covariance matrix.

To ensure the absence of the storage effect in the fluctuation-independent niche model, the covariance matrix \mathbf{V} was adjusted to allow all elements to be as close as possible to the same value (implying that responses to the environment are perfectly correlated, and thus no storage effect can occur). This scenario is unlikely in natural systems, where species will respond differently to various environmental conditions to at least some degree. However, this was necessary to ensure that the storage effect was not operating in these communities and that coexistence was strictly due to niche

partitioning. The diagonal elements were slightly higher, by 0.001 to ensure elements were positive semi-definite. Five values were chosen to represent different levels of environmental variation. For the storage effect model, the elements in the λ matrix were the same value, at five different strengths of competition. This allowed for different magnitudes of interactions between species but maintained complete niche overlap. Each mechanism had 25 combinations of parameters. 50 simulations were run for each of the 50 parameter sets, at five different community sizes, to generate 12,500 distinct community time series. The time series were 2,000 years and then the community statistics were calculated from each coexisting community on the last 1,000 years. This ensured the timeseries had reached a stationary distribution and the calculations were not sensitive to arbitrary initial conditions. Five time series from each community size and parameter set were randomly selected and visually inspected to check for stationarity. All simulations and statistical calculations were conducted in R (R Core Team, 2016).

Table 2.1: Parameter values used in the community models. Each model had 25 different parameter sets. These values ensured that a range of coexistence mechanism strengths were samples and that communities were sufficiently distinct.

Parameter	Symbol in Eq. 1	Value	Justification
All models			
Mortality	M	Random values from a uniform distribution from 0.0 to 0.5, to represent annual mortality rates but varied from year to year and were species-specific.	The values of the calculated community statistics are sensitive to mortality rates, so a range of low to high mortality rates were used and differed with each timestep.
Growth rate	r	Normal distribution with a mean of 0, defined by the variance-covariance matrix Σ	Generated using a lognormal distribution within the exponential growth function.
Initial population size	N_n	7	This population size allowed for most communities to reach a stationary distribution

			of abundances, fluctuating around the equilibrium abundances, within the first 1000 time steps of the simulation.
Niche model			
Interspecific competition	$\lambda_{ij}, i \neq j,$	0.05	This value is consistently smaller than intraspecific competition, ensuring there is niche differentiation among species, but species still compete through a minor degree of niche overlap.
Intraspecific competition	λ_{ii}	Five matrices with all elements as one of the following: 0.1, 0.15, 0.2, 0.25, 0.3	These values are larger than interspecific competition, as members of the same species compete more with themselves for resources than with other species, because the individuals within a species occupy the same niche.
Covariance matrix diagonals	$\text{var}(\mathbf{X})$	Five matrices with all elements as one of the following: 0.101, 0.201, 0.301, 0.401, 0.501	These values ensure that species experience an increasing degree of environmental fluctuation.
Covariance matrix off diagonal	$\text{cov}(\mathbf{X})$	Five matrices with all elements as one of	The slightly lower value in the off

		the following: 0.1, 0.2, 0.3, 0.4, 0.5	diagonal elements ensures that the matrix is positive semi-definite, while also making species respond the same way to environmental fluctuations.
Storage effect model			
Covariance matrix off diagonals	$cov(\mathbf{X})$	Five matrices with all elements as one of the following: 0.05, 0.1, 0.15, 0.2, 0.25	These values represent a range of covariance so that species' responses to environmental variation differ strongly (0.05) or only moderately (0.25).
Covariance matrix diagonal	$var(\mathbf{X})$	Five matrices with all elements as one of the following: 0.1, 0.2, 0.3, 0.4, 0.5	Each species within a community experiences the same moderate amount of environmental variation between years.
Interspecific and intraspecific competition	λ	Five matrices with all elements as one of the following: 0.1, 0.2, 0.3, 0.4, 0.5	The values of all elements within the competition matrix are the same; therefore, there is complete niche overlap but increasing degrees of competition.

The parameter values for the niche-based communities are such that a range of niche partitioning is evaluated, but species in communities of all sizes are still able to coexist. Coexistence is rare in communities of ten species when the interspecific competition value is greater than 0.3. The values

within Σ increase from 0.1 to 0.5 to subject the communities to different degrees of environmental fluctuations. The values of the diagonals are slightly higher to ensure the matrix is positive semi-definite. The values are sufficiently close to preclude the storage effect from facilitating coexistence, as species respond to fluctuations in the environment to approximately the same degree. Three examples of the competition and covariance matrices for a niche-based community of two species are as follows:

Parameter set 1

$$\lambda \begin{pmatrix} 0.1 & 0.05 \\ 0.05 & 0.1 \end{pmatrix}$$

$$\mathbf{V} \begin{pmatrix} 0.101 & 0.1 \\ 0.1 & 0.101 \end{pmatrix}$$

Parameter set 2

$$\lambda \begin{pmatrix} 0.1 & 0.05 \\ 0.05 & 0.1 \end{pmatrix}$$

$$\mathbf{V} \begin{pmatrix} 0.201 & 0.2 \\ 0.2 & 0.201 \end{pmatrix}$$

Parameter set 6

$$\lambda \begin{pmatrix} 0.15 & 0.05 \\ 0.05 & 0.15 \end{pmatrix}$$

$$\mathbf{V} \begin{pmatrix} 0.101 & 0.1 \\ 0.1 & 0.101 \end{pmatrix}$$

The \mathbf{V} values are set to allow for different levels of covariance, and the correlation coefficient, rho, is equal to 0.5 in all parameter sets. Rho is calculated by dividing the variance by the covariance. The values in the competition matrix increase to subject communities to increasing inter- and intraspecific competition. The values in this matrix are the same, to inhibit coexistence via niche partitioning. Three examples of the competition and covariance matrices for a storage effect-based community of two species are as follows:

Parameter set 1

$$\mathbf{V} \begin{pmatrix} 0.1 & 0.05 \\ 0.05 & 0.1 \end{pmatrix}$$

$$\lambda \begin{pmatrix} 0.1 & 0.1 \\ 0.1 & 0.1 \end{pmatrix}$$

Parameter set 2

$$\mathbf{V} \begin{array}{cc} 0.1 & 0.05 \\ 0.05 & 0.1 \end{array}$$

$$\lambda \begin{array}{cc} 0.2 & 0.2 \\ 0.2 & 0.2 \end{array}$$

Parameter set 6

$$\mathbf{V} \begin{array}{cc} 0.2 & 0.1 \\ 0.1 & 0.2 \end{array}$$

$$\lambda \begin{array}{cc} 0.1 & 0.1 \\ 0.1 & 0.1 \end{array}$$

2.3 Results

There was no difference in the community coefficient of variation, CV_n^c , between the niche and storage effect models of different species richness (Figure 2.1a). While the mean values of CV_n^c differ slightly, all points are in a range from approximately 0.125 to 0.25. Furthermore, the strengths of the mechanisms did not strongly affect the value of CV_n^c (see Figures 2.1b and 2.1c). There is no significant difference in the CV_n^c values calculated from niche-based coexistence based on the degree of niche separation (Figure 2.1b). There is, however, a slight trend of increasing CV_n^c with increasing covariance, which would represent a weaker storage effect (Figure 2.1c). Species richness has a negligible effect on the CV_n^c value in communities generated by either mechanism.

However, mechanism type and species richness did affect the other community statistics. For example, synchrony was consistently lower in storage effect models than niche-based models (Figure 2.2a). Additionally, increasing species richness decreases the average synchrony value in communities governed by either mechanism (Figure 2.2a). The strength of the mechanism had a more noticeable impact on synchrony in the niche models than the storage effect models (Figures 2.2b and 2.2c). In niche-based communities, the mean value of synchrony increases slightly with increased niche separation (Figure 2.2b). Though, species richness has a greater impact on the value of synchrony in niche-based communities, and this is more pronounced among communities with fewer species (Figure 2.2b). In communities generated through the storage effect, the degree of covariance has a negligible impact on the mean value of synchrony (Figure 2.2c). There is a slight effect of species richness, which also has more pronounced impact on smaller communities, most notably on the two-species community (Figure 2.2c).

Mechanism type affected the values of evenness calculated from the timeseries, where evenness was lower among niche-based communities than storage effect-based communities (Figure 2.3). In niche

models, the median value of evenness is affected primarily by species richness, particularly among communities with less niche separation. The values of evenness are also much more constrained when calculated from niche communities, whereas there is a considerable spread to the distribution of evenness values in storage-effect communities (Figures 2.3).

Overyielding occurred in communities generated by niche coexistence, but on average, underyielding occurred in communities generated by the storage effect (Figure 2.4a). The values of x , used to determine overyielding, ranged from approximately 0.2 to 0.8 in niche-based communities, implying that biomass increases with diversity in niche-based communities. In storage effect-based communities, x ranged from approximated 0.95 to 1.15, indicating underyielding in most storage effect-based communities. Therefore, instances of overyielding in storage effect-based communities were rare and limited to some communities with a low covariance of 0.05 or a few communities with other covariances but a community size of only two species (Figure 2.4c). Species richness did not make a difference in the average overyielding values in the storage effect model but did impact the value in niche models (Figures 2.4b and 2.4c). The magnitude of the mechanism did influence overyielding in both the storage effect and niche models (Figures 2.4b and 2.4c). In storage effect-based communities, however, covariance has a slight effect on the mean value of x but the data points have considerable spread, particularly in communities with high covariance, so this effect is negligible (Figure 2.4c).

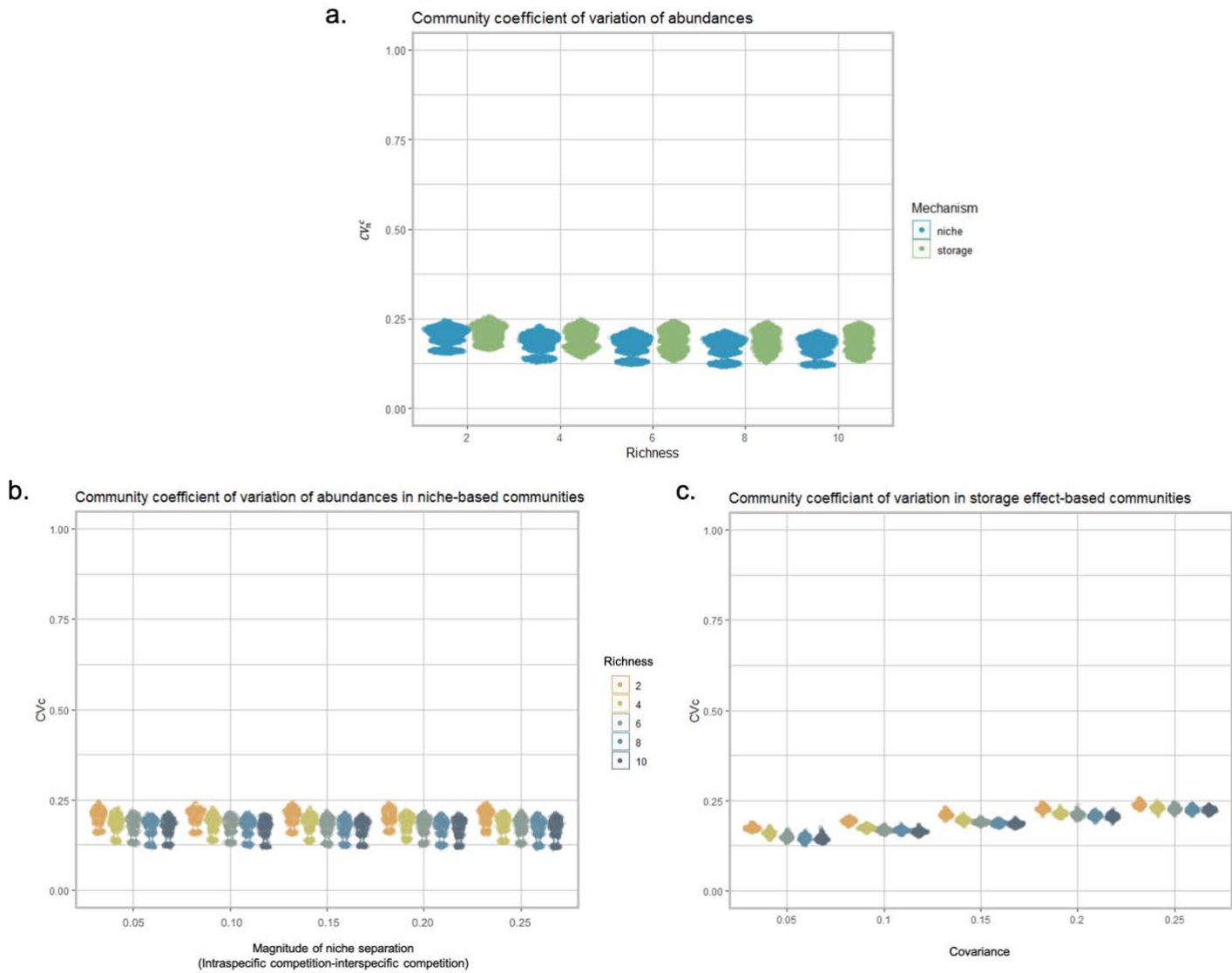


Figure 2.1: The violin plots represent the distribution of community coefficient of variation, CV_n^c , values calculated from the 12,500 simulations. In panel a, each violin represents a cloud of 1,250 data points, jittered horizontally to minimise overlapping points. The blue points represent values from simulations generated by the niche mechanism and green points represent values from simulations generated by the storage effect. Panels b and c show the same data, separated into different plots by mechanism type to show the effect of mechanism strength, on the x axis, and community size, which are differentiated by colour. Each violin in these panels represents a cloud of 250 data points, jittered to minimise overlapping points.

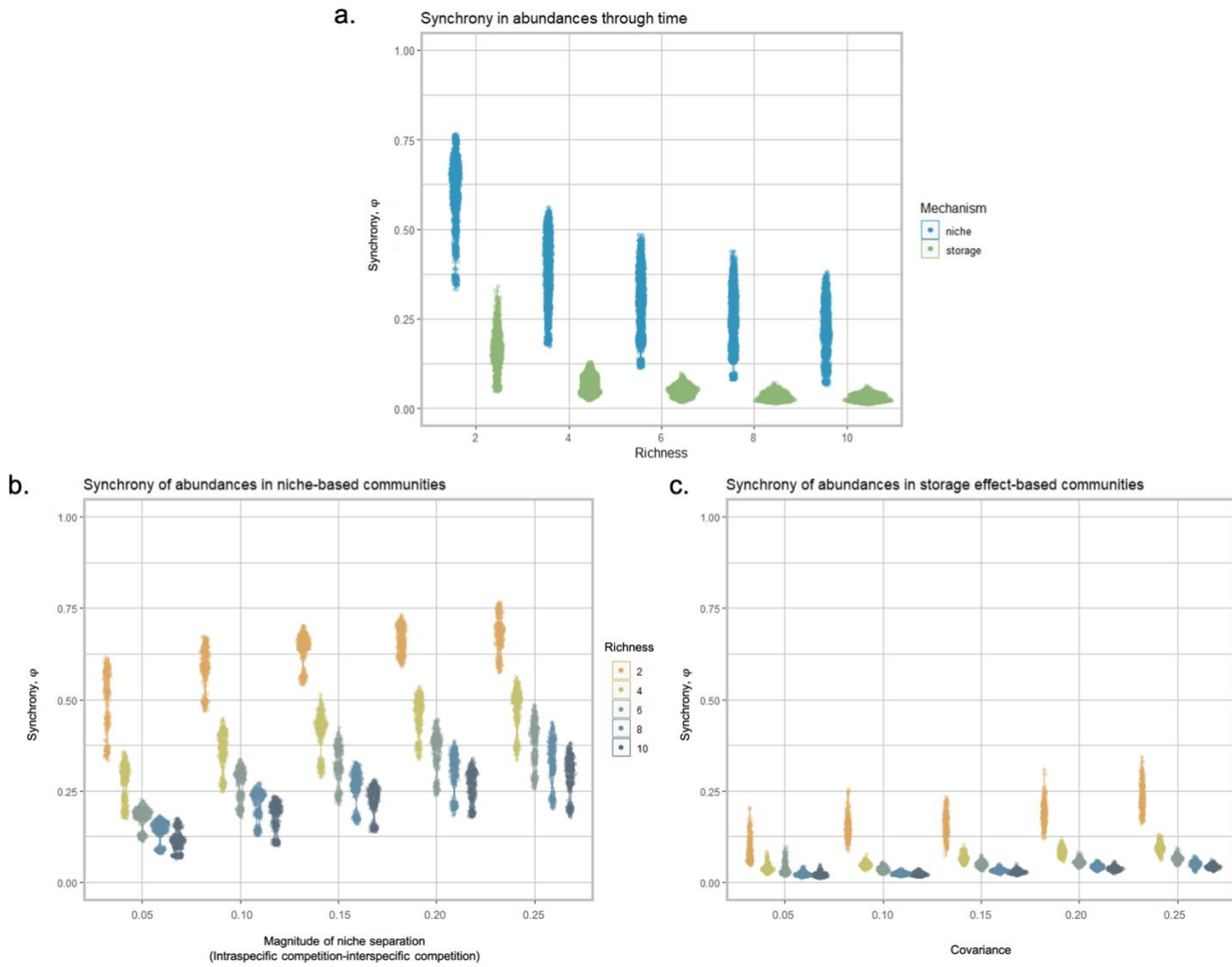


Figure 2.2: Panel a demonstrates the distinct difference in the synchrony, ϕ , values between mechanism. Panels b and c represent the synchrony values separated by niche and storage effect mechanisms, respectively.

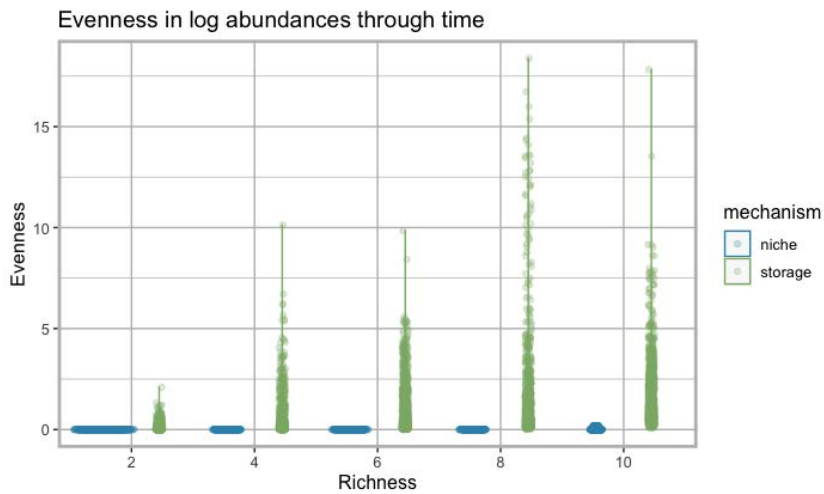


Figure 2.3: *Evenness is affected by mechanism type; the value of the evenness index is lower in communities generated by the niche mechanism than storage effect-based communities. There is significant variability in the values of the evenness index in communities generated by the storage effect community, particularly in communities with higher species richness.*

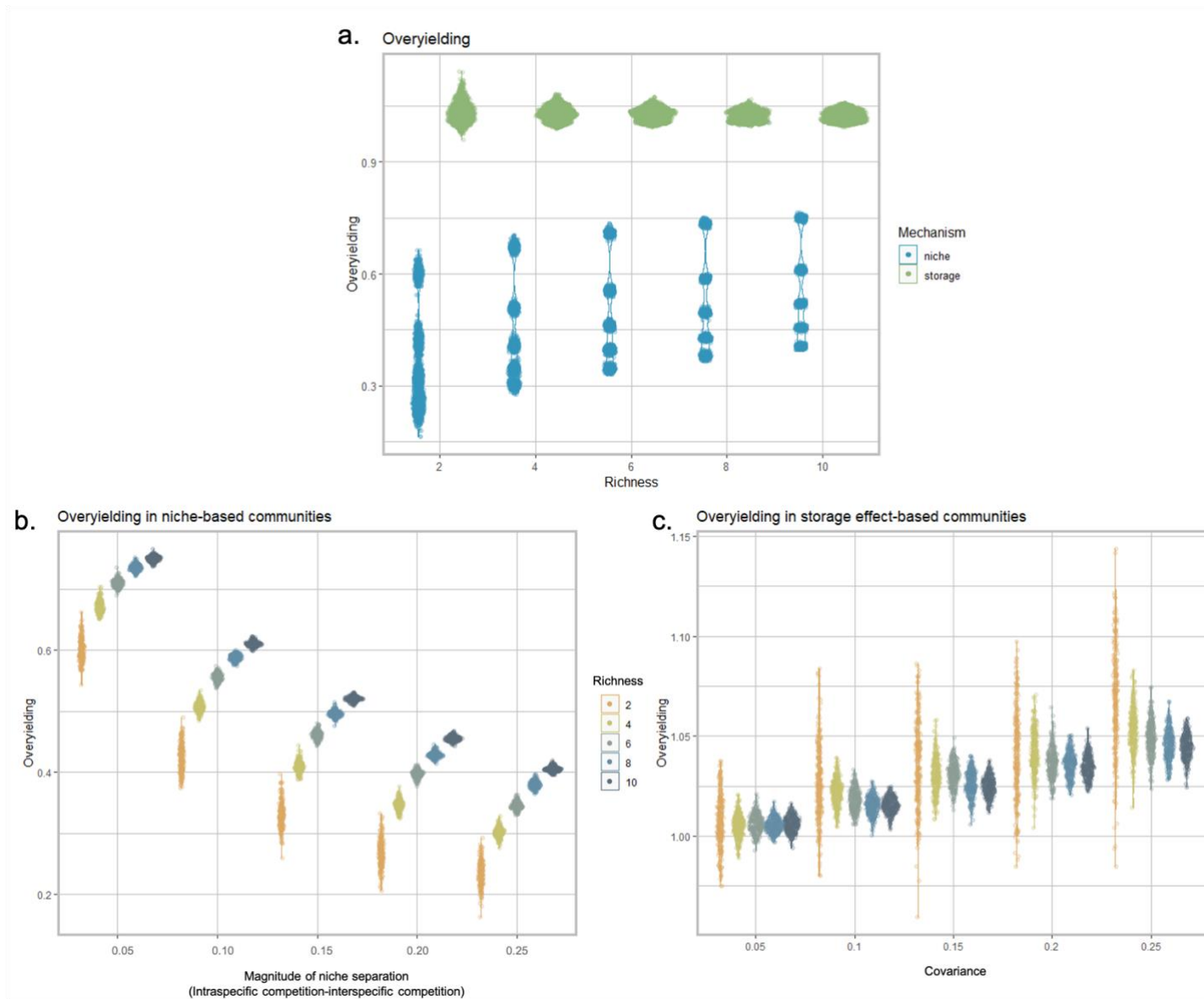


Figure 2.4: Panel a shows that overyielding is occurring in communities generated from niche-based coexistence whereas storage effect-based communities exhibit underyielding. Panels b and c demonstrate the effect of mechanism strength and species richness on overyielding in communities generated by the different mechanisms.

2.4 Discussion

The results from my simulated communities and subsequent statistical analyses on timeseries data found no effect of mechanism type, strength, or species richness on the community coefficient of variation, which was my proxy for community stability (Figure 2.1). The lack of an effect of community attributes such as mechanism type, strength, and species richness on community stability underscores the notion that these attributes are less important in influencing the aggregate property of stability. Many different natural communities persist and function, despite having different community sizes and being shaped by disparate combinations of different mechanisms operating

simultaneously at different strengths. Evenness and synchrony, however, were impacted by the type of mechanism shaping the simulated communities and, to an extent, by mechanism strength and species richness (Figures 2.2 and 2.3). Evenness and synchrony both affect the spatial and temporal patterns of communities and ecosystem functions. High evenness and low synchrony combine to decrease community variation when it is calculated over large time periods.

My findings indicate that the value of overyielding is affected by the number of species present in a community and the strength of mechanisms, but only in niche-based communities (Figure 2.4). Overyielding is an indicator of community productivity, and the values calculated from my timeseries demonstrate that overyielding is occurring in niche-based communities (that is, α is less than one), but not in storage-effect based communities. This supports the assertion that if species are competing less for the same resources, they are more likely to take advantage of resources within the environment and increase abundances or biomass despite the presence of other species.

Overall, my research supports other findings that the processes that affect community assembly do not have a straightforward impact on ecological stability. Furthermore, the effects of these mechanisms on stability and other community attributes depends on other factors. By altering the type of species interactions through manipulating patterns of competition, Hughes and Roughgarden (2000) showed that diversity-stability relationships varied. Similarly, by using stochastic models with niche-based coexistence to generate randomly assembled communities, Lehman and Tilman (2000) found that stability significantly varied among communities with equivalent species richness, indicating that community composition is also a significant contributor to temporal stability. In contrast to my results, through using numerical simulations to model fluctuation mediated coexistence mechanisms, Tredennick et al. (2017) determined that the storage effect can result in an increase of community stability with not only diversity but also the strength of the mechanism. However, their results also indicated that the effects of relative nonlinearity, another fluctuation mediated coexistence mechanism, depended in part on the traits of species. The species that immigrated into the local pool that were inherently more stable helped to buffer community variability.

Out of the community statistics I calculated, the most reliable to calculate from data based on ecological surveys is synchrony, as it simply requires comparing the relative abundances of species through time. However, synchrony may be difficult to discern due to environmental noise and changes in relative abundances may be undetectable in shorter time series (Cazelles & Stone, 2003). CV_n^c is also a reliable statistic to calculate from empirical data (Ives and Hughes, 2002). However, the magnitude of CV_n^c is influenced by large abundances, which is further exacerbated by the difficulty in detecting rare species in ecological surveys (Emlen et al., 2003). Evenness is a critical statistic in describing species diversity, however, there is a lack of consensus regarding how it should be

calculated. I used a straightforward evenness index based on species' variances. However, conventional calculations of evenness can be considered problematic as they incorporate species richness into the calculations, which should be separate from evenness as richness independently affects diversity (Heip, 1974; Smith and Wilson 1998). Furthermore, unbiased sampling for evenness indices necessitates that species are randomly distributed and are independent of other species, which is unrealistic in natural environments (Heip et al., 1998). Finally, overyielding is difficult to observe in nature and requires an experimental set up. To calculate overyielding, the abundance or biomass of a community must be compared to the average biomass of each of those species in isolation under identical conditions. Though overyielding has proven to be a considerable outcome of resource partitioning, it is a calculation that does not lend itself to study in natural systems (Tilman et al., 2006).

Community statistics are reliable in predicting mechanisms despite not having intuitive linear relationships. Synchrony and evenness are both community statistics that may be helpful in discerning which mechanisms are operating if time series data are only available. Evenness is very close to zero when niche partitioning is operating, and the difference between communities governed by niche coexistence and the storage effect are more pronounced as species richness increases. Therefore, it may be particularly useful in evaluating large communities. While there is a distinct difference in the ϕ values when calculating synchrony from communities, the difference is more distinct among those with smaller community sizes. Provided it is feasible to compare abundances of species in isolation with those within a community, overyielding can indicate niche partitioning is occurring if the calculated value for x is below one. Even in complicated data collected from ecological surveys and experiments, these statistics may aid in my ability to explain the processes that are occurring and how they impact that system.

CHAPTER 3: Using ensemble modelling to predict the impacts of assisted migration on recipient ecosystems (*in press, Conservation Biology*)

3.1 Introduction

Many species face extinction as a consequence of habitat and environmental changes which they cannot escape. Assisted migration (often called assisted colonisation; IUCN, 2013) is a conservation intervention which moves a portion of a threatened population beyond its indigenous range, when such a movement is unlikely to occur naturally (Vitt et al., 2010). Assisted migration and related interventions are often proposed as a response to anthropogenic impacts such as climate change or habitat loss (McLachlan et al., 2007; Hoegh-Guldberg et al., 2008; Vitt et al., 2010; McDonald-Madden et al 2011). While it is a radical action, in some cases assisted migration may be the only way to prevent extinction due to human-driven environmental change. Advocates of assisted migration argue that humans have been translocating plants and animals throughout history (Vitt et al., 2010), and point out that assisted migration has been successfully applied in the past without negative repercussions (Schlaepfer et al., 2009; Willis et al., 2009).

Despite its proponents, assisted migration remains a contentious conservation action (McLachlan et al., 2007; Hewitt et al., 2011; Gallagher et al., 2015; Webster et al., 2017), with experts identifying three primary risks. First, assisted migrations are costly and resource-intensive, expending resources and time that could have been invested elsewhere (Ricciardi & Simberloff, 2009). Second, removing individuals from extant populations increases the extinction risks facing those source populations (Wootton & Pfister, 2013). Finally, assisted migration will perturb the ecosystem that individuals are moved into (the “recipient ecosystem”), with the potential for seriously ecological disruption, and even extinctions (Javeline et al., 2015; Bucharova, 2017; Catford et al., 2018). Negative consequences of assisted migrations are common for invasive species (Kolar & Lodge, 2001; Gurevitch & Padilla, 2004), but have also been observed following the assisted migration of other species (Ricciardi & Simberloff, 2009; Bucharova, 2017; Catford et al., 2018; Barrio et al., 2019).

Formal risk analyses are required for assisted migration (Hoegh-Guldberg et al., 2008; Ricciardi & Simberloff, 2009; IUCN 2013), and both qualitative and quantitative techniques have been applied to the decision. Reviews of the ecological literature have detailed the wide range of positive and negative consequences of assisted migration, both for the translocated species and for the recipient ecosystem (Richardson et al., 2009; Hewitt, et al., 2011; Schwartz and Martin, 2013). However, because these approaches are qualitative, they cannot calculate the aggregate effect – that is, whether the benefits of assisted migration outweigh the costs. In contrast, quantitative risk analyses have estimated and compared the magnitude of the different benefits and impacts. Unfortunately, their scope has been

narrow, focusing on the risks to the species being translocated, rather than potential ecosystem-level impacts (Hällfors et al., 2015). For example, in the risk analysis proposed by Hoegh-Guldberg et al. (2008), collateral impacts on the recipient ecosystem are dealt with by a single yes-or-no question. Similarly, in the decision-support tools proposed by McDonald-Madden et al. (2011) the impact on the recipient ecosystem are not mentioned at all, while Rout et al. (2013) encapsulate the collateral impacts in a single parameter. While this parameter could potentially take any value, their analyses only explored the possibility that assisted migration would cause 0.2, 1, or 2 extinctions (Rout et al., 2013).

There is an accepted need to incorporate the potential impacts of assisted colonisation on the recipient ecosystem, but previous quantitative risk analyses have not included this factor because it is very difficult to forecast ecosystem dynamics (Dexter et al., 2012; Barrio et al., 2019). Ecosystem models are complex and highly nonlinear (May, 2001; Benton et al., 2006), and accurate predictions are impossible in the face of high levels of parametric and structural uncertainty (Levins, 1974; Dexter et al., 2012; Barrio et al., 2019). Even in intensively studied systems, ecosystem models cannot predict whether assisted migration will cause species in the recipient ecosystem to increase or decrease (Baker et al., 2019). Additional uncertainty is introduced by the novel habitats and novel species interactions created by assisted migration.

In this paper, we describe a risk analysis of assisted migration that incorporates the dynamics of the recipient ecosystem, as well as the translocated species itself. Importantly, we estimate the range of collateral impacts that could affect the recipient ecosystem by applying ensemble ecosystem modelling (Baker et al., 2017), an approach that is designed to investigate the ecosystem-scale consequences of decisions made under severe uncertainty. Our goal in this work is not to make predictions for a specific example, but to instead estimate the distribution of outcomes across a wide range of assisted migration projects. We ask: Is assisted migration generally a low-risk conservation intervention, with few serious consequences for the recipient ecosystem. Or, should we expect it to frequently destabilise recipient ecosystems, causing a cascade of primary and secondary local extinctions (Moir et al., 2012)?

3.2 Methods

3.2.1 Ecosystem-based risk assessment framework

Assisted migration will have a range of conservation consequences. For the translocated species, it will alter the dynamics of the source population, and potentially create a new population. In the recipient ecosystem, function and dynamics will change following the introduction, certainly in the short term, and potentially in perpetuity. We focus our analyses on a straightforward measure of utility – the number of extinctions, aggregated across both species being translocated and the species in the recipient ecosystem. For parsimony, our utility function considers all species to have equal value. Thus, assisted

migration could not be recommended if the action is expected to cause one or more local extinctions (on average) in the recipient ecosystem. However, in real assisted migration projects, it is unlikely that all species would be valued equally. Practitioners could value particular species based on their role in maintaining ecosystem functions or providing services, or on threatened status. We further assume that decision-makers are risk neutral, and are therefore interested in minimising the expected number of extinctions.

Our risk assessment requires quantitative estimates of three critical factors. We first describe each of these elements, and explain how they are integrated into single combined assessment. We then describe how we estimate their values to draw our quantitative conclusions. First, we must consider the probability p that the source population of the translocated species will go extinct. A radical intervention like assisted migration is easier to justify if the threatened species faces a high probability of extinction in its current location. We also consider the possibility that removing individuals from this source population for assisted migration will increase its probability of extinction by a factor δ . Second, we have to estimate the probability q that the assisted migration will be successful for the translocated species. That is, whether the species will be able to establish itself with a positive abundance in the recipient ecosystem. Finally – and conditional on successful assisted migration – we need to estimate how many (if any) of the S species originally persisting in the recipient ecosystem will go extinct, as a consequence of the assisted migration. We define this outcome using the discrete probability distribution $E(i)$, where i is the number of local extinctions within the recipient ecosystem.

Figure 3.1 shows the possible combinations of these three factors, their associated probabilities and consequences. Averaging over all these potential outcomes, the expected change in the number of extinctions within the recipient ecosystem and the source population of the translocated species as a consequence of undertaking assisted migration is:

$$\langle \Delta \rangle = (1 - q)(p\delta + S) + q \sum_{i=0}^S E(i)(1 - S - i) - pS + (1 - S - p).$$

Equation 3.1

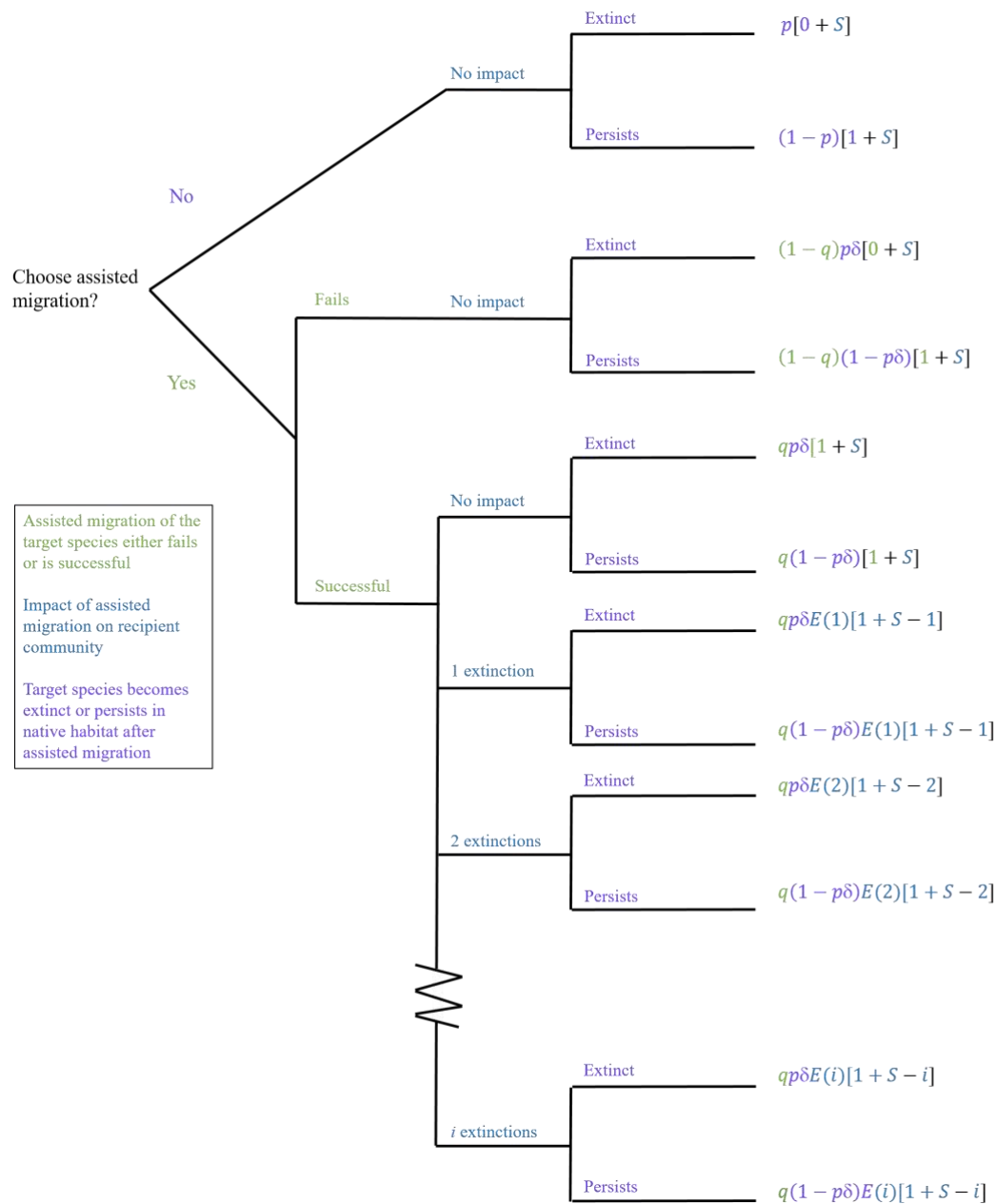


Figure 3.1: Decision tree representing all possible outcomes of assisted migration. The source population of the translocated species goes extinct with probability p (shown in purple). Assisted migration succeeds with probability q (shown in green). If successful, the translocated results in $0 \leq i \leq S$ extinctions with probability $E(i)$ (shown in blue). At the terminals of the tree, the terms describe the consequences of each outcome (in square brackets), and the associated probability of each event. (Note the break in the tree).

3.2.2 Model parameterisation

I am not applying these techniques to any particular assisted migration project (e.g., Baker et al. 2019), and so our results will show an *a priori* estimate – essentially a null expectation – of the net

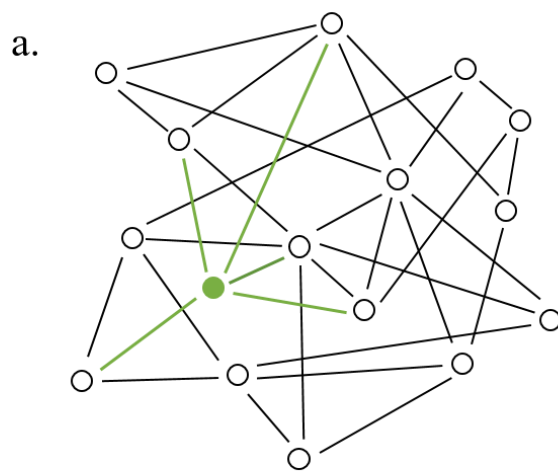
consequences of translocating an average new species, into an average ecosystem containing 15 interacting species. The most significant challenge is making quantitative predictions about impacts on the recipient ecosystem following assisted migration (i.e., estimating $E(i)$). We parameterise this element of the risk analysis using ensemble ecosystem modelling (EEM), a form of exploratory computational modelling that is particularly useful under conditions of severe uncertainty (Raymond et al., 2011; Dexter et al., 2012; Baker et al., 2017). By creating and simulating a large number of ecosystems, EEM can capture and quantify the range of consequences that could result from intervening in particular complex ecological systems.

Our ensemble comprises 1.5×10^6 Lotka-Volterra ecosystems, each representing a unique combination of a novel translocated species and a complex, stable, recipient ecosystem (Fig. 3.2). For our main results, we choose to use a stable recipient ecosystem to simplify the assumptions and interpretations of our results. Recipient ecosystems that are candidates for assisted migration as refuge for species vulnerable to climate change are chosen due to their stable environmental conditions, that will remain suitable over long periods of time (Hoegh-Guldberg et al., 2008; McDonald-Madden & Martin 2011). However, as all natural ecosystems are vulnerable to change, we also modelled two types of nonequilibrium recipient ecosystems. First, an ecosystem subject to a slow “press” perturbation, representing a gradual impact such as warming. Second, a recipient ecosystem that is in the process of re-equilibrating following the recent removal of a species. Eradication of threatening species – generally invasives – is common practice before proceeding with assisted migration (Bellingham et al., 2010; Smith et al., 2010). This also represents a more sudden perturbation to the recipient ecosystem than the gradual change modelled in the other non-equilibrium scenario. The full methods and results for both non-equilibrium ensembles are given in the *Supplementary Information*.

The elements of the ensemble vary both parametrically and structurally, including ecosystems with both sparse and dense networks of interactions, as well as interaction strengths that range from strong to weak. The magnitude and sign of the interactions are randomly chosen and do not adhere to any predetermined hierarchy, and can represent competition, mutualism, and predation (see *Supplementary Information* for full model details). We choose 15 species in the recipient ecosystem, as this is sufficient to create a realistic web of complex interactions, while remaining computationally feasible. By comparison, the reintroduction analyses by Baker et al. modelled 20 species and functional groups (2019); Dexter et al. modelled 17 species (2012); and Hunter et al. model 16 species (2015). In each case, these previous models only considered a single ecosystem structure.

Each of our ecosystems is initialised at its stable equilibrium \mathbf{n}^* , and then a new species is added at an initially low abundance. In many of our ecosystem simulations, the translocated species cannot successfully establish, and its abundance declines to zero. The frequency of this outcome allows us to

estimate the probability q that assisted migration will succeed. If the translocated species can successfully establish, the ecosystem dynamics are simulated until a new equilibrium \mathbf{n}^\dagger is reached. The impact of the assisted migration on the recipient ecosystem is determined by the difference between these two equilibria. Across all ensemble elements, we estimate $E(i)$ as the proportion of ensemble members where i species are negatively impacted (see below). The final parameters in the risk assessment are the probability p that the species targeted for assisted migration goes extinct in its source population, and the degree δ to which assisted migration exacerbates this risk. We choose two contrasting combinations of these parameters.



b.

$$\begin{bmatrix} x_{1,1} & x_{1,2} & \dots & x_{1,S} \\ x_{2,1} & x_{2,2} & \dots & x_{2,S} \\ \vdots & \vdots & \ddots & \vdots \\ x_{S,1} & x_{S,2} & \dots & x_{S,S} \end{bmatrix}$$

c.

$$\frac{dn_i}{dt} = r_i n_i + \sum_{j=1}^S x_{i,j} n_i n_j$$

Figure 3.2: Ensemble ecosystem modelling approach. (a) An example interaction network of a 15 species recipient ecosystem following assisted migration (the green node). Black lines represent interactions present before the intervention, and the green lines represent interactions created by

assisted migration. (b) The interaction matrix following assisted migration, with translocated species interactions shown in green. (c) The governing Lotka-Volterra ecosystem equations, where the change in abundance n of species i depends on the species specific growth rates, r_i and interaction matrices, α , whose elements $x_{i,j}$ measure the per-capita interaction strength of species j on individuals of species i for S species. The values for the parameters are given in Appendix 1.

I define an upper and lower bound of risk by performing the analysis under two contrasting sets of conditions. The first set is particularly favourable to undertaking assisted migration. The species targeted for assisted migration is Critically Endangered in its source location and could easily become extinct if the action is not taken ($p = 0.5$, according to IUCN Red List criterion E). Removing individuals of this species does not increase its probability of extinction (i.e., $\delta = 1$), further encouraging intervention. Moreover, we set a high threshold for impact in the recipient ecosystem, and only consider a species i to be “negatively impacted” if it goes extinct: $n_i^\dagger = 0$. The second set of conditions is unfavourable to assisted migration. The translocated species is only IUCN Red List Vulnerable in its source location ($p = 0.1$) and is therefore quite likely to persist without assisted migration. Removing individuals substantially increases this probability of extinction, however, with $\delta = 2$. We also consider a species in the recipient ecosystem to be impacted if its population declines by more than 90% (that is, if $n_i^\dagger/n_i^* < 0.1$), making negative impacts more likely to be registered, as well as incorporating vulnerability to genetic bottlenecks and demographic stochasticity at low abundances. We repeat the analyses and report the results for both scenarios.

3.3 Results

The models in our ensemble exhibit three categorically different types of outcome. In the best case, the assisted migration is successful, and no species become extinct in the recipient ecosystem. The total number of extant species then remains at $S + 1$, although abundances in the recipient ecosystem may change substantially (Figure 3.3a). In the worst case, a number of species in the recipient ecosystem are driven to extinction by negative direct and indirect interactions with the successfully translocated species (Figure 3.3b). In this case, the total species richness may drop substantially. Finally, it is possible that the assisted migration fails, with only transient effects on species in the recipient ecosystem (Figure 3.3c) – a loss of one species from the system. Our model ensemble contains a diverse range of each outcome, and so it is therefore important to but determine the relative likelihood of each scenario.

In both scenarios, successful assisted migration of the translocated species has a probability of $q = 82\%$. The summed value of all $E(i)$ for $i > 0$, which is the probability of at least one extinction in the recipient ecosystem, is 25% for the favourable scenario. There is a 13% probability of at least 2 extinctions, a 4% probability of at least 4 extinctions, and a 1% probability of 6 or more extinctions.

The extinction of a large portion of the recipient ecosystem is very rare but possible; for example 10 species go extinct in 48 of the models.

Poor outcomes were obviously more common in the unfavourable scenario. The recipient ecosystem experiences at least one extinction in 30% of simulations, and there is a 17% probability of at least 2 extinctions, a 7% probability of at least 4 extinctions, and a 3% probability of 6 or more extinctions. See Table 1 in Supplementary Information and Figure 4 for the full results.

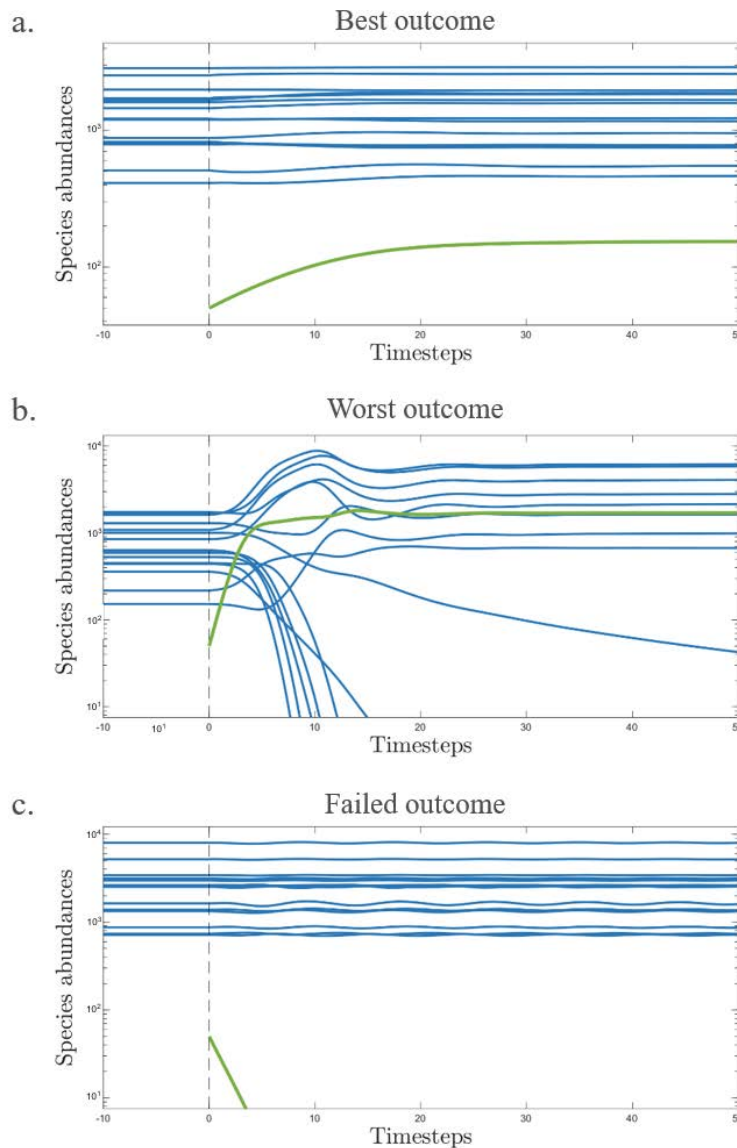


Figure 3.3: Assisted migration consequences. The green line indicates the abundance of the translocated species, and the blue lines indicate the abundance of species in the recipient ecosystem. (a) Successful assisted migration, recipient species experience minimal changes in abundance, and there are no extinctions. (b) Successful assisted migration, but recipient species experience

substantial changes in abundance with some extinctions. (c) Unsuccessful assisted migration, with no long-term changes to the recipient ecosystem.

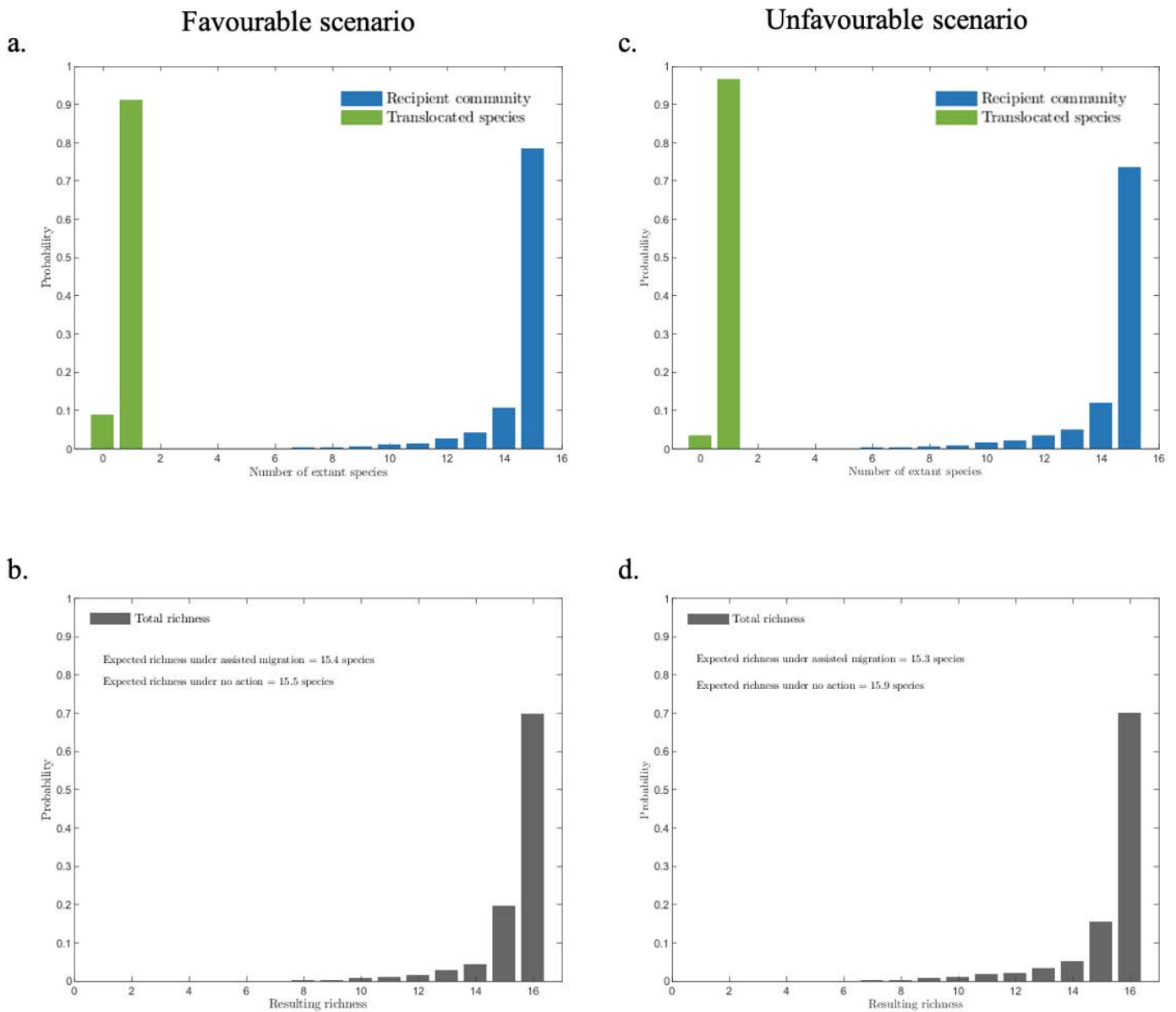


Figure 3.4: Aggregate outcomes of assisted migration in the favourable scenario. In panel (a), the probability distribution for number of extant species in the translocated and recipient ecosystems is distinguished. The translocated species (green), can either survive following successful assisted migration, where the assisted migration success is given by the probability q , or survive in its native habitat following a failed assisted migration, which is given by the probability $1 - p$. Or, the assisted migration can fail ($1 - q$) and the translocated species may go extinct in its native habitat (p). Species in the recipient ecosystem (blue), can be unaffected by assisted migration, maintaining a richness of 15, or may experience one or more extinctions, given by $E(i)$. Panel (b) shows the probability density for the change in overall richness following assisted migration (i.e., the aggregate of the green and blue distributions in panel a).

Assisted migration results in fewer extant species overall, in all modelled scenarios. This is true for the favourable and unfavourable parameterisations, and for both dense and sparse interaction networks (see Appendix 1). In the favourable scenario, the average expected richness if assisted migration is chosen is 15.4, whereas the average richness if no action is taken is 15.5 species (Figure 3.4b). In the unfavourable scenario, the expected richness following assisted migration is 15.2 species, but 15.9 species if no action is taken.

3.4 Discussion

The primary objective for assisted migration is to improve the persistence of a translocated species. Our analyses suggest that the action will likely achieve this, as assisted migration reduces the probability of extinction for the translocated species (assuming we can accurately identify suitable habitat). However, our results also predict that, given the magnitude and likelihood of the collateral impacts on the recipient ecosystem, assisted migration is likely to drive more species to extinction than it saves. The average increase in extinctions caused by assisted migration (compared to no action) is small – less than a single species in both favourable and unfavourable scenarios – but the probability distribution of extinctions has a long and thin tail, warning of large potential losses in the recipient ecosystem. Essentially, the benefits of assisted migration are likely but small, and the costs are rare but acute. The tail of extinctions visible in Figure 4 was anticipated by the critics of assisted migration; our model ensemble shows that their expectations are plausible and show that its effects may be large enough to outweigh the benefits of the intervention.

Our findings mirror and extend the conclusions about ecosystem complexity first drawn by May (1972). Large, complex ecosystems are statistically unlikely to be stable (May, 1972; Pimm, 1984; May, 2001; Jacquet et al., 2016); for similar reasons, the assisted migration of a new interacting species into a stable ecosystem is statistically unlikely to create a larger, more complex, stable equilibrium. Thus, while our ensemble of ecosystem models do not represent any particular project, they create a statistical null expectation about the outcomes of any proposed assisted migration. The average outcome of the action is expected to be negative, and the long-tail of the richness distribution (Figure 4) indicates the potential loss of multiple species, therefore practitioners must carefully weigh the benefits and costs before proceeding with an assisted migration project. The technique presented here quantitatively predicts the potential for unanticipated impacts from assisted migration, allowing practitioners to be more informed during the decision making process.

As our ensemble of ecosystem models are not parameterized for any particular system, we acknowledge that some trophic dynamics that can affect outcomes in real assisted migration projects were not represented. The “biological resistance” hypothesis states that, due to competitive interactions with

other species and predation, introduced species have limited scope for negatively impacting recipient ecosystems (Elton, 1958). This is because introduced species are translocated at low abundances, which reduces the magnitude of their impact on the recipient ecosystem (Elton, 1958). Our models do not predict that this will always be the case. Furthermore, our results indicate that, although novel antagonistic interactions that arise can negatively impact the translocated species, these can also negatively impact the recipient species and disrupt higher order interactions to affect other recipient species indirectly.

Prey switching occurs when a native predator switches its prey preference to the introduced prey, native prey are relieved of pressure from predation as well as competition from the introduced species (Carlsson et al., 2009). This is a potential mechanism for “biotic resistance” against the establishment of an introduced species (Carlsson et al., 2009; Cuthbert et al., 2018). Our model ensembles did not overtly include prey switching, but in Lotka-Volterra models, the proportion of a predator’s diet that is composed of each prey species will vary with the relative abundance of that prey species (Vance, 1978; Weisberg & Reisman, 2008). However, predator preferences for different prey species are determined by a constant interaction parameter, so our model ensembles did not include its potential impact on the probability of establishment or the downstream impacts on the recipient ecosystem. Additionally, the extent to which prey switching occurs when a new species is introduced to an ecosystem is not solely dependent on the relative abundances of the prey species; it is also conditional on the composition and structure of each trophic network and species-specific attributes (Carlsson et al., 2009; Jaworski et al., 2013; Cuthbert et al., 2018).

The specific outcomes following assisted migration will vary based on the attributes of both the recipient ecosystem and the translocated species (Kumschick et al., 2015). We did not calculate the trophic position of the translocated species in our ensemble models as our networks of interacting species are based on the general Lotka-Volterra model, which does not specify interaction type or particular trophic structure (Weisberg & Reisman, 2008). Instead of distinguishing between interaction types, our ensemble of models employs the sum magnitude of interactions that are constant through time. Further, in natural systems, these interactions are dynamic, and the type of interaction can change over time (Thompson, 1988; Chamberlain et al., 2014). Therefore, the type and magnitude of trophic interactions at different times could also affect the outcomes of real-world assisted migrations. Indeed, the outcomes of assisted migration will likely depend on the trophic role of the species being translocated, as well as the trophic structure and functional redundancy within the recipient ecosystem (Ricciardi et al., 2013; Kumschick et al., 2015). Building on our general framework, a promising future direction is to consider multiple interaction types at different times in the recipient community, and the structure of those ecological networks.

We used a very simple utility function in our analyses, assigning equal weight to the translocated species, and to each of the species in the recipient ecosystem. While parsimonious, this utility function is unlikely to be true for any particular project, where a higher value would likely be associated with some species, particularly the target of assisted migration (since that species clearly attracts attention and resources). In our study, we gave the same weight to global and local extinctions. If the source population of the translocated species goes extinct and assisted migration is not chosen or that species fails to establish following translocation, we consider this a global extinction. We made no assumptions regarding the endemism of species within the recipient ecosystem and thus only considered local extinctions in our utility function. Managers may seek to prioritise avoiding global extinctions over local extinctions, but this would depend on the identity of the species within the focal system. Endemic or functionally-important species in the recipient ecosystem may also be associated with higher utility. Alternatively, functional redundancy could make the loss of some species less important. In any case, by assuming equality, we asserted an equivalence between the extinction of the translocated species (whose global population may be threatened), and the extinction of species in the recipient ecosystem (which may be very abundant, or common in other locations). However, we equally did not assume that the ecological damage caused by the translocated species would propagate more broadly, which can occur when translocated species turn into invasives (Ricciardi & Simberloff, 2009). Finally, the reduction of population sizes in the recipient ecosystem was a common outcome of translocation, but one that we generally did not consider (unless the decline was of sufficient magnitude). If the loss of some ecosystem functions or services are more problematic than gains in other functions, then our results present a relatively conservative estimate of impacts on the recipient ecosystem (Dee et al., 2019).

Before proceeding with assisted migration, decision makers must consider if the benefit of establishing a particular species justifies the risk to the recipient ecosystem. When all species are valued equally, our results suggest that the impacts to the recipient ecosystem outweigh the benefits. The potential for the loss of many species will be particularly concerning for risk-averse decision-makers. Two changes could make the action more palatable: a reduction in the impact on the recipient ecosystem, and an increase in the probability of a successful assisted migration. Improving ecological information about the translocated species can help managers improve the efficacy of assisted migrations, and may assist in estimating values to quantify the interactions between translocated species with the proposed recipient ecosystem. The greater impact however would be specifically researching the potential recipient ecosystem's response rather than further studying the translocated species. Endangered and threatened species that are candidates for conservation interventions are generally well-monitored and studied (Campbell et al., 2002). Provided there is enough time and funding, the scoping process for finding suitable recipient ecosystems should involve detailed monitoring of those communities.

CHAPTER 4: Risk analysis of faunal reconstruction decisions on Dirk Hartog Island

4.1 Introduction

Faunal reconstruction, or “refaunation” on islands is a powerful conservation initiative because the geographic isolation limits anthropogenic impacts and enables the elimination of non-native predators or competitors, providing refuge to threatened species (Burbidge et al., 2018). The first translocations to islands for the sake of conservation were two kiwi species in New Zealand between 1903 to 1919 (Bellingham et al., 2010). To improve the likelihood of establishment success, eradications of non-native mammals such as goats, cats, and pigs are often deemed necessary (Simberloff, 2008; Glen et al., 2013). Island refaunation programs are commonplace throughout Australia and have been instrumental in the conservation of multiple threatened native mammals sensitive to non-native predators and competitors (Armstrong et al., 2015; Burbidge et al., 2018; Legge et al., 2018). Translocation of the rufous-hare wallaby, (*Lagorchestes hirsutus*), which had previously been considered extinct in the wild, to Trimouille Island in Western Australia proved successful with post-release surveys indicating the population was breeding and expanding its range (Langford & Burbidge, 2001). Similarly, the translocation of dighters (*Parantechinus apicalis*) to Escape Island in Western Australia yielded successful wild breeding populations, as determined from surveys three years after release (Moro, 2003).

Dirk Hartog Island (DHI) was chosen for an ambitious refaunation project of multiple species for its diversity of habitats, large area as the largest island in Western Australia, and its location within the Shark Bay World Heritage area (Morris et al., 2017). The refaunation project on DHI is the largest in Australia to date (Morris et al., 2017). The first stage involved the removal of populations of non-native species from the island: sheep were declared eradicated in June 2016, goats in November 2017, and feral cats in October 2018 (Cowen et al., 2019). The removal of grazing pressure allowed vegetation to increase across the island (Cowen et al., 2019), while feral cat predation was a key driver of native mammal declines and extinction on DHI (Algar et al., 2011). The removal of these non-native species, therefore, was necessary to facilitate successful translocations and subsequent establishment of the native species proposed for refaunation (Algar et al., 2011). As these eradications were being completed, the translocation of native species began with a trial release of the rufous hare wallaby (*Lagorchestes hirsutus bernieri*) and banded hare wallaby (*Lagostrophus fasciatus*) on the island in August/September 2017, followed by a full-scale translocation in 2018 (Cowen et al., 2019). Translocations have also been recently undertaken for the Shark Bay bandicoot (*Perameles bougainville*) in September/October 2019 and dightler in October 2019 (Cowen et al., 2019).

The Western Australian Department of Biodiversity Conservation and Attractions Western Australia (DBCA) aims to translocate 10 additional native vertebrates to the island by 2025 (Table 4.1; Cowen et al., 2019). The translocation of such a large number of species to an insular ecosystem will be challenging, and multi-species translocation theory is relatively undeveloped in reintroduction ecology (Armstrong and Seddon, 2008). A commonly raised question in the translocation of multiple species how does the order and timing of translocations impact success (Armstrong and Seddon, 2008; Plein et al., 2015). These decisions, which are collectively labelled as the “Translocation Alternatives”, may affect the chances of a successful outcome through their influence on population dynamics and species interactions (Plein et al., 2015). To give the simplest example, in a two-species translocation of a specialist predator and its prey, the predator species should not be translocated before the prey species is present at the site. Therefore, the order and possible interactions between species has been explicitly included in the planning and adaptive management process for restocking DHI.

The Translocation Alternatives that DBCA have proposed all contain the same suite of new species, but they occur in a different order, with varying delays between species, and potentially at different release locations. My risk analysis process first estimates the relative probability that each scenario will successfully establish each of the 13 translocated species by the end of the project. Once these probabilities have been calculated, I identify the weak-points in each alternative – the species most at risk of failed translocation – and assess which ecological processes (e.g., high competition or predation, insufficient resources) are most likely to be the cause of the failure. These modelled outputs provide quantitative support for future translocayions on DHI, and to provide guidance for ongoing, adaptive management and monitoring.

Table 4.1. *The proposed vertebrates for translocation to DHI.*

Common name (WA)	Latin name
Dibbler	<i>Parantechinus apicalis</i>
Shark Bay bandicoot	<i>Perameles bouganville</i>
Woylie (brush-tailed bettong)	<i>Bettongia penicillata</i>
Chuditch (Western quoll)	<i>Dasyurus geoffroii</i>
Rufous hare-wallaby	<i>Lagorchestes hirsutus bernieri</i>
Banded hare-wallaby	<i>Lagostrophus fasciatus fasciatus</i>
Heath mouse	<i>Pseudomys shortridgei</i>

Shark Bay mouse	<i>Pseudomys fieldi</i>
Brush-tailed mulgara	<i>Dasyercus blythi</i>
Boodie (burrowing bettong)	<i>Bettongia lesueur lesueur</i>
Greater stick-nest rat	<i>Leporillus conditor</i>
Desert mouse	<i>Pseudomys desertor</i>
Western grasswren	<i>Amytornis textilis textilis</i>

4.2 Methods

In this chapter, I used ensemble ecosystem modelling to simulate the possible outcomes from the set of proposed Translocation Alternatives. The ensemble ecosystem modelling process offers insights at a range of levels. At the broadest scale, it estimates the range of plausible outcomes for each of the Translocation Alternatives, and their relative performance in terms of overall richness and species abundances. Essentially, it predicts which Translocation Alternative is most likely to achieve a complete faunal reconstruction on DHI. It also indicates how many local extinctions may be possible under worst-case scenarios for each Translocation Alternative.

The objective of the DHI refaunation program is complex and multifaceted. However, to effectively compare strategies managers must focus on critical and measurable outcomes. The primary objective of the project is to minimise the number of extinctions or near extinctions, to create persisting, secure populations of as many translocated species (listed in Table 4.1) as possible by 2050. There are two primary mechanisms by which a translocated population may fail. The first is deterministic – interactions among species drive one unlucky species' population lower and lower, until it falls to zero. The second is stochastic – even if a species' abundance eventually reaches high levels, it can be driven to low abundance in the short-term by transient dynamics (e.g., population cycles, initially high predation, or dispersal dynamics). During this low abundance stage, the population is vulnerable to demographic and environmental stochasticity. The measured outcome from the model ensembles is therefore the expected number of species that experience dangerously low abundance, either temporarily or permanently. This is defined as having occurred if a population declines below 50% of its translocation number at any point in the first 30 years of the project (i.e., before 2050).

4.2.1 Translocation Alternatives and constraints

The overall objective of the faunal reconstruction is to translocate up to 13 species of vertebrates to DHI. However, there are many ways in which this can be undertaken. Specifically, this is varied by changing the (1) dates on which each species is brought to the island; (2) the number of individuals translocated to the island on those dates; (3) the location on DHI where the animals are released. The combination of these choices, across the set of 13 species, are the “Translocation Alternatives”. The general differences between the Translocation Alternatives are in Table 4.2.

Table 4.2: *The proposed Translocation Alternatives to DHI. The differences in the alternatives are fine-scale adjustments to timing or location of the release.*

#	Name	Scenario description
1	Status quo	Existing plan for the order and location of releases (Morris et al., 2017).
2	Move stickies	Release greater stick-nest rats to a zone further from boodies to reduce interactions.
3	Cheapest boodie A	Translocate some species earlier than the status quo (Shark Bay mouse, chuditch, heath mouse) to reduce the number of trips to Bernier and Dorre Islands; boodies released in single zone (option A)
4	2 nd Bernier collection	Cheapest option if collections from Bernier Island two years in a row required.
5	Cheapest boodie B	Same as alternative 3 but also translocate the desert mouse later than the status quo.
6	No boodies	All species are translocated except boodies.
7	No mulgara	All species are translocated except mulgara.
8	Boodies & chuditch last A	Boodies and chuditch are released in the final two years of the translocations (2024 and 2025).
9	Boodies & chuditch last B	Same as alternative 8 but boodie releases are equally distributed in all zones (option B).
10	2 nd to last boodies & chuditch last A	Boodies are released the second to last (2022 and 2023) and chuditch are released last (2024 and 2025).
11	2 nd to last boodies & chuditch last B	The same as 10, but boodies are released equally at all sites.
12	Boodies after chuditch	Boodies are released in 2025 and 2026, and chuditch are released in 2023 and 2024.
13	Delay mulgara	Mulgara are released in 2025 and 2026.

14	Delay chuditch	Chuditch are released in 2026 and 2027.
15	Desert mouse after heath mouse	Desert mouse is released in 2025 and 2026, and the heath mouse is released in 2023 and 2024.

Expert elicitation with biologists at DBCA was used to develop the 15 different Translocation Alternatives for the DHI project. The proposed Alternatives were shaped by the suitability of nearby habitat; the overall and annual project budget allocation; logistical and time constraints on the managers, and limits on the availability of source animals. For example, boodies need an appropriate substrate to establish warrens (Short & Tuner, 1999), and so most Translocation Alternatives proposed release of boodies at the northern end of DHI, which is predominantly limestone habitat. Additionally, the funding schedule for the project requires that all translocations be completed within a relatively short timeframe, so many Translocation Alternatives undertake most of the translocations in a few years, and to only a few sites. The most easily accessible translocation site is in the vicinity of the Dirk Hartog Homestead, which has a nearby airstrip and is also the only permanent camp on the island (see Figure 4.2), so quite a few of the translocations are proposed, or have already been undertaken, there. Another accessible site is in the vicinity of Herald Bay where DBCA have an operational base and campsite. Here, there is also spinifex habitat nearby that is suitable for many of species, such as the Shark Bay mouse and greater stick-nest rat (Morris et al., 2000; Short et al., 2019). The feasibility of monitoring species also influenced the selection of release locations, primarily in relation to accessibility. Finally, the Translocation Alternatives implicitly consider species interactions, by, for example, delaying the translocation of predators (e.g., chuditch and mulgara) until the populations of susceptible prey species have had a chance to establish.

4.2.2 Model of the system dynamics

I used a suite of 19 Lotka-Volterra (LV) equations to model the abundance n_{im} of each species i in each zone m (Baker et al., 2017). The 19 equations represent the 13 translocated species, and six species groups that are already present on the island. These groups include vegetation, invertebrates such as insects, varanid reptiles that may prey on some of the small mammals, other small rodents that would potentially compete with the translocated mammals, other small vertebrates, and larger natural predators such as birds of prey. As the island has been divided into five distinct zones, I extend the model into the spatial dimension to allow dispersal of individuals between adjacent zones.

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

Equation 4.1

The dynamics of each species are governed by their growth rate, r_i , their interaction with other species x_{ij} , and their dispersal from and to different zones, d_{pm} and d_{mp} respectively. Both the growth rates and species interactions are considered constant across the island.

These dynamics allow for antagonistic and beneficial interactions between species using the interaction matrix \mathbf{X} with elements x_{ij} . The elements x_{ij} of \mathbf{X} reflect the per capita impact of species j on each individual of species i . On DHI, experts expect that these interactions will be predominantly competitive, which is antagonistic for both species, since the translocated species cohort contains species with substantial niche overlap (e.g., the species of hare-wallabies). Predation is also expected to be common, particularly between native predators already on the island (e.g., birds of prey) and the translocated species. LV equations also allow for possible positive interactions such as mutualism, where both benefit, and commensalism, where one species benefits and the other is not impacted positively or negatively. A potential example of commensalism on DHI would be greater stick-nest rats using old burrows made by boodies. However, these two species may also compete for refugia, particularly in poor conditions.

Equation 4.1 also allows for dispersal between each of the five zones, although in practice only dispersal between adjacent zones was considered. The final summation of the equation considers the effects of both emigration out of, and immigration into, each of the zones. The dispersal parameters d_{mp} indicates the rate of movement from zone m into zone p . These parameters are time-dependent, since for each of the species I assumed a different fixed delay between the translocation date, and the onset of dispersal between zones.

4.2.3 *Creating sign-structured interaction matrices*

The first step in generating the species interaction matrices began with the creation of a sign-structured matrix. Qualitative analysis often assumes that ecologists can state with some certainty whether a direct ecological relationship exists between two species (or species groups), and if a relationship existed, whether it is positive or negative. This required the experts to identify predator-prey relationships, competition, and so on, based on their ecological knowledge about, and experience with, these species. Multiple factors were considered when defining the sign-structure of the interaction matrices. Species whose expected habitat distribution did not overlap, for example, might be assumed not to directly interact ($x_{ij} = 0$). Species that were too large to be consumed by a predatory species throughout their lifespan, might also have a zero-interaction term. Four conservation biologists working on the project at DBCA (i.e. experts) separately developed sign-structured matrices following these instructions. In some cases, even this qualitative information was uncertain, and the experts were then allowed to create multiple matrices that corresponded to different potential

ecosystem structures. For example, one expert constructed two matrices – one where boodies played an important role as ecosystem engineers, the other where they did not. In total, the process yielded six different sign-structured matrices. The differences in the interaction networks generated from the sign structured matrices is visually demonstrated in Figure 4.1.

Within each of the six sign-structured interaction matrices, I also allowed for additional uncertainty about the sign of individual pairwise interactions. Following Raymond et al. (2011), the experts therefore identified uncertain pairwise interactions as “positive or negative”, “positive or zero”, “zero or negative”, or “positive, negative, or zero”. Like the six different interaction matrices, these uncertainties represent structural uncertainty about the proposed DHI ecosystem. However, because they are independent uncertainties (e.g., “I’m not sure whether this interaction is positive or zero”), rather than overarching (e.g., “I’m not sure if this ecosystem will be top-down or bottom-up regulated”), I did not create a new matrix for each uncertainty.

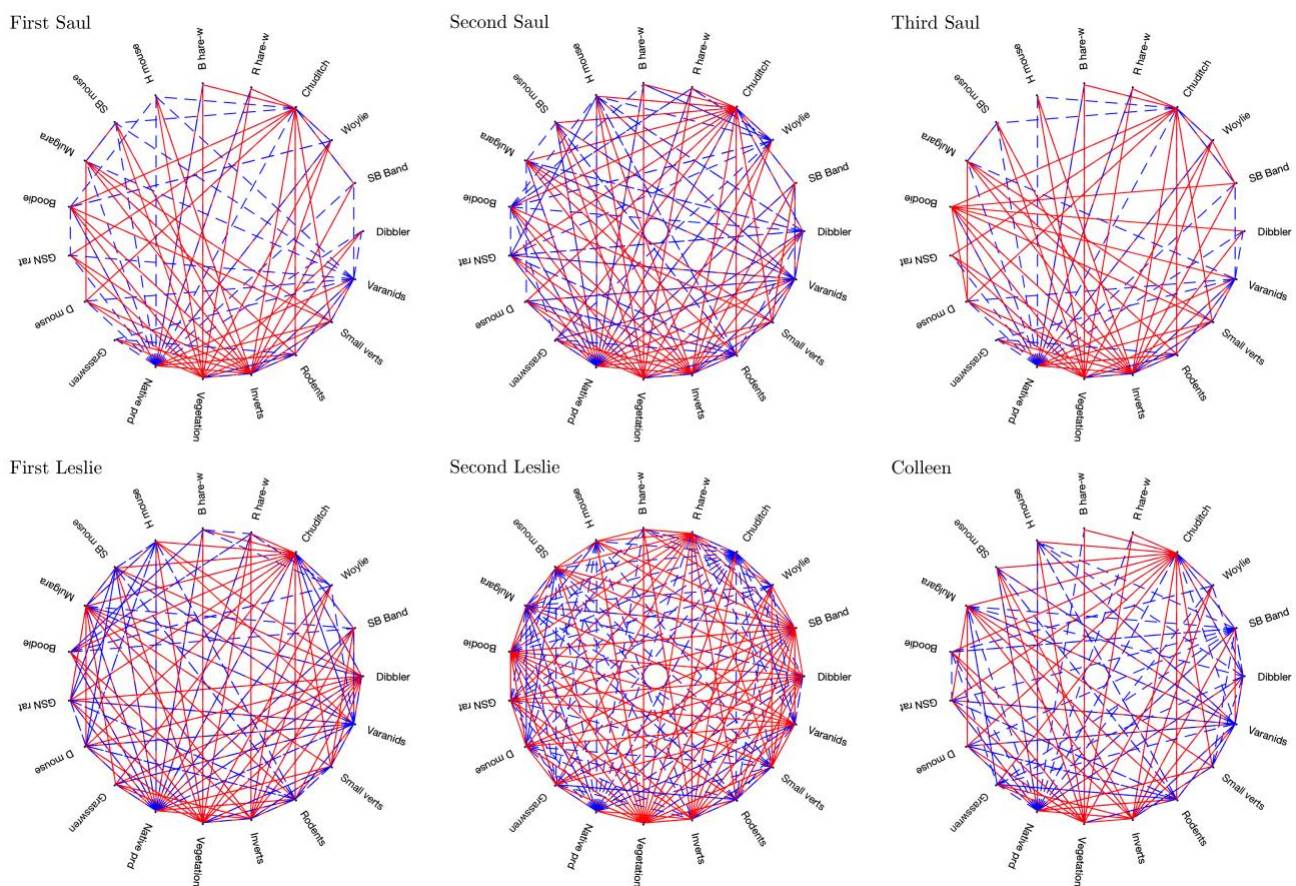


Figure 4.1: Six elicited interaction networks for DHI. Red lines indicate a positive interaction (e.g., Heath mice consume vegetation). Dashed blue lines indicate a negative interaction (e.g., Shark Bay mice are consumed by native predators). These networks do not indicate directionality of interactions,

and instead aim to represent the relative density of interactions between the elicited sign structured matrices.

4.2.4 Assigning strengths to the interaction matrices

Once the sign-structured matrices were created, the next step was to determine the strengths of each interaction. The exact values of the interaction terms are important. In large ecosystems (i.e., containing more than a few species), the sign structure alone does not allow the ecosystem dynamics to be predicted unambiguously. For example, one cannot answer a simple question such as “What would happen to albatrosses if I eradicated cats from this island?” without knowing all of the quantitative strengths of many of the terms in the interaction matrix. Traditionally, these values would be selected by either expert opinion (Martin et al., 2012), experimentation (Roemer et al., 2002), or literature surveys (Hunter et al., 2015). However, this approach was challenging for the DHI ecosystem, and there are compelling arguments that it is equally challenging for any ecosystem. In the case of DHI, managers are attempting the reconstruction of an extinct ecosystem, which by definition cannot be observed. Not all of the species destined for DHI currently co-occur or co-occur in the Shark Bay region (Algar et al., 2011). Observational studies where all 13 species co-occur are therefore not possible, and experimental manipulations are outside the scope of the DHI project. More generally, parameterisation of ecosystem models is an enormously difficult problem. The expert elicitation process identified 38 pairwise interactions between species on DHI, each of which is hard to measure with any accuracy. Even in microcosm experiments where confounding factors (e.g., temperature, resources) can be easily controlled, where observations are highly accurate, and where populations lack spatial, age, and sex structure, these estimates have coefficients of variation greater than one. This is too much uncertainty to allow unambiguous predictions.

Rather than making and using the best-estimates of these interaction terms, which are known to be inadequate for prediction, I adopted an ensemble ecosystem modelling approach to risk analysis. Computational simulation generated many different models of the ecosystem, which each fit with the knowledge and observations of the ecosystem dynamics determined through expert elicitation but offering a different explanation for those dynamics. The creation of these models involved first simulation, and then filtering. In the simulation step, I randomly generated millions of candidate models with unique parameter sets. Using these random parameter sets, I calculated the equilibrium state of the model, and a timeseries of future ecosystem dynamics under each translocation scenario. In the filtering step, I discarded any of those models that did not agree with expected properties of the ecosystem based on prior knowledge and expert judgement (See Table 4.3).

Simulation: I began by selecting values for the species growth rates r_i and the interaction terms x_{ij} from uniform distributions $U(0,1)$. For the interaction matrices, these uniform values were then assigned the sign indicated by the expert-elicited sign-structured matrix. The unit interval may seem restrictive, but all possible parameter sets can be re-parameterised without loss of their behaviour (in terms of changes in relative abundance) to fit within this range. Thus, any possible LV ecosystem model could be constructed by this process. The uniform distribution also seems specific, but experiments with different probability distributions (e.g., normal and Gompertz) did not show a substantial impact on the relative frequency of the model predictions (Baker et al., 2017). I then used simple forward Euler simulation to solve the population equations in each zone from the present day, through to 100 years after the final translocation. This random generation process was repeated many tens of millions of times for each of the sign-structured matrices created by my experts.

Filtering: I then considered whether each of these models in turn could recreate three sets of observed phenomena, which I called “filters”, since they were used to discard unsuitable models from my ensemble (Table 4.3). These model filters were defined by the experts and they represent known behaviour of the system that the model should recreate (Bode et al., 2017). Only one in 3.2 million models were able to satisfy all the filters; the remainder were rejected. Models that satisfied the filters provide a “good fit” to the known information about the DHI ecosystem, since they are able to recreate all known features of the system.

Full coexistence filter: I assumed that full coexistence of the 13 translocation species is possible, therefore any simulated communities that did not allow for the whole suite of translocated species to coexist at some point during the time series were removed

Subset coexistence filter: There are subsets of the translocation species that are known to coexist in other locations. For example, five of the translocation species currently coexist on Bernier Island, and four on Dorre Island. There are seven other islands or conservation areas where subsets of a combination of two to five species have or currently do coexist. Additionally, nine species have been identified as coexisting at the same time within the subfossil record at nearby Peron Peninsula (Francois Peron National Park).

Growth rate filter: Another model filter that was used is that each species growth rate must be within a certain range. The experts at DBCA estimated the upper and lower bounds for the doubling times for each species, based on demographic rates in the literature. In my ecosystem models, the growth rates were set to zero so that increases in population size depended on consumption of vegetation or prey. To compare the simulated growth rates with the ranges given by the experts, I checked the maximum

possible per-capita rate of increase that each species could attain. To calculate this, I used only the positive interactions for each species, and I omitted any negative interactions:

$$r_i = \sum_{j \in P} x_{i,j} n_j^*, \text{ where } P \text{ is the set of } j \text{ for which } x_{i,j} > 0,$$

Equation 4.2

where n_j^* is the equilibrium abundance for species j when all species coexist. By only including the positive interactions and assuming no explicit growth rates, the Lotka-Volterra system of equations becomes:

$$\frac{dn_i}{dt} = \sum_{j=1}^S x_{i,j} n_j^* n_i = r_i n_i, \text{ when } x_{i,j} > 0.$$

Equation 4.3

I was then able calculate upper and lower bounds for the growth rates by solving Equation 4.3 given that the population must double in each time period (doubling time). The maximum possible per-capita rates of increase are then calculated using Equation 4.2. Models that had species with growth rates that were too low or too high were not included in further analyses.

Table 4.3: *The model filters limit the simulated models that are further evaluated. Only models that match these criteria are used in the subsequent analyses.*

Model filter	Explanation
Stability	The community has a stable equilibrium at some point in time.
Growth Rate	Growth rates for species are bound between low and high expert estimates of doubling times.
Coexistence 1 – total	All translocated species can coexist on the island.
Coexistence 2 – extant species	The species that have already been translocated (the rufous hare-wallaby and banded hare-wallaby) can coexist.
Coexistence 3 – island subsets	There are other islands, such as Bernier Island, that support a subset of the translocation species, therefore these species are assumed to coexist on DHI.

4.2.5 The spatial dispersal model

The above model (Equation 4.1) was extended to a spatial model to incorporate the effects of translocating species to different zones across DHI and the movement of individuals. Dispersal data, also from expert elicitation, was used to parameterise the spatial model. The dispersal data includes the lower and upper bounds of the percent of a species' carrying capacity that will disperse each year, a time delay before a species is likely to begin dispersing after translocation, maximum dispersal distance, and the percentage of dispersing individuals that would cross permeable barriers on the island. Species are unlikely to disperse until it is necessary to seek more refugia or food, therefore it was necessary to include a time delay for nearly all species, which varies from no time-delay (e.g., chuditch) to 30 years (e.g., heath mouse).

Dispersal rates differed across the island. A swath of dune habitat exists in the south of DHI. For some species, this is expected to reduce the dispersal between the southernmost zone of DHI and the remainder of the island (e.g., the experts at DBCA assume that the dune will reduce heath mouse dispersal by 95%). A fence also crosses the island, although it is currently in disrepair. The impact of this barrier will differ between species (e.g., the experts at DBCA assume that desert mouse dispersal will reduce by 5%, but from rufous hare-wallaby and banded hare-wallaby dispersal will be stopped entirely if the fence remains intact). This barrier to dispersal may be removed as the fence integrity diminishes with time, however a scenario that included removal of the fence was not modelled.

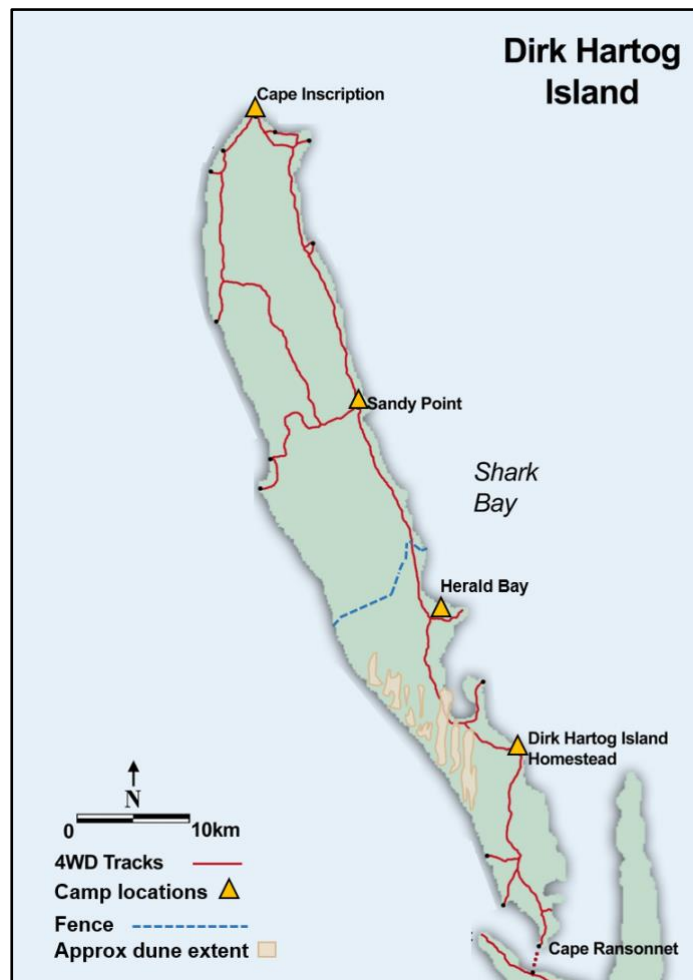


Figure 4.2: Map of Dirk Hartog Island. The approximate locations of the fence barrier and dune system are indicated, as well as some camp locations. Most species will be (or have been) released near the Dirk Hartog Island Homestead or in the vicinity of Herald Bay.

4.2.6 The simulation process

Following the filtering of unviable models, the simulations were run to determine total species richness for each Translocation Alternative for each sign-structured matrix, and to produce envelopes of potential timeseries for each matrix and Translocation Alternative. This allowed the production of 90 time series with the average abundance through time for each species, and envelopes of trajectories within the 99% and 80% confidence intervals (see Figure A1.1). I also calculated the probability for failure for each species for each Translocation Alternative and sign structured matrix. Additionally, I evaluated the strength of important positive and antagonistic interactions for each species when a translocation failure occurred. These analyses allowed me to predict which Translocation Alternatives are the best options, determine which species benefit the most from each option and which species are most vulnerable, and identify what interactions in particular contribute to the vulnerability of a species. The threshold for translocation failure for a species in my model is defined as a decline in abundance of 50% or greater of translocated individuals. The target number of translocated

individuals for each species is approximately 100 individuals, with roughly 50 brought to the island in the first translocation and 50 in the second translocation. The second translocation is either the following season or year, as per the Translocation Alternatives. Dibblers, however, are an exception with 23 individuals brought to DHI in the first year and 23 to 27 individuals to be translocated in subsequent years. The exact number of translocated individuals depends on the abundances and genetic diversity of source populations, but for the purposes of the model, I used 100 for each species. Translocation of 100 individuals is estimated to be approximately 1% of the carrying capacity for most species on DHI, based on scaled up estimates from Bernier and Dorre Islands. For chuditch, however, this represents 15% carrying capacity.

4.3 Results

The Translocation Alternatives performed very similarly when averaged across the sign-structured matrices proposed by the experts (see Figure 4.3). The model ensemble consistently suggests that almost all the species are likely to be successfully translocated to DHI. In 50% of models in the ensemble, one species translocation will fail as a result of species interactions and stochastic population fluctuations. Multiple local extinctions are possible but unlikely. Translocation Alternatives 6 (boodies are not translocated) and 7 (mulgara are not translocated) result in the lowest number of persisting species with approximately one to two failed translocations (see Figure 4.3 and Figures A2.2-A2.8 in Appendix 2). However, the worst of these two alternatives depends on the sign structured matrix. For example, in Figure A2.3, which are the outcomes based on Expert 1's matrix to represent realistic interactions between species, Translocation Alternative 7 is the worst with an average of approximately 1.5 failed species establishments. Conversely, Translocation Alternative 6 is slightly worse than Translocation 7 among the outcomes from Expert 1's third matrix, which represents eco-engineer dynamics within the ecosystem (Figure A2.5). All other Translocation Alternatives result in a nearly full assemblage of persisting species, with an average failed translocation of 0.5, which represents the failed translocation of one species possible approximately half of the time. There are long "tails" on the Translocation Alternatives, which represent the very small but not impossible chance that multiple species could fail to successfully establish. For example, when all interaction matrices are considered, though unlikely, up to seven species can fail to establish for all Translocation Alternatives. The exception is Translocation Alternative 7, where up to 8 species can fail to establish. (Figure 4.3).

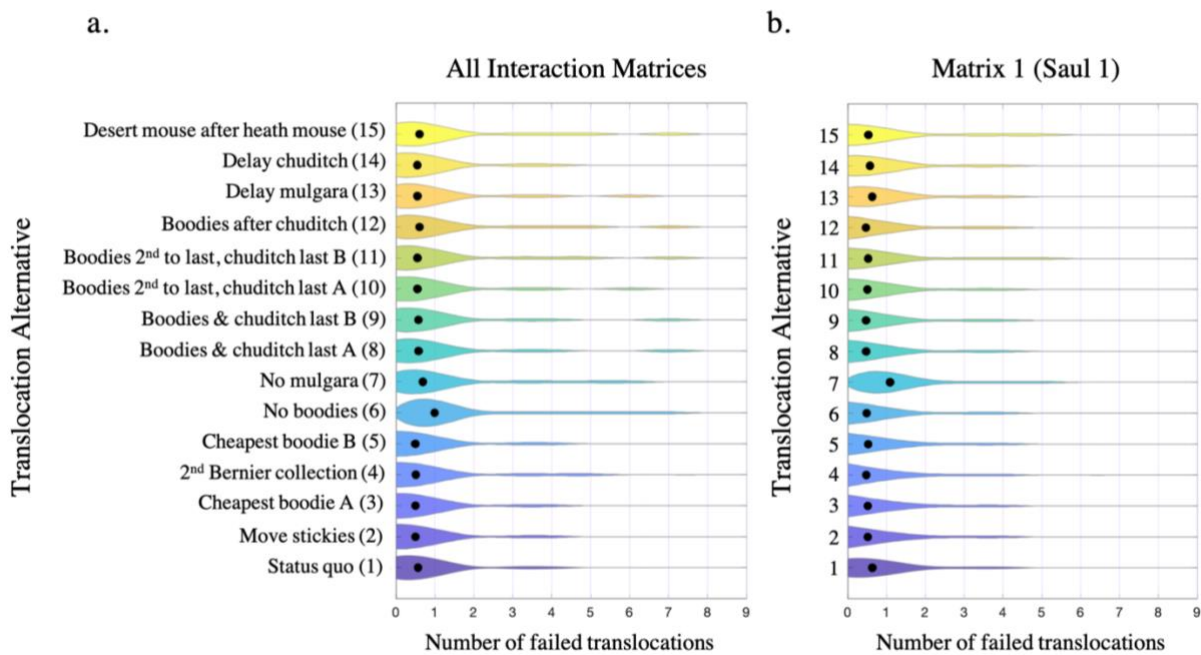


Figure 4.3: *The number of local extinctions for each Translocation Alternative averaged across all models (a), and the result from only Matrix 1 (b). When averaging across the outcomes of all sign structured matrices, the results of the Translocation Alternatives are approximately equal, with Translocation Alternative 6 being slightly worse among all of the options. However, when only considering one sign structured matrix, the results are slightly different. The results from only using Matrix 1 show that Translocation Alternative 7 is the worst option (b).*

The outcomes of the modelling process also reveal significant variability due to the sign structured matrices. The sign structured matrices predict that different species will be vulnerable and will respond differently to the Translocation Alternatives (see Figures 4.4 and 4.5). Most species had slightly heterogeneous responses to different Translocation Alternatives within the result for a particular sign structured matrix, as seen in Figure 4.4. For example, most species in the first sign structured matrix made by Expert 1 respond differently to the Translocation Alternatives. The heath mouse responds positively to Translocation Alternative 6 but has moderate to poor responses for the other alternatives. Most notably, however, is that different species are predicted to be consistently vulnerable to translocation in general. For example, in the first matrix by Expert 1, the western grasswren responds poorly to every Translocation Alternative. It is also vulnerable in the second and third matrices by Expert 1, but the second sign structured matrix by Expert 1 also predicts that the heath mouse and greater stick-nest rat will do poorly while the third sign structured matrix by Expert 1 identifies dibblers and the Shark Bay bandicoot as other consistently vulnerable species. Mulgara are vulnerable species in both sign structured matrices by Expert 2, but the first predicts the desert mouse will respond poorly to the translocations while the heath mouse and Shark Bay mouse are the other

vulnerable species in the second matrix by Expert 2. The species that are vulnerable as predicted by Expert 3's sign structured matrix are the dibbler and heath mouse. The only species with a fairly consistent response across sign structured matrices is the chuditch; it fares well in nearly all instances. The chuditch averages a value of -5.5, which is the log likelihood of extinction, for every Translocation Alternative except those generated from Expert 2's first matrix, where it still fared well, with values no less than approximately -3.75. The second most robust species is the woylie, which responds well to most Translocation Alternatives no matter the matrix. In general, the western grasswren is the most vulnerable species, but this is biased towards the sign structured matrices generated by Expert 1. Dibblers are also highly vulnerable to most Translocation Alternatives. The desert mouse had the most variability in responses to Translocation Alternatives, no matter the matrix used.

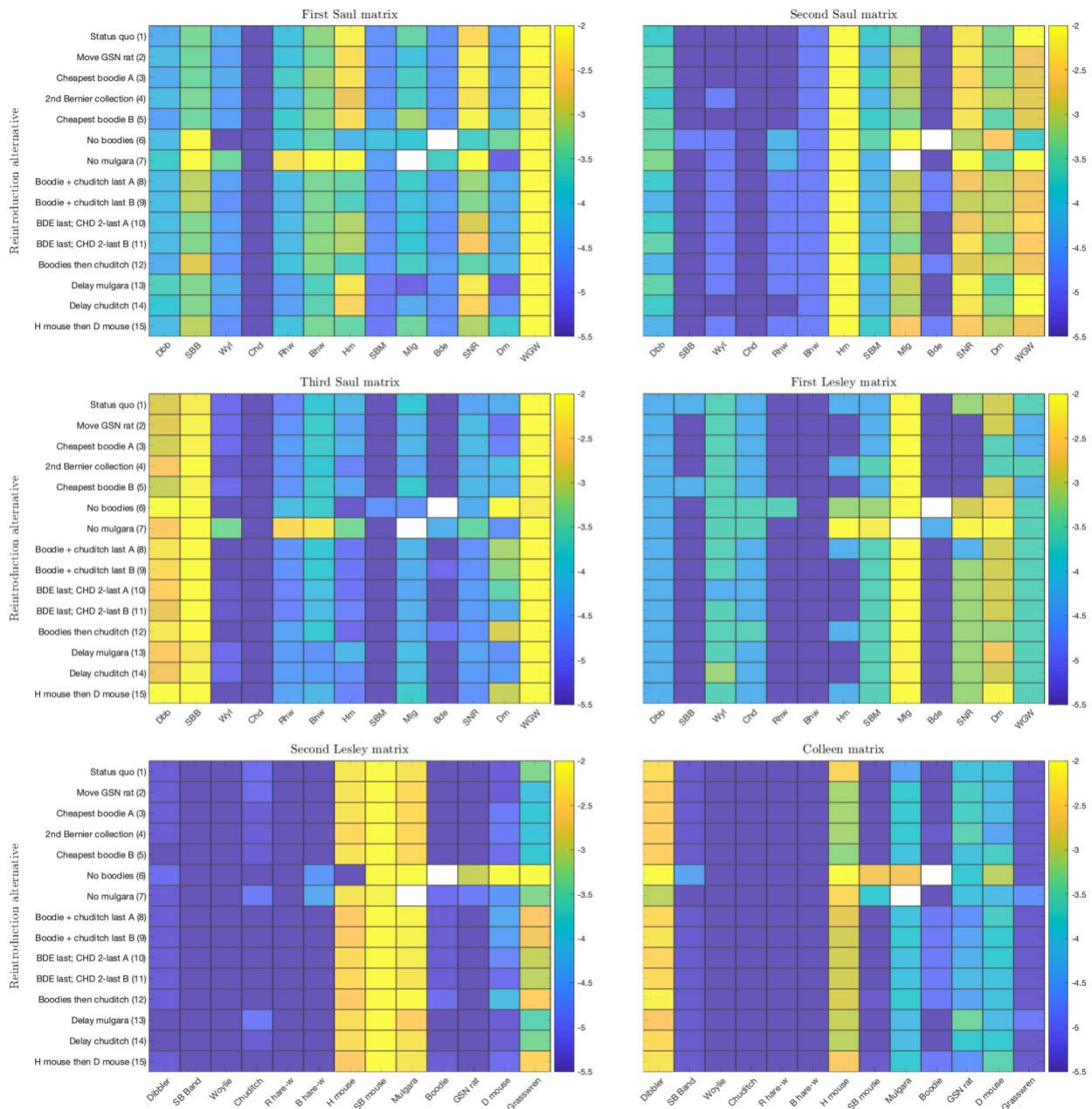


Figure 4.4: Species outcomes for each sign structured matrix. How individual species fare in each Translocation Alternative varies significantly between sign structured matrices. The colours represent the log likelihood of extinction, where warmer colours equate to higher extinction risk. For example, in the first matrix (First matrix by Expert 1), chuditch fares the best for all Translocation Alternatives, while the western grasswren is the worst off in all cases. Conversely, in the sixth matrix (Expert 3's matrix), the western grasswren responds well to all Translocation Alternatives. However, dibblers and the heath mouse do not do well in any Translocation Alternatives in this matrix, with some variability.

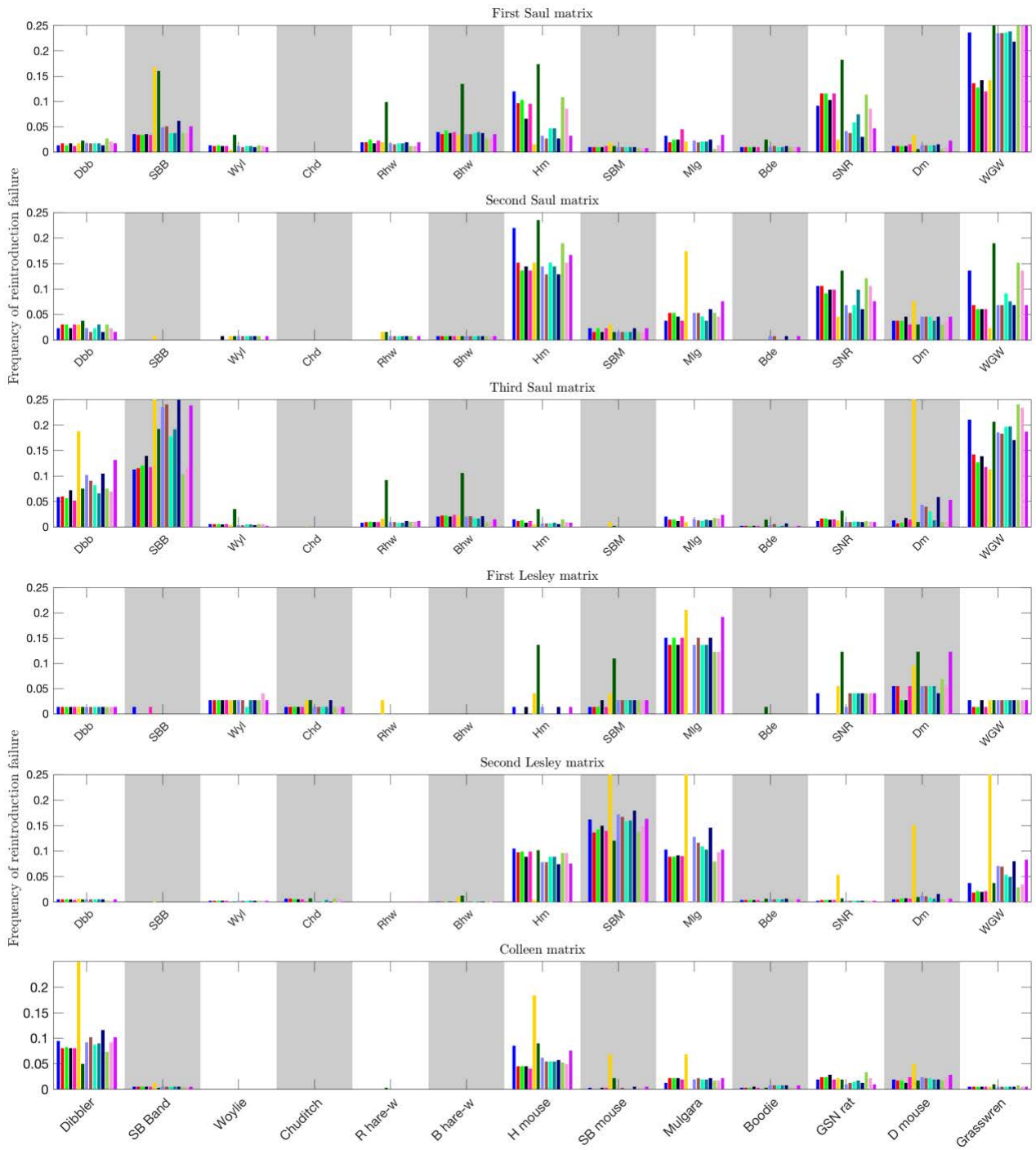


Figure 4.5: Species' responses to Translocation Alternatives. There is significantly variability in how each species responds to Translocation Alternatives, based on the underlying sign structured matrix. The coloured bars represent different Translocation Alternatives, (ascending from left to right). Species are listed along the x-axis and the frequency with which translocations fail is shown on the y-axis.

The two matrices that assume that the ecosystem-engineer function of boodies have slightly different results. Translocation Alternative 6 does not involve the translocation of any boodies, so it follows that if species benefit from boodies, those species will be worse off for this Translocation Alternative. In Expert 2's eco-engineer matrix, the greater stick-nest rate and desert mouse are significantly worse off when boodies are not translocated compared to all other alternatives. The western grasswren is similarly worst off in that Translocation Alternative, but the difference from other Translocation Alternatives is less pronounced. The heath mouse is the only species that benefits from the lack of boodies. Similarly, in the boodies as ecosystem engineers by Expert 1, Expert 1's third matrix, the heath mouse benefits from the lack of boodies as indicated by a better response to Translocation Alternative 6 than other Translocation Alternatives. The desert mouse, however, is the only species that fares poorly due to the lack of boodies in Translocation Alternative 6.

Species extinctions are caused by negative interactions (competition, predation) outweighing positive interactions that contribute to population growth (consumption of vegetation or prey). The dynamics that contribute to translocation failure for particular species appears to be primarily due to predation from species extant on DHI. Eight species of the 13 were subject to stronger interactions with varanids in instances of translocation failure, although varanids may be a greater source of competition than predatory pressure on brush tail mulgara. Native predators such as hawks also impacted species; six translocated species had increased negative interactions with native predators in instances translocation failure. Negative interactions with other translocated species were minor, which some Translocation Alternatives were designed to accomplish. Most of the Translocation Alternatives explicitly translocate predatory or strongly competitive species such as chuditch and boodies to allow vulnerable species to establish. However, boodies impacted other translocated species more than chuditch. Three species had stronger interactions with boodies when their translocations failed, but the chuditch only affected the rufous hare wallaby. Similarly, stronger negative interactions with the mulgara only affected the Shark Bay mouse.

The magnitude of interactions that are linked to occurrences of translocation failure vary widely among species, indicating some species may be more vulnerable than others. For most species, translocation failure occurred when there were particularly strong interactions from predators extant on DHI, such as varanids or other native predators like predatory birds. For example, translocation failure of dibblers is associated with a negative interaction with varanids that was on average 285% stronger than non-failure cases. Failures of brush tail mulgara, however, are due to increased negative interactions with varanids, by 110%, but also weaker interactions with prey such as small vertebrates (45% weaker), desert mouse (70%), and the Shark Bay mouse (35%). Chuditch failures had no pattern

in stronger or weaker interactions. A visual representation of the failure analysis results for the western grasswren is shown in Figure 4.6, and the results for the other species are in Appendix 2.

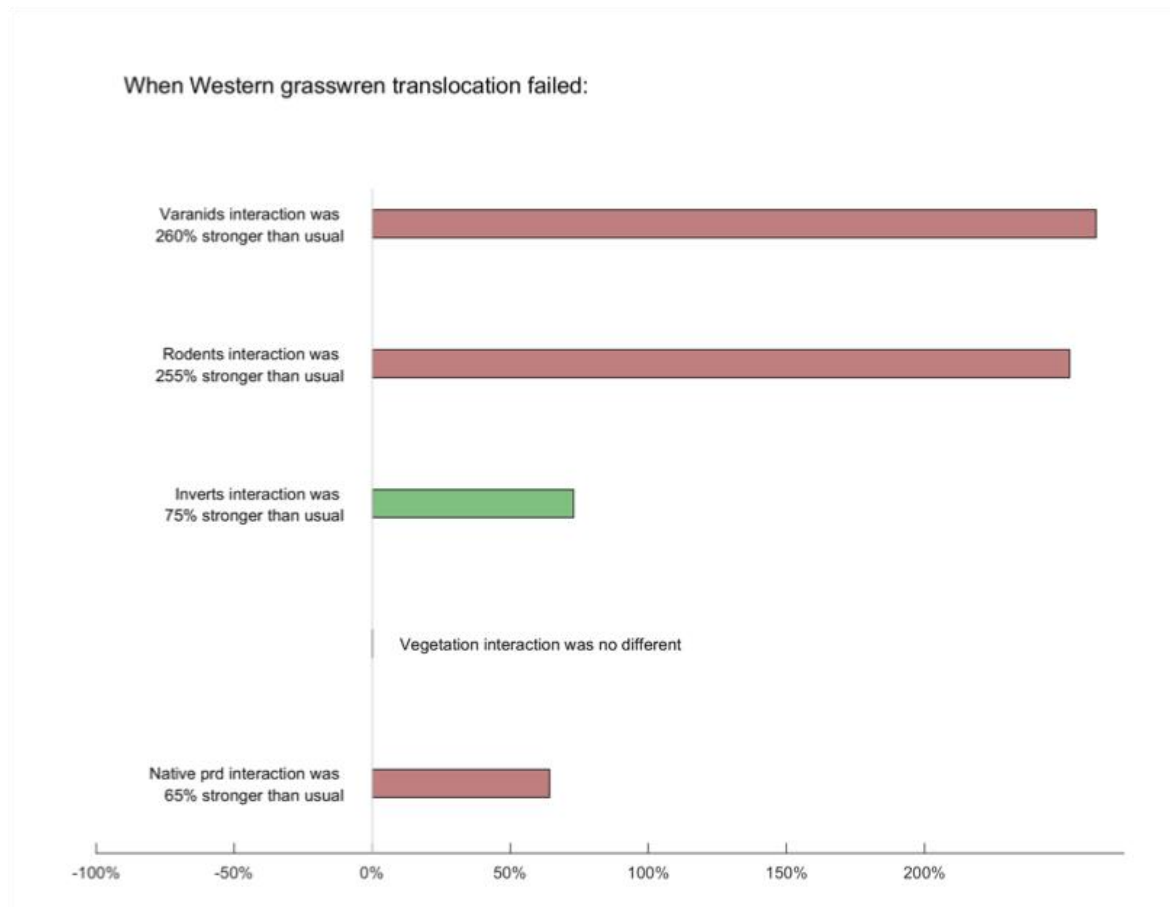


Figure 4.6: *The western grasswren translocation failures are associated with stronger antagonistic interactions. Despite having an increased interaction with a food source, strongly negative interactions from varanids, rodents, and native predators affected the success of the western grasswren in some simulations. Rodents are a source of competition with western grasswren, and it is vulnerable to predation by varanids and native predators such as hawks.*

4.4 Discussion

Modelling faunal reconstruction of a large scale, complex system is unprecedented. Using ensemble modelling allowed for many simulations of a multi-species interacting community. This method enables a quantitative analysis that would otherwise be intractable. Simultaneously evaluating 19 interacting equations is complicated, and then evaluating those over 90 scenarios representing different ecological dynamics and conservation actions, is simply not feasible with conventional modelling techniques.

There are limitations to the conclusions drawn from this analysis. The assumption that all species can coexist at equilibrium has a strong influence on the results. While this assumption is supported by

observations of similar species or subsets of species coexisting, coexistence in one context does not necessarily guarantee coexistence in other contexts (Chamberlain et al., 2014; Cazelles et al., 2016). Additionally, the DHI project evaluation timeline is too short to observe all potential population dynamics (Courchamp et al). Species with high annual population growth rates such as the northern quoll do not reach a regulation phase in population dynamics within five years; it is longer for much slower growing animals (Griffiths et al., 2017). Additionally, this timeline does allow for the consideration of long term dynamics and slow competitive exclusion. Furthermore, it does not consider long term changes in vegetation abundance or habitat quality (Armstrong & Seddon, 2008).

Choosing the Translocation Alternative strictly on the number of species that persist indicates that the Status Quo (Translocation Alternative 1), which is most logistically feasible option, is sufficient. However, if particular species are prioritised, then the Translocation Alternative and the sign structured matrix must both be taken into account. For example, Translocation Alternatives 2, 3, 4, and 5 should be the first choices if greater stick-nest rats are the prioritised species, and the ecological dynamics are assumed to follow those outlined by Expert 2's first matrix. If Expert 3's matrix is assumed to reflect the true interactions within the ecosystem and the Shark Bay mouse is prioritised, then any Translocation Alternative but alternatives 6 and 7 are acceptable. However, decisions made regarding the particular Translocation Alternative that is implemented is highly sensitive to the kind of sign structured matrix that is assumed to represent the system.

Translocation failure cannot be directly attributed to specific interactions in the model ensembles. I was, however, able to identify which interactions and their relative magnitudes were associated with translocation failures. These are aggregated across Translocation Alternatives and sign structured matrices. The analysis nevertheless allows one to identify potentially problematic interactions, which is important for refining Translocation Alternatives and adaptive management. Subsequent work with the biologists at DBCA will involve separating these dynamics by interaction matrix and Translocation Alternative to determine finer resolution of impacts and better attribute causes of translocation failure. Annual monitoring of the populations on DHI will contribute to updated model constraints and improved interaction matrices, which will allow for additional simulations of the model ensembles. Updated model ensembles could potentially change which Translocation Alternative is considered optimal, thereby informing passive adaptive management.

Uncertainty regarding the ecological dynamics of the system is underscored in the variability in results between the sign structured matrices. Determining the actual magnitude and nature of interactions between species in complex systems is notoriously difficult (Novak et al., 2011; Aufderheide et al., 2013). Many species had consistent responses to Translocation Alternatives given a particular sign structured matrix but differed in their vulnerability or robustness depending on the

ecological dynamics that were assumed. For example, the Shark Bay mouse is extremely vulnerable to any translocation action in Expert 2's second sign structured matrix but is generally robust to translocation if other sign structured matrices are assumed. Therefore, without knowing the true dynamics of the system, managers cannot anticipate which species may need additional support to ensure their persistence.

CHAPTER 5: General discussion

5.1 Thesis summary

In this final chapter, I synthesise the main findings of my data chapters, and discuss how these findings contribute new knowledge to the way interactions affect ecological communities. I also review how these findings relate to how one draws conclusions from ecological models in a broader context, and the inextricable role of uncertainty. I then discuss the implications this has for managing and conserving natural systems. Finally, I comment on the limitations of my work, and identify areas of future research in using theoretical quantitative ecology in applied environmental science.

In Chapter 2, I examined how two types of coexistence mechanisms affect aggregate community properties. The functional form is the same in the niche-based community model and the storage effect-based community model. However, the underlying dynamics differ as the storage effect-based model relies on species responding to stochasticity differently to confer coexistence. While the species in the niche-based community model are affected by stochasticity, they coexist in spite of it, rather than because of it. The coexistence in the niche-based community is instead due to incomplete competition between species. Though niche-based communities are well studied, and storage effect-based communities are increasingly evaluated, this chapter is novel in that it directly compares these two mechanisms. By using the same functional form, I was able to directly compare the effects of a fluctuation-independent and a fluctuation-dependent mechanism. This allowed me to draw conclusions as to how fluctuation independent mechanisms may affect aggregate community properties differently. Indeed, there is a distinct difference in the effect of these two classes of mechanisms on some properties. Additionally, the statistical indices used in this study to evaluate the simulated timeseries data are based on the framework established by Thibaut and Connolly (2017), and included the community coefficient of variation, which is this study's proxy for ecological stability, synchrony, an evenness index, and overyielding. The community models resulted in different values for synchrony, the evenness index, and overyielding, and this was generally robust to the magnitude of the coexistence mechanism and community size. Therefore, fluctuation-mediated and fluctuation-independent produce recognisable signatures on the statistical indices. However, there was no discernible difference in the community coefficient of variation between the two community models. Though this is not ideal if using the community coefficient of variation as a diagnostic to identify the underlying dynamics of timeseries data, it is important for ecological functioning. This finding demonstrates that there is not a type of coexistence mechanism that is necessarily better at ensuring ecological stability. Therefore, as long as coexistence mechanisms are in place to a sufficient degree in a community, then the community can be stable.

Chapter 3 focuses on the effects of assisted migration on recipient communities. Overall species richness is slightly lower when a hypothetical decision-maker proceeds with assisted migration than if they had chosen not to. This was examined in two scenarios, but the results are similar. The favourable scenario represents one in which the candidate species would stand to benefit from assisted migration, as it has a 50% chance of extinction in its native habitat and would not be damaged by the removal of individuals for translocation. In the unfavourable scenario, the species has a 90% chance of persisting in its native habitat but is negatively affected by removal of individuals for translocation. I considered modelling a “high risk” scenario, where the candidate species is highly endangered (50% chance of extinction), but removal of individuals would also damage the original population. This is more realistic for very rare, endemic species. However, in this scenario total species richness would likely be even lower as it would effectively preclude the possibility for the candidate species to survive in its native habitat if assisted migration was chosen.

Interestingly, the supplementary results for Chapter 3 in Appendix 1 indicate that the density of the interaction network has some impact on overall species richness. Overall species richness following assisted migration is lower among communities with higher density of interactions, implying that the translocated species is more disruptive to the recipient community the more tightly linked species are. For example, species richness is 14.8 (favourable) and 14.5 (unfavourable) in low-density interaction matrices, where there are about 25% interactions out of the community that are not zero. The moderate and high density have the same expected richness with 14.2 species for favourable scenarios and 13.9 for unfavourable scenarios. In the main text, we used a random uniform distribution to determine the density of interactions, so the interaction network ranges from dense to sparse. Therefore, if practitioners have some idea of the level of density of the interactions, they would be able to better predict the impact of translocation to the recipient community.

Additional scenarios of Assisted Migration to reflect more realistic environmental conditions are also presented in Appendix 1. The first scenario represents a community that is not in equilibrium as it is subject to a press perturbation, such as climate change. Here, the disruption of the recipient community from translocation exacerbates the background species loss from the perturbation. The other scenario represents a refaunation project, where a species from the recipient community had been eradicated and a new species is translocated before the recipient community reaches equilibrium. In this scenario, Assisted Migration improves overall species richness in dire circumstances, such as when the target species is highly endangered. These scenarios provide important context for when Assisted Migration may cause more damage or be beneficial.

In Chapter 4, the outcomes of each Translocation Alternative are approximately similar: roughly one species fails to persist following translocation, half of the time. Translocation Alternatives 6 and 7 are

the exception, though the outcomes from these alternatives are not significantly worse: one species fails to persist on average. The similarity in species richness outcomes is likely because the Translocation Alternatives are not extremely different. The differences between some alternatives are simply the postponement of a translocation of one species by a year or two, or moving one species to a different location. The two Translocation Alternatives that did have a relatively higher impact on richness were those that did not involve translocating a species, either the boodie or chuditch. This is not an artefact of leaving a species out of the translocation process, because species richness was calculated out of 12 species rather than 13 for these alternatives. This result indicates that the presence of boodies or chuditch have the potential to facilitate the persistence of other species. Positive impacts of boodies as ecosystem engineers were explicitly accounted for in two sign structured matrices, but chuditch were not. Chuditch may have had an indirect positive impact on some species through the consumption of other species' natural predators.

Despite the fairly consistent results among Translocation Alternatives, the species that were vulnerable to failed translocation varied significantly, depending on the sign structured matrix that was used. In general, the species that were particularly vulnerable were the western grasswren and many of the rodent species. Stronger antagonistic interactions, particularly from varanids and natural predators, were generally the case for failed translocations. Varanids and natural predators were not originally included in the sign-structured matrices, but in a workshop with the biologists at DBCA, we concluded that it was important to include these in the model. Not including these would have resulted in more optimistic results for the biologists at DBCA, but clearly these interactions have a significant impact on the outcomes.

5.2 Implications

The overarching objective of conservation is to preserve species. However, ecological communities are fundamentally complex, and by proxy, uncertain. Coexistence is important for conservation as it provides a mechanistic framework for examining how interactions between species affect their persistence. Modern coexistence theory accurately describes many of the underlying processes that govern communities, but as a quantitative approach, it is not always useful. By employing statistical decomposition of community properties, and using ensemble models to incorporating heavy uncertainty, I am able to gain useful insights about community dynamics.

This research shows that overall richness can be greatly affected by some conservation interventions (Chapter 3), and not necessarily others (Chapter 4). In both cases, if a particular species is considered more important, we must proceed carefully. In Chapter 3, the identities of the species that become extinct following assisted migration, is irrelevant because the model was not parameterised to

represent any particular community. However, this can have significant ramifications in real communities. The loss of one species in 12% of cases may be a non-issue if the lost species is functionally redundant or has little impact on the environment and other species. If the lost species is a keystone species, however, this could catalyse a shift of the entire community to a qualitatively different state (Simberloff, 2003). Furthermore, the results imply that in the rare cases that five or more species are lost, assisted migration can have catastrophic consequences by causing the local extinction of at least a third of the species within the community. A loss of species of this magnitude would undoubtedly eliminate ecosystem functions, which further threatens the persistence of other species. However, climate change jeopardizes the persistence of species in nearly every community (Burkett et al., 2005; Vasseur et al., 2014). It is well established that increased temperature affects the survivability of species, but changes in ranges and increased environmental variability further strain species by causing the decoupling of species or changing the magnitude of interactions between them (Vasseur et al., 2014). However, the fragility of ecosystems as conditions worsen will have to be taken into consideration, as practitioners are forced to consider “conservation actions of last resort”. These actions include risky and challenging interventions, such as assisted migration and multi-species translocations.

5.3 Limitations and future directions

A limitation of the studies in this thesis is the use of models at equilibrium (Chapters 3 and 4) or approximate stationarity (Chapter 2). Ecological communities are often dynamic and equilibrium is not realistic for many systems (DeAngelis & Waterhouse, 1987). Moreover, May (2001) demonstrated mathematically that complex ecosystems are inherently unstable. Anthropogenic impacts such as climate change, pollution, and habitat degradation further push ecological systems away from their natural equilibria. Conservationists would only consider introducing species to relatively intact communities in exceptional circumstances. Also, assisted migration is often proposed as a way to provide future refugia for species facing climate change. Therefore, the proposed recipient ecosystem is usually projected to change and become more suitable for the translocated species. Consequently, modeling equilibrial systems has the potential to result in unanticipated outcomes if this is not taken into account during decision-making.

Ecological models are increasingly including more complex types of interactions and dynamics (Burkett et al., 2005). This includes nonlinear interactions (Tredennick et al., 2017), explicitly incorporating variability in interaction strength (Novak et al., 2011), including nonadditivity (Clark & Neuhauser, 2018), and moving beyond pair-wise mechanisms (Levine et al., 2017). Different kinds of interactions are occurring simultaneously in natural communities, particularly as species richness increases. Nonlinear dynamics are exceptionally important to include in ecological models, as it has

been demonstrated responses to change in natural ecological systems are predominantly nonlinear, rather than gradual and linear (Bazykin, 199; Burkett et al., 2005; Blasius et al., 2007). Nonlinear systems can be defined as systems where the interactions between components are not directly proportional (Burkett et al., 2005). Organisms often exhibit threshold-type responses to changes in physical and chemical properties in an environment, as well as in interactions with other species (Burkett et al., 2005). Finally, though Lotka-Volterra models are useful due to their generality, they are also not the best fit with most empirical data. This is in part due to its structural form: Lotka–Volterra models simplify systems into a series of linear interactions. This linearisation causes analyses that use Lotka-Volterra models to be subject to extra uncertainty (Clark & Neuhauser, 2018).

Finally, the models in this thesis are limited to the community scale. Ecological problems, like climate change and habitat loss, can impact species at multiple scales. Also, some dynamics exceed the community scale. Dispersal is an important process in ensuring the local and regional persistence of many species. Therefore, to ensure models are useful, they must be at the correct spatial resolution (Schuwirth et al., 2019). Metacommunity ecology, which is the study of linked and interacting communities, has advanced significantly as an important area of theoretical ecology in recent decades (Leibold & Chase, 2017). Despite a general consensus regarding the ecological importance of metacommunity ecology, there remains considerable scope to incorporate metacommunity concepts into applied ecology and conservation (Leibold & Chase, 2017). Models that incorporate dispersal and movement of populations as well as environmental process have considerable implications for conservation and management strategies, particularly as anthropogenic impacts on natural systems continue to escalate.

Despite the potential limitations of ecological models, they are critical in helping to develop ecological theory and improve decision-making ability (Getz et al., 2018). The most significant way models support the decision-making process is through enabling practitioners to evaluate the consequences of alternative management decisions (Schmolke et al., 2010). This is particularly crucial when the temporal or spatial scale of a problem is large (Schmolke et al., 2010). Finally, the complexity of ecological systems further necessitates the use of models to distil a conservation problem to its more essential components and processes (Pielke, 2003). Due to this, however, ecological practitioners and managers are certainly underestimating uncertainty to some degree. Elaborate models that more accurately represent natural systems have the potential to reduce structural uncertainty (Jackson et al., 2000). This often comes with the cost of adding more parameters, which increases uncertainty or requires higher resolution and better-quality data (Hermoso et al., 2013). Furthermore, increasing the complexity of models also introduces the possibility of using the incorrect functional form to relate components within models.

There is a sweet spot of parsimony and representativeness that practitioners and modelers should strive for when developing models for applied conservation problems (Jackson et al., 2000; Pielke, 2003). This, in particular was an issue during the development of the model for Chapter 4. When one is invested in an ecological system, often one feels compelled to include every relevant dynamic. Therefore, model development must be an iterative process and modelers must be assertive and transparent about the potential of increased complexity to make a model unwieldy and impractical (Gordon et al., 2013; Kark et al., 2015). Once a sufficiently realistic but tractable model structure is agreed upon, then parameter uncertainty should be tackled. Ensemble modeling, though, is an excellent method for evaluating multiple management options while also allowing for uncertainty in parameter values (Jones-Farrand et al., 2011). Ensemble modeling is computationally intensive, however, which limits its applicability. Whichever method practitioners and modelers use to tackle conservation problems, it is necessary to explicitly include uncertainty (Langford et al., 2009). Practitioners do not have the luxury of limitless time or resources to reduce uncertainty (Getz et al., 2018; Schuwirth et al., 2019). To successfully conserve species and biodiversity, ecologists therefore must address uncertainty head on.

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Appendix 1. Supplementary information for “Using ensemble modelling to predict the impacts of assisted migration on recipient ecosystems.”

A1.1 Supplementary methods

We constructed a large ensemble of Lotka-Volterra ecosystems, each comprising 15 coexisting and interacting species (Fig. 1, main text):

$$\frac{dn_i}{dt} = r_i n_i + \sum_{j=1}^S x_{i,j} n_i n_j$$

Equation A1.1

These were the recipient ecosystems that received the translocated species. A 15-species ecosystem was large enough to offer substantial and complex interactions networks, but not so large that creating a large model ensemble was computationally infeasible. Candidate ecosystems were created using randomly-generated growth rates, $r \sim U[0,1]$, and interaction matrices, α , whose elements $x_{i,j}$ measure the per-capita interaction strength of species j on individuals of species i . These are sampled from a mixed distribution $x_{i,j} \sim \text{Bernoulli}(D) \times U[0,1]$, with randomly allocated signs. That is, we first used a Bernoulli random variable to decide whether a particular interaction occurred in a particular direction (i.e., whether $x_{i,j}$ was nonzero), then used another Bernoulli random variable to decide whether that interaction was positive or negative, and then finally used a uniform random variable to determine the magnitude of the interaction strength (note that the signs and values of $x_{i,j}$ and $x_{j,i}$ are generated independently). Both the r_i and $x_{i,j}$ values were therefore bounded, but this did not limit the ecosystems that were created, since any Lotka-Volterra model can be rescaled so that all parameters fall between 0 and 1 (Baker et al., 2017).

The density of interactions within the ecosystem was controlled using the Bernoulli parameter D , which determined the proportion of possible species interactions that were nonzero. Ecosystems constructed using small values of D had fewer interactions, while large- D ecosystems exhibited dense webs of interactions. For each simulation, D was a random number chosen from a uniform distribution $D \sim U[0,1]$. In addition to letting D vary, we modelled scenarios with three separate and specific D values, to determine if our results were sensitive to this parameter. The low-density network allowed for $D = 0.25$ of the interactions to be non-zero. The medium-density network had non-zero values for $D = 0.5$ of the interactions, and the high density interaction network had $D = 0.75$.

The resulting ecosystems were then tested for the existence of stable equilibria. Fewer than one in every million random parameter sets created an ecosystem that was able to coexist with all 15 species present;

the others were discarded. Once 100 equilibrial recipient ecosystems with coexistence were found, we simulated assisted migration (AM). A single randomly-generated species, our translocated species, was added to each ecosystem, and the response of the ecosystem was monitored. We then repeated this process with 100 different new species in turn, for a total of 10,000 simulated assisted migrations. For each combination simulation, we recorded whether the assisted migrations was successful, and also recorded the response of the recipient ecosystem.

Assisted migration scenario parameterisation

The outcomes of assisted migration will be sensitive to the circumstances of the translocated species, and to our measure of impact on the recipient ecosystem. We modelled two main scenarios – one with conditions that were favourable for AM, the other with unfavourable conditions.

The favourable scenario is biased towards choosing assisted migration: (i) the translocated species faces a high risk of extinction, (ii) the removal of assisted migration individuals is less likely to impact the source population, and (iii) we only consider a species to be impacted in the recipient ecosystem if that species is driven to extinction. The high risk of extinction is given by the probability of extinction of 50% in three generations, as per IUCN criteria for Critically Endangered species (Mace et al., 2008). The exact extinction criteria is when a species' population is less than 0.1% of pre-introduction abundances.

In the unfavourable scenario, the parameters were biased against choosing assisted migration: (i) the species was at less risk in its source population, but (ii) the removal of assisted migration individuals was more likely to have negative viability consequences for the source population, doubling the risk of extinction. Finally, (iii) we considered species in the recipient ecosystem to be impacted if their population declined by 30% or more. That is, species in the recipient ecosystem could be impacted even if they did not get driven to extinction. The Vulnerable category from IUCN Criterion E was used to inform the extinction probabilities for this scenario, which assumes 10% chance of going extinct within 100 years (Mace et al., 2008)

Modelling non-equilibrium communities subject to press perturbations

An impact on communities from climate change or any sort of “press” perturbation are achieved in the models through an incremental annual change of 1% in the values for growth rate, r_i , and the elements $\alpha_{i,j}$ of the interaction matrices, α . The direction of this change can increase or decrease the A and r value for each species. The direction is randomly chosen for each species in each model community, but it remains in the same direction throughout time.

Modelling non-equilibrium communities subject to rapid assembly change from eradications

To model the removal of a species from the recipient ecosystem prior to assisted migration, a random species was removed from the community when that community had reached equilibrium. The translocation then occurs 10 years following the removal of the species, before the recipient community is able to re-equilibrate. The highest possible total richness is 15 species, instead of 16 due to the prior removal of a species within the recipient community.

Both non-equilibrium ensembles are further analysed using scenarios of different levels of threatened status for the target species for translocation and different thresholds of acceptable impact to species within the recipient community, producing 12 scenarios for each non-equilibrium ensemble. We evaluate the outcomes when the target species' source population is at an abundance that qualifies it as Vulnerable, Endangered, and Critically Endangered according to IUCN guidelines (Mace et al., 2008). For each of these scenarios, the impact to the recipient community is considered at different thresholds. The most conservative threshold counts a loss of species when the abundance declines to an extent to qualify that species as Vulnerable. The least conservative threshold for qualifying a species as lost is when a species' abundance declines to zero and it is extinct. The other thresholds of loss are declines in abundances to qualify species as Endangered and Critically Endangered.

Measuring the ensemble outcomes

The three repercussions of assisted migration we were most concerned with were: (1) extinction of the translocated species in its source population, (2) failure of the assisted migration, and (3) negative impacts on species in the recipient ecosystem. We constructed a decision tree to visually and mathematically represent all possible combinations of these three potential repercussions, under both decisions. That is, if the assisted migration goes forward, or if the managers choose to take no action. The combinations are shown in Figure 2 in the main text, and are described mathematically in Equations A1.1, A1.2, and A1.3.

There are two possible choices managers can make, indicated by the first branching of the decision tree: to translocate a translocated species or not (Figure A1.1).

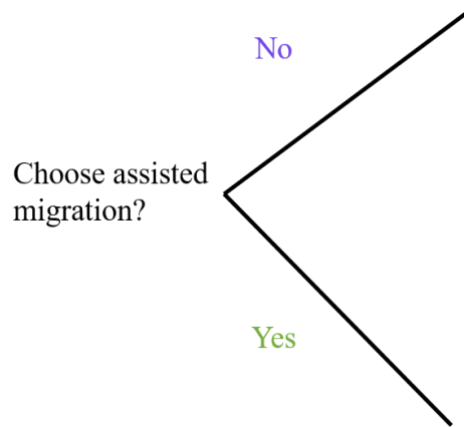


Figure A1.1: The beginning of the decision tree. The subsequent outcomes depend on managers choosing to undertake assisted migration

By choosing to not move the candidate species, the manager risks the species going extinct, with probability p given by its IUCN designation. With probability $1 - p$, the species does not.

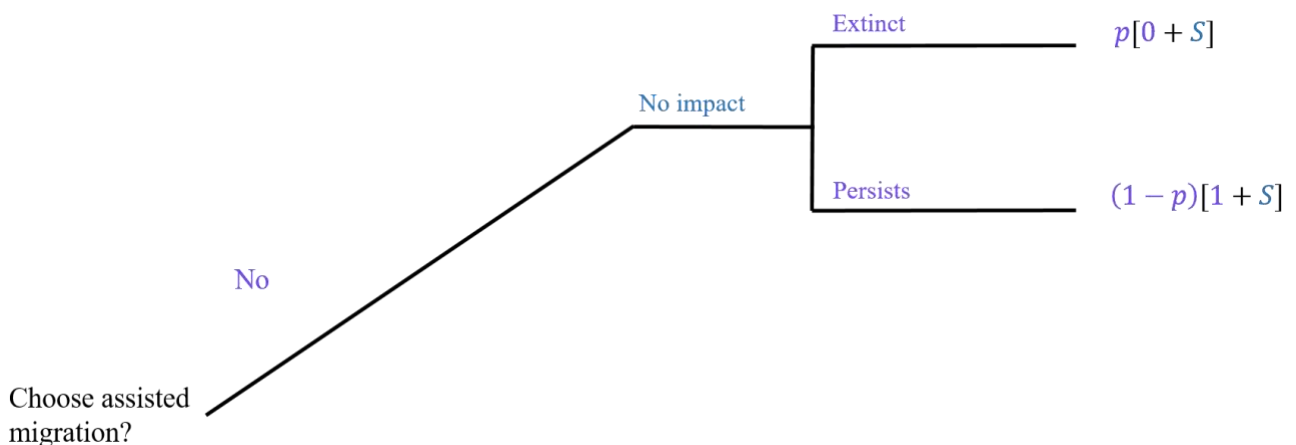


Figure A1.2: No assisted migration. If assisted migration is not undertaken, there is no impact on the recipient ecosystem (in blue), but the species that was the candidate for assisted migration may either go extinct or persist in its native habitat.

If assisted migration is chosen, this branch is further divided by the failure or success of assisted migration. The probability that the translocated species succeeds in becoming established in the recipient ecosystem is given by the probability q .

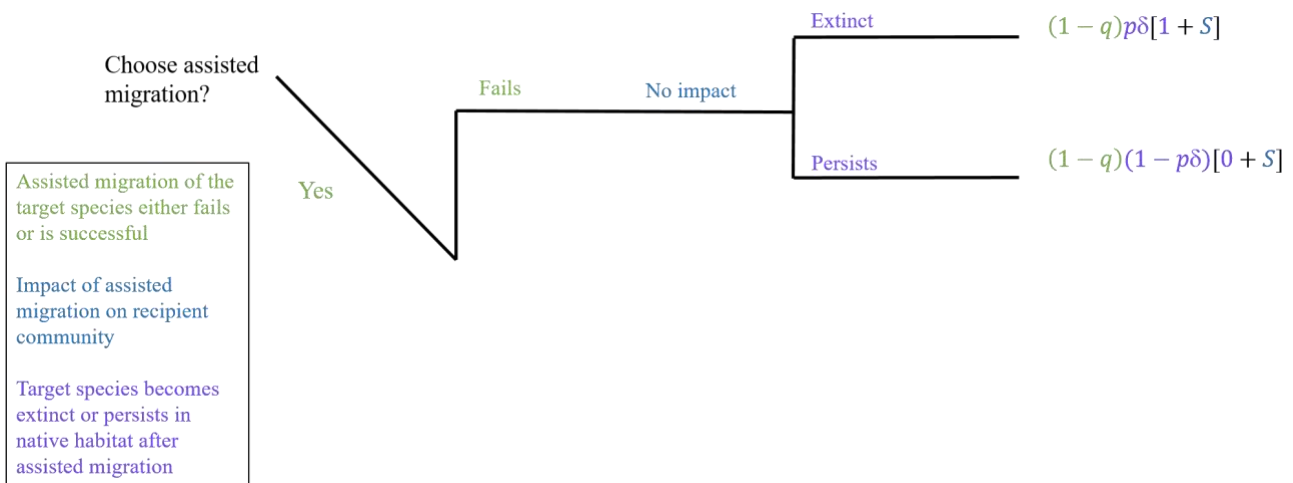


Figure A1.3: Assisted migration chosen, but fails. If managers elect to move the species, it may not establish in the recipient ecosystem. In this outcome, it would not impact the recipient ecosystem (blue), and the final outcome would again depend on the probability of its extinction in its native habitat (purple).

Following assisted migration, the source population of the moved species can still become extinct or survive, but the probability p is increased by the removal of individuals for assisted migration, by a factor δ . The number of species originally coexisting in the recipient ecosystem is given by S . Once the translocated species is established, it can impact these species either directly or indirectly. The probability that those interactions will drive i species to extinction is $E(i)$.

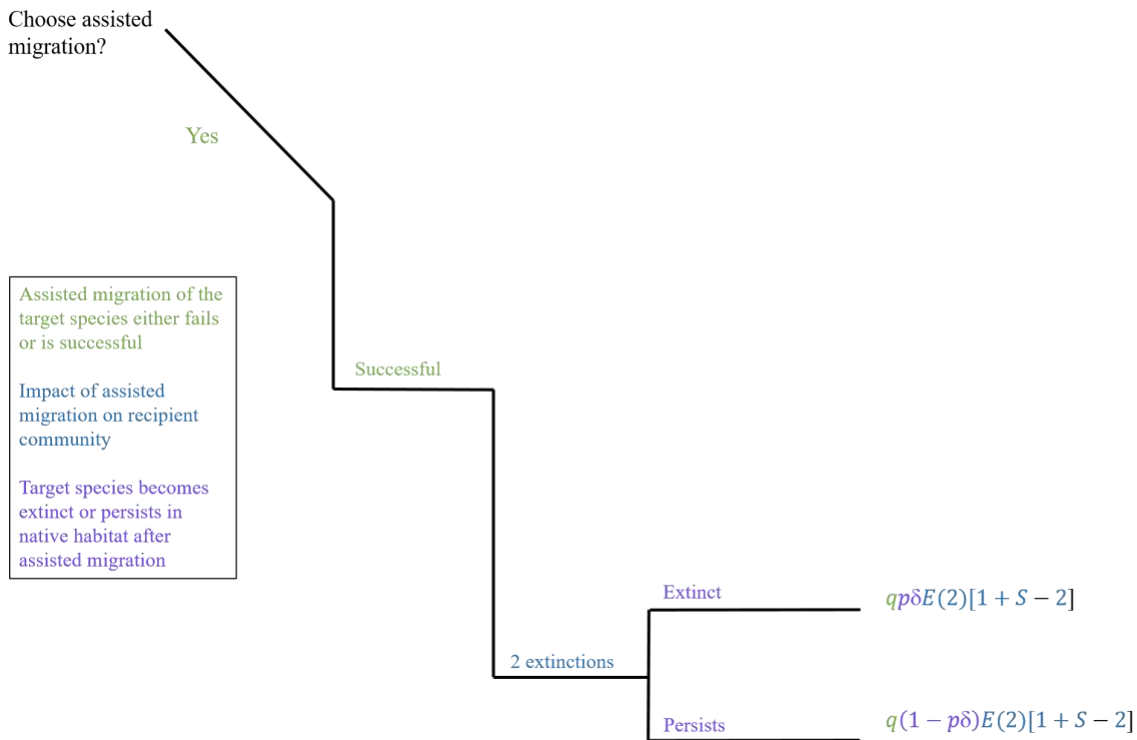


Figure A1.4: Successful assisted migration, but negative impacts on 2 species in the recipient ecosystem. This branch of the decision tree gives an example of assisted migration negatively impacting two species in the recipient ecosystem. The ecosystem gains one species (the translocated species), but loses two species due to interactions with the translocated species. Additionally, the probability of the translocated species persisting in its native habitat or becoming extinct is still incorporated (purple).

Equations A1.2 and A1.3 represent the expected outcome of undertaking assisted migration $\langle S_A \rangle$, or taking no action $\langle S_D \rangle$. These equations combined all possible outcomes depicted in Figure 3.1.

$$\langle S_D \rangle = pS + (1 - S - p)$$

Equation A1.2

$$\langle S_A \rangle = (1 - q)(p\delta + S) + q \sum_{i=0}^S E(i)(1 - S - i)$$

Equation A1.3

Supplementary Results

Constraining the density of the interaction network to particular values of D made little difference to the outcomes of AM. The scenarios with the lowest fixed density of interactions ($D = 0.25$) had slightly higher expected species richness in both the favourable and unfavourable scenarios, see Figure S6b and S6d. Results were the same for moderate ($D = 0.5$) and high ($D = 0.75$) interaction densities for the favourable, as well as the unfavourable scenarios (Figures A1.7b, A1.7d, A1.8b, A1.8d).

The general result of a rare but significant impact on many species in the recipient ecosystem following assisted migration was found in all equilibrium scenarios, see Table A1 and Figures 3.4, A1.5, A1.7, and A1.7. This generally held true for the non-equilibrium scenario of prior eradication (Figure A1.9). In the press perturbation scenarios, the loss of many species following assisted migration was much more probable. The loss of nearly five species within the recipient ecosystem was nearly 20% in some press perturbation scenarios (Figure A1.8). In the non-equilibrium scenarios, overall species richness on average was higher in no action was taken instead of proceeding with assisted migration in nearly all cases (Figures A1.8 and A1.9). The exceptions to this were in some eradication scenarios and conditional on the thresholds for extinctions and the IUCN status of the translocation species (Figure S9). Assisted migration improves overall richness slightly only if the threshold of loss is at the least conservative level (abundance must decline to zero or low enough to qualify that species as Critically Endangered). For example, if species loss is counted only when abundance is zero and the target species for translocation is Critically Endangered, the species richness following assisted migration is on average 14.3 whereas the species richness with no action is 14.1, out of a possible maximum of 15 species (Figure A1.9). The non-equilibrium scenarios differ from the equilibrium scenarios in that there is a loss of species in the recipient ecosystem even when assisted migration is not chosen. However, the scale of this loss is generally lower compared to when assisted migration is chosen, and this is particularly true in nearly all of the press perturbation scenarios (Figure A1.8). In the most conservative scenario of press perturbations, where the target species for translocation is Critically Endangered and a species in the recipient community is counted as lost if it qualifies for Vulnerable status, the average richness following assisted migration is 10.9 species, whereas the average richness if no action is taken is 13.9 species (Figure S8).

Table A1.1. The probabilities of successful assisted migration, q , extinction of translocated species in its native habitat, p , and number of extinctions in the recipient ecosystem, $E(i)$ in an ecosystem where the interaction density varied randomly and in an ecosystem with a moderate ($D = 50\%$) density interaction network.

	Random density network $D \sim U[0, 1]$		Moderate density network $D = 0.5$	
	Favourable	Unfavourable	Favourable	Unfavourable
q	0.83	0.83	0.63	0.63
p	0.5	0.1	0.5	0.1
E(1)	0.12	0.12	0.1	0.08
E(2)	0.04	0.05	0.09	0.08
E(3)	0.03	0.03	0.09	0.09
E(4)	0.01	0.02	0.07	0.08
E(5)	0.01	0.06	0.06	0.06
E(6)	6.1×10^{-3}	8.8×10^{-3}	0.04	0.05
E(7)	2.7×10^{-3}	6.1×10^{-3}	0.03	0.02
E(8)	1.9×10^{-3}	3.0×10^{-3}	0.01	0.01
E(9)	8.0×10^{-4}	2.0×10^{-3}	4.9×10^{-3}	4.4×10^{-3}
E(10)	1.0×10^{-4}	1.0×10^{-4}	1.9×10^{-3}	1.2×10^{-3}
E(11)	0	2.0×10^{-4}	4.0×10^{-4}	5.0×10^{-4}
E(12)	1.0×10^{-4}	0	0	8.0×10^{-4}
E(13)	0	1.0×10^{-4}	0	1.3×10^{-3}
E(14)	0	0	0	4.0×10^{-4}

Low interaction density ($D = 0.25$)

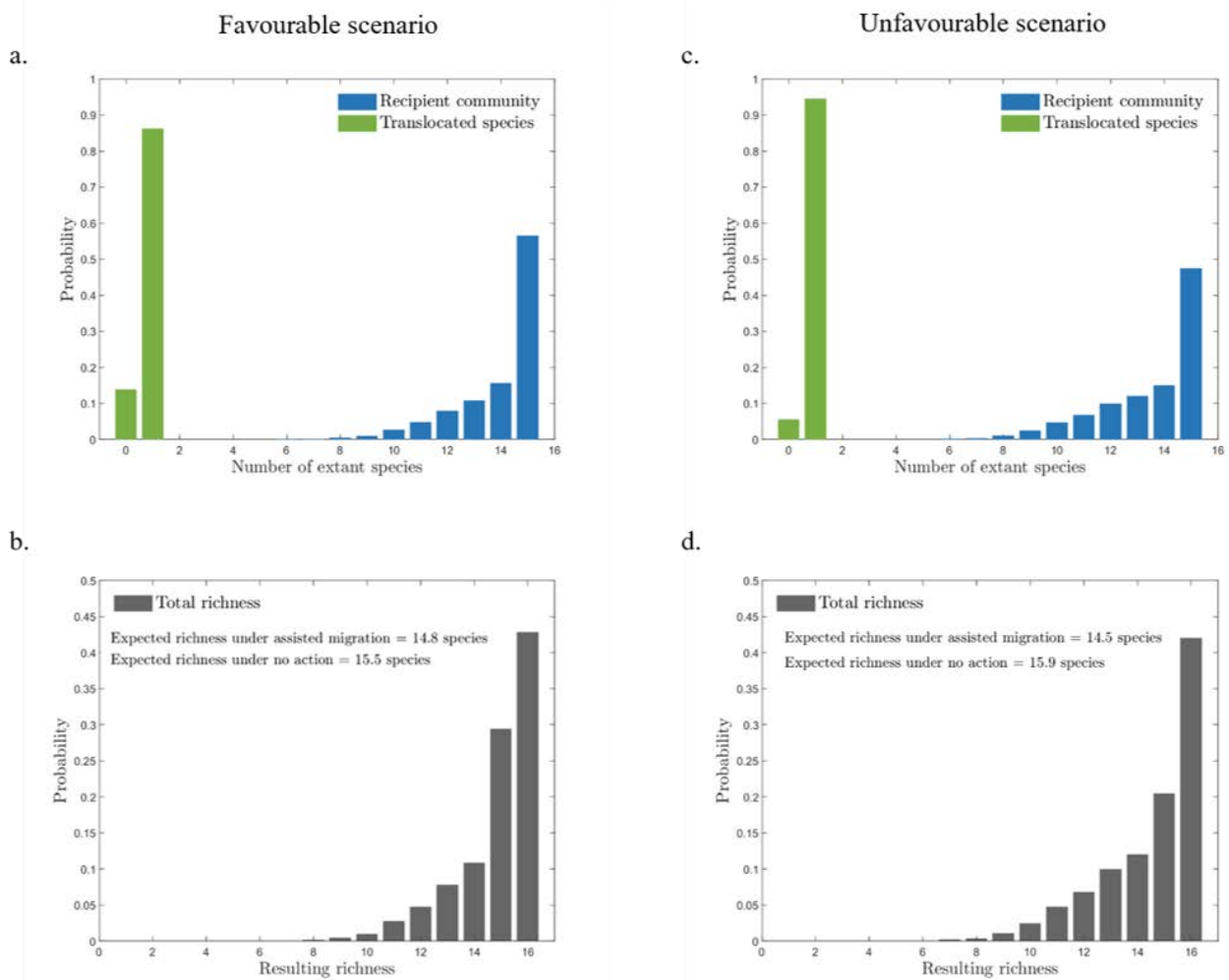


Figure A1.5. Aggregate outcomes of modelled ecosystems with low density interaction networks, $D = 0.25$. Panels (a) and (b) show the favourable scenario, and (c) and (d) show the unfavourable scenario. In panels (a) and (c), probability distributions for number of extant species in the translocated and recipient ecosystems are distinguished. The translocated species (green), can (i) survive following assisted migration and survive in its native habitat, (ii) survive following assisted migration and go extinct in its native habitat, (iii) assisted migration can fail and the species survives in its native habitat, (ii) assisted migration can fail and the species goes extinct in its native habitat. Species in the recipient ecosystem (blue), can be unaffected by assisted migration, maintaining a richness of 15, or may experience one or more extinctions. Panels (b) and (d) show probability distributions for the change in overall richness following assisted migration (i.e., the aggregate of the green and blue distributions in the upper panels).

Moderate interaction density ($D = 0.50$)

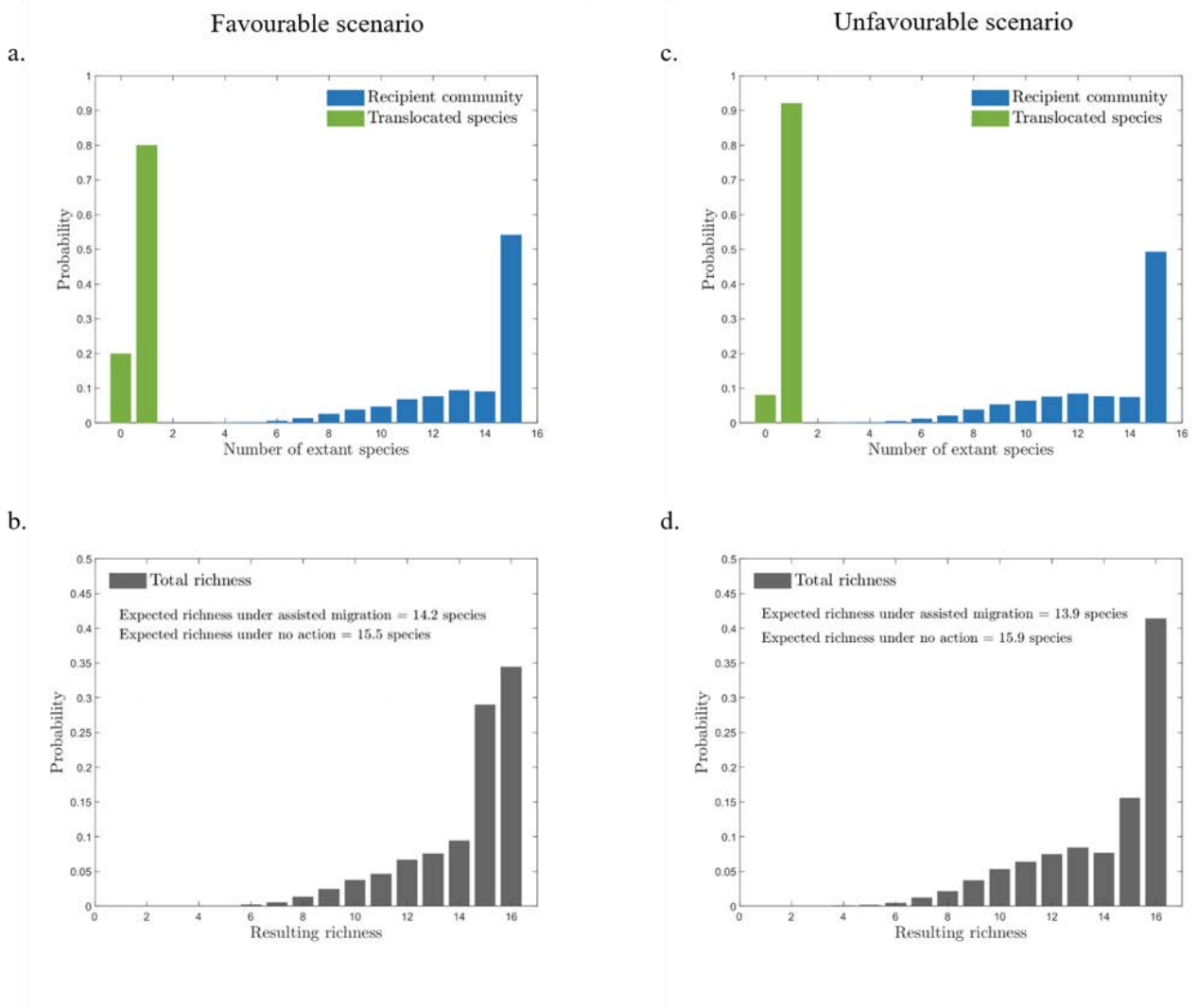


Figure A1.6. Aggregate outcomes of modelled ecosystems with moderate density interaction network $D = 0.50$. Panels (a) and (b) represent the outcomes for the favourable scenario, and (c) and (d) show the unfavourable scenario. The favourable scenario has a slightly better outcome simulations for expected species richness than the unfavourable scenario.

High interaction density ($D = 0.75$)

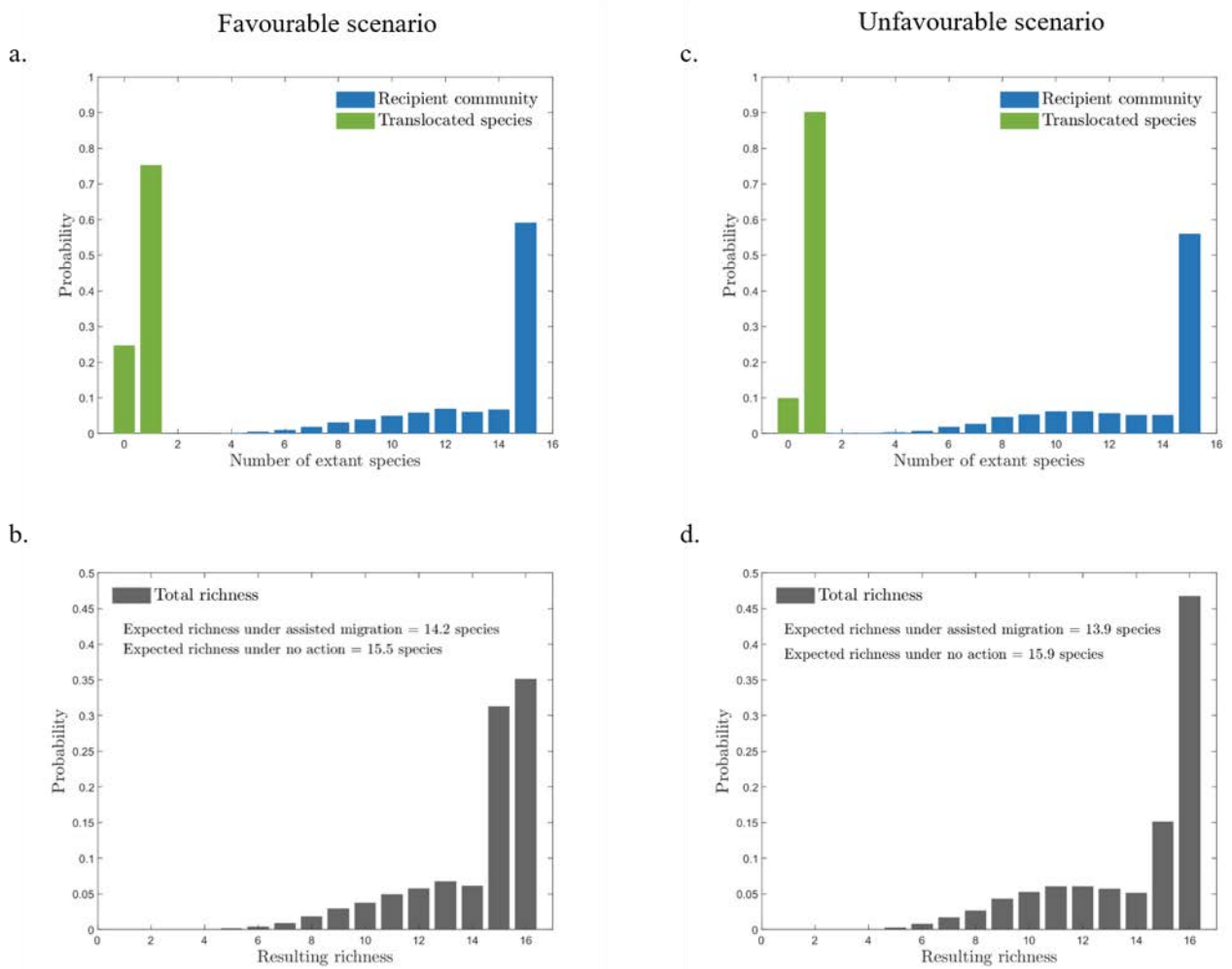


Figure A1.7. Aggregate outcomes of modelled ecosystems with high density interaction network, $D = 0.75$. Panels (a) and (b) show the favourable scenario, and (c) and (d) show the unfavourable scenario. There is a low, but not impossible chance of the loss of many species following AM in both scenarios.

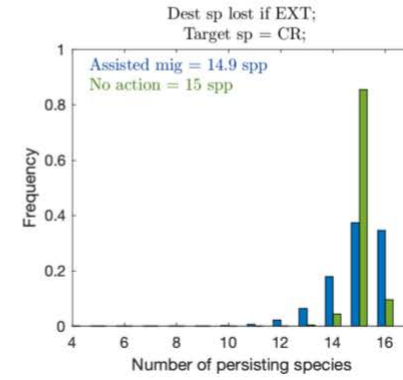
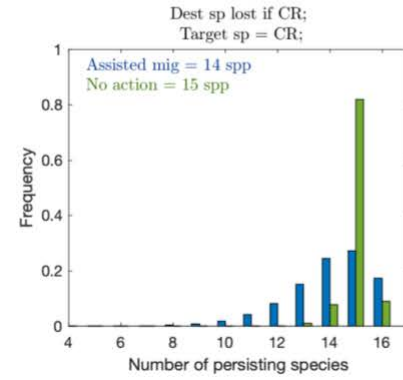
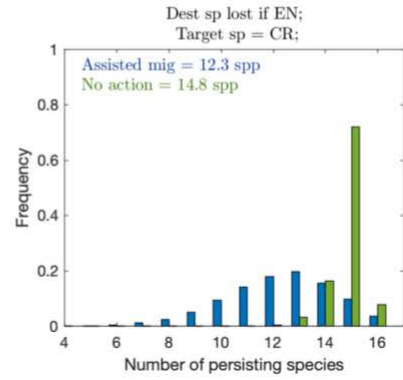
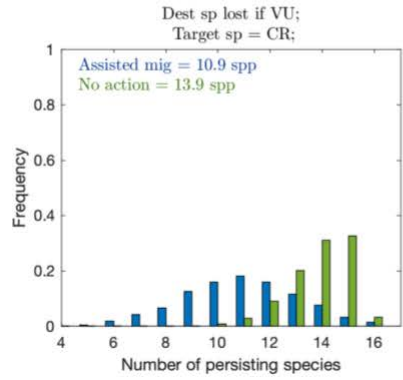
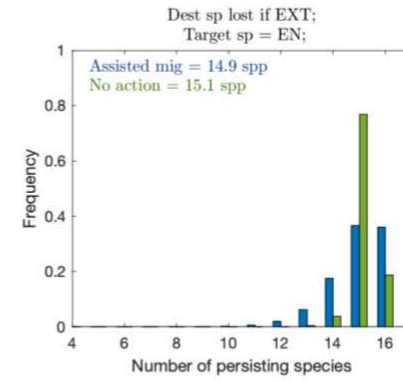
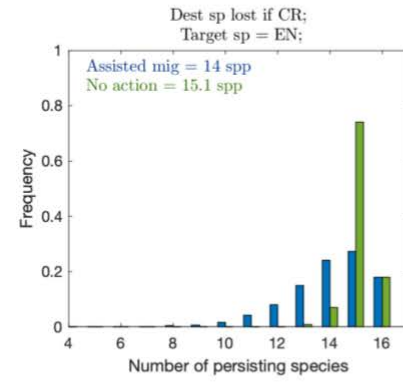
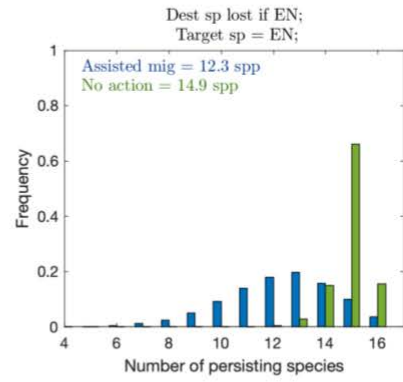
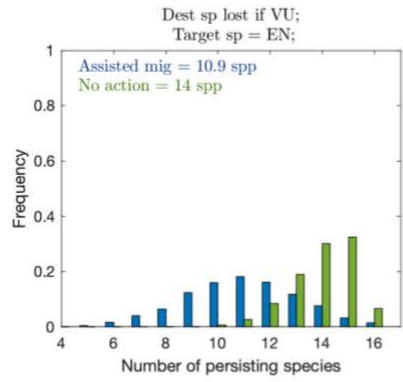
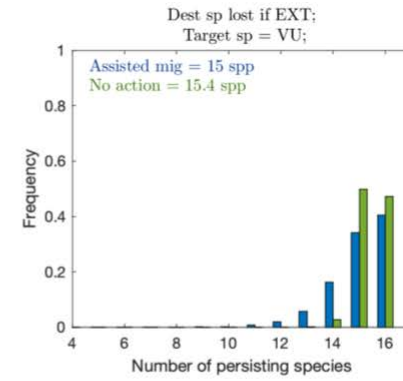
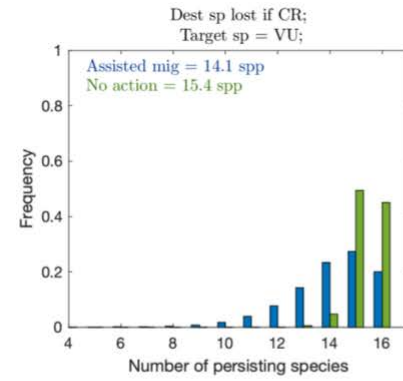
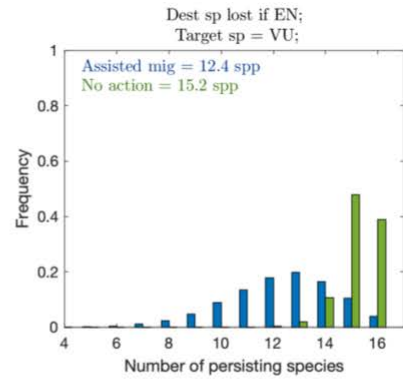
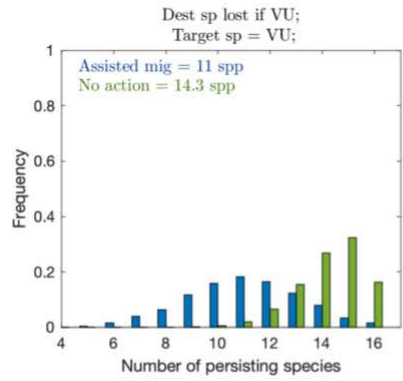


Figure A1.8. Aggregate outcomes of modelled ecosystems affected by press perturbations such as climate change. In all scenarios, species richness is on average higher when no action is taken. There is still a loss of species due to climate change, but the magnitude of loss is on average far lower than the magnitude of species loss if managers proceed with assisted migration. Demographic rates and interactions between species are already being affected by the press perturbation, assisted migration exacerbates the effects on the recipient ecosystem. The loss of many species in the recipient ecosystem is relatively common following assisted migration, except in the least conservative scenarios where species loss is only counted if abundance is zero.

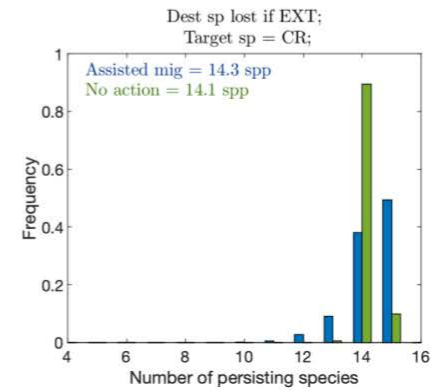
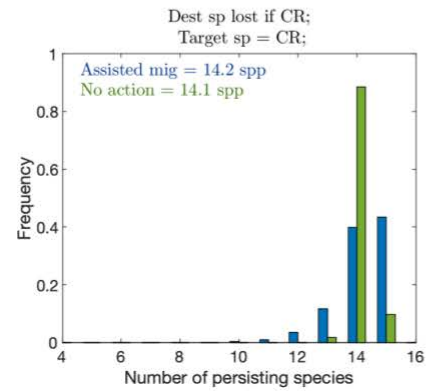
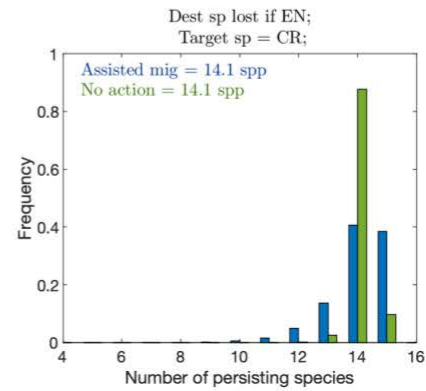
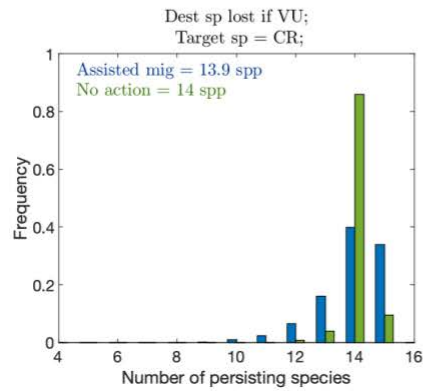
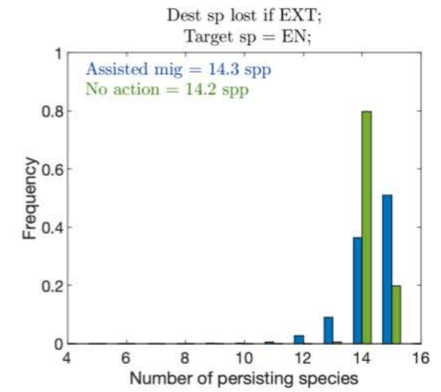
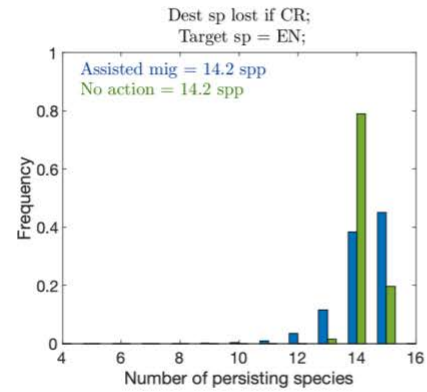
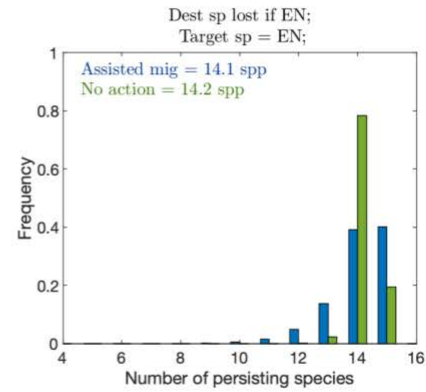
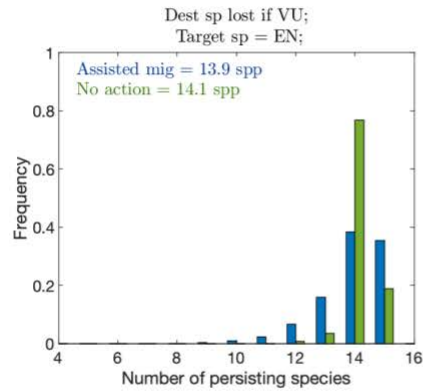
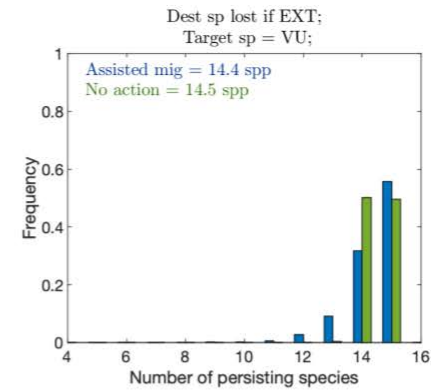
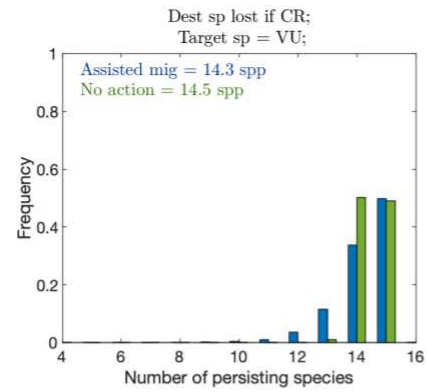
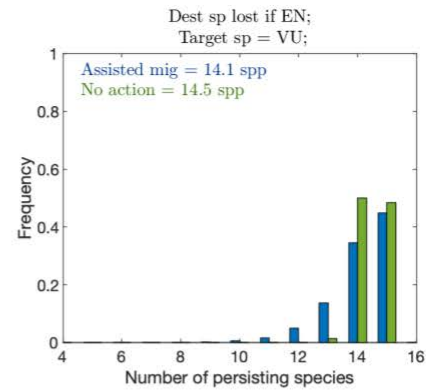
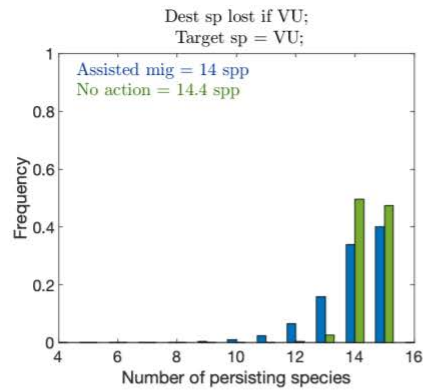


Figure A1.9. Aggregate outcomes of modelled ecosystems affected by a prior species eradication. *The difference in species richness is low between taking no action or proceeding with assisted migration, following a species eradication. There is a rare but possible chance of losing multiple species when assisted migration is chosen. In the least conservative scenarios, overall species richness is the same or slightly higher if assisted migration is chosen (bottom right panels).*

Supplementary references for Appendix 1

Baker, C. M., Gordon, A., & Bode, M. (2017). Ensemble ecosystem modeling for predicting ecosystem response to predator reintroduction. *Conservation biology*, 31(2), 376-384.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C. R. A. I. G., Akçakaya, H. R., Leader-Williams, N. I. G. E. L., ... & Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation biology*, 22(6), 1424-1442.

Appendix 2. Supplementary figures for “Risk analysis of faunal reconstruction decisions on Dirk Hartog Island”

Figure A2.1 shows an example of one of the panels of 13 species population trajectories for one interaction matrix and one Translocation Alternative. There are 90 panels giving a total of 1,170 population projections, available upon request. This appendix also includes figures showing the predicted species richness outcomes from all Translocation Alternatives for all interaction matrices together (Figure A2.2), and then each interaction matrix separately (Figures A2.3 through A2.8). The average magnitude of antagonistic and positive interactions associated with translocation failure for each species are graphically represented in Figures A2.9 through A2.21.

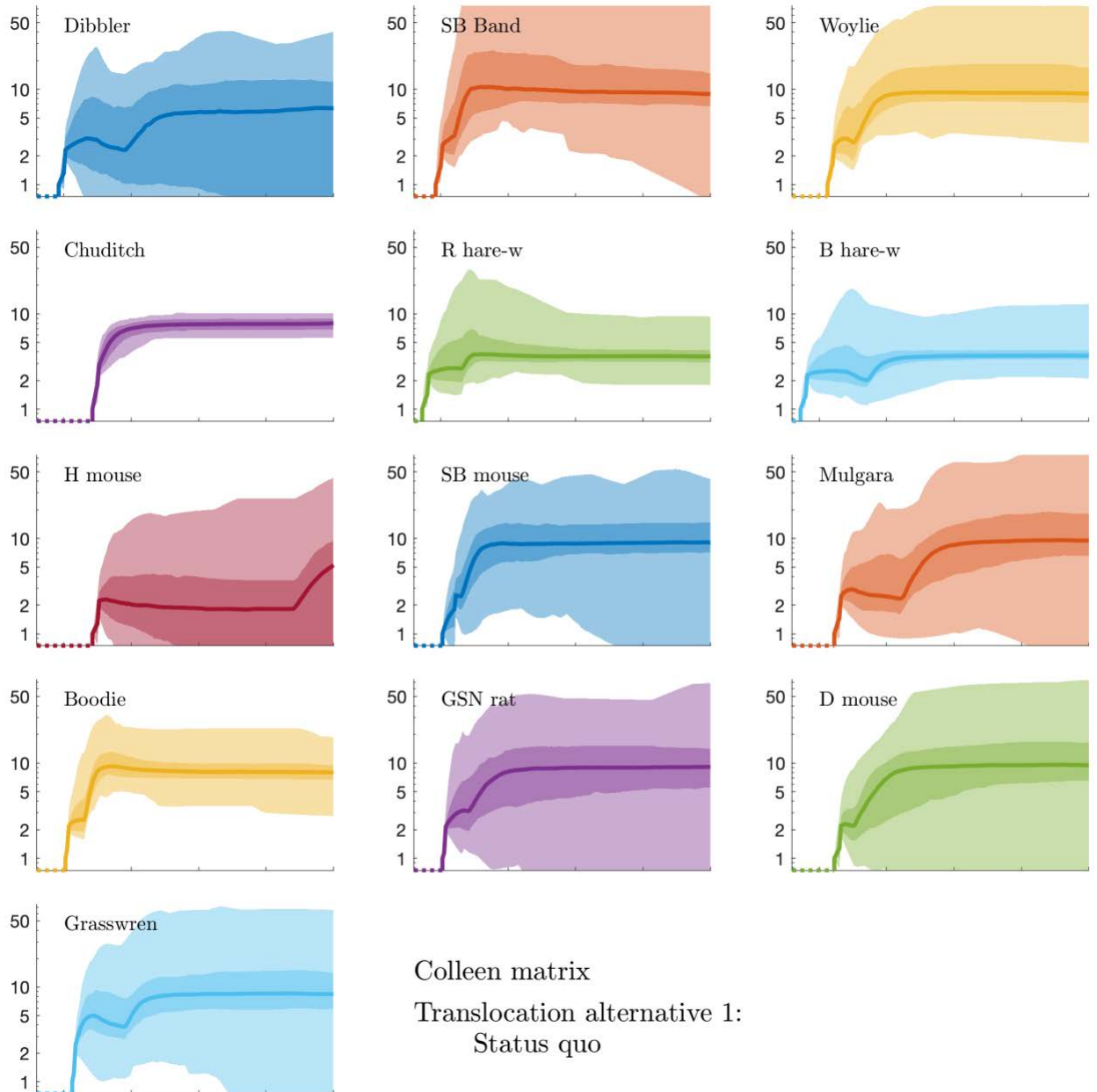


Figure A2.1: Simulation abundance timeseries for the 13 translocated species. Dark line shows the average abundance through time for all simulations, using Expert 3’s matrix (the sixth expert-elicited sign-structured matrix) and the “status quo” translocation alternative. Surrounding shading indicates the 99% and 80% confidence intervals. The timeseries for the remaining species are in the appendix.

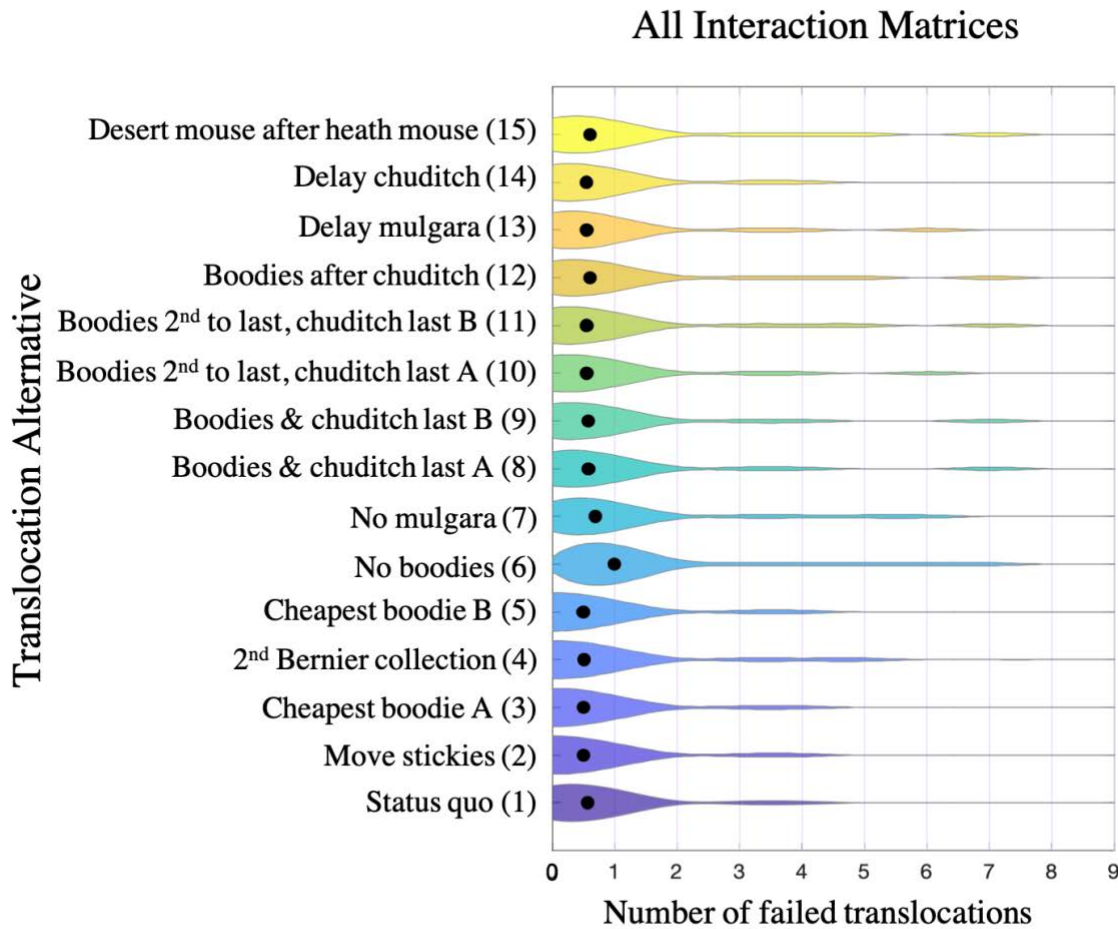


Figure A2.2: The number of local extinctions for each Translocation Alternative averaged across all sign structured matrices. Translocation Alternative 6 is slightly worse among the options with an average number of one failed translocation. The long tail of the violin plots, however, represent the very unlikely but possible chance of many failed translocations.

Matrix 1 (Saul 1)

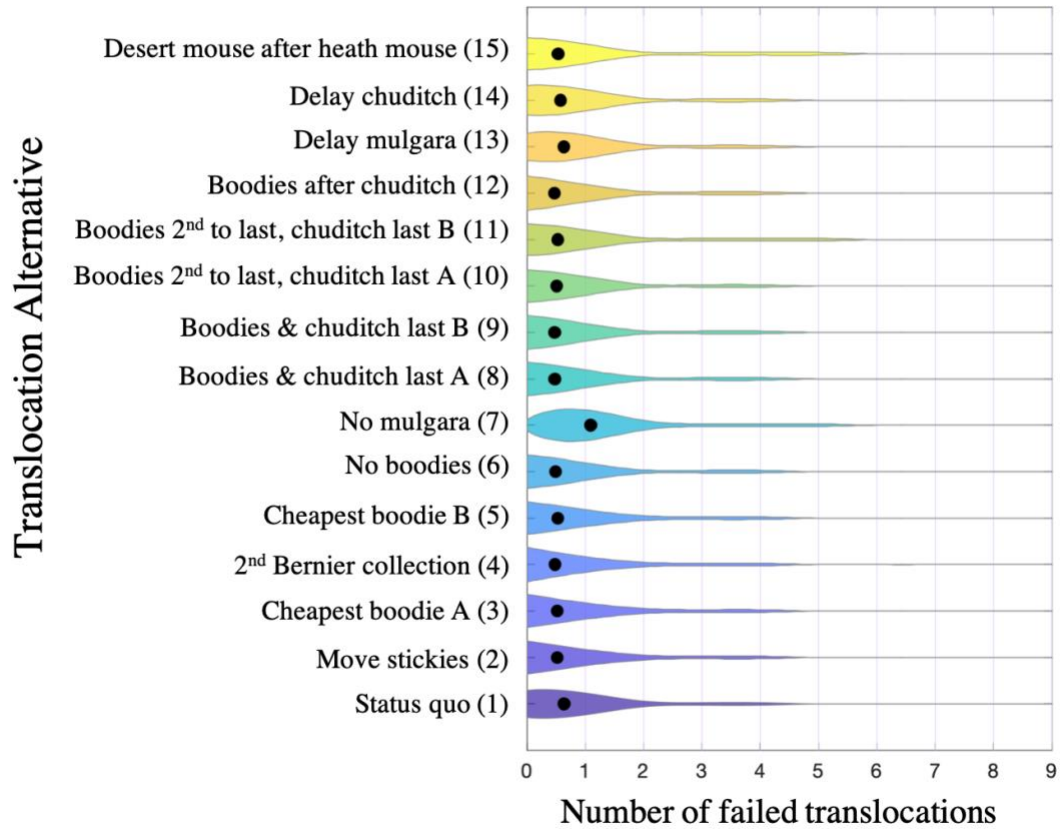


Figure A2.3: The number of local extinctions for each Translocation Alternative using Interaction Matrix 1. Translocation Alternative 7 is slightly worse among the options with an average number of one failed translocation.

Matrix 2 (Saul 2)

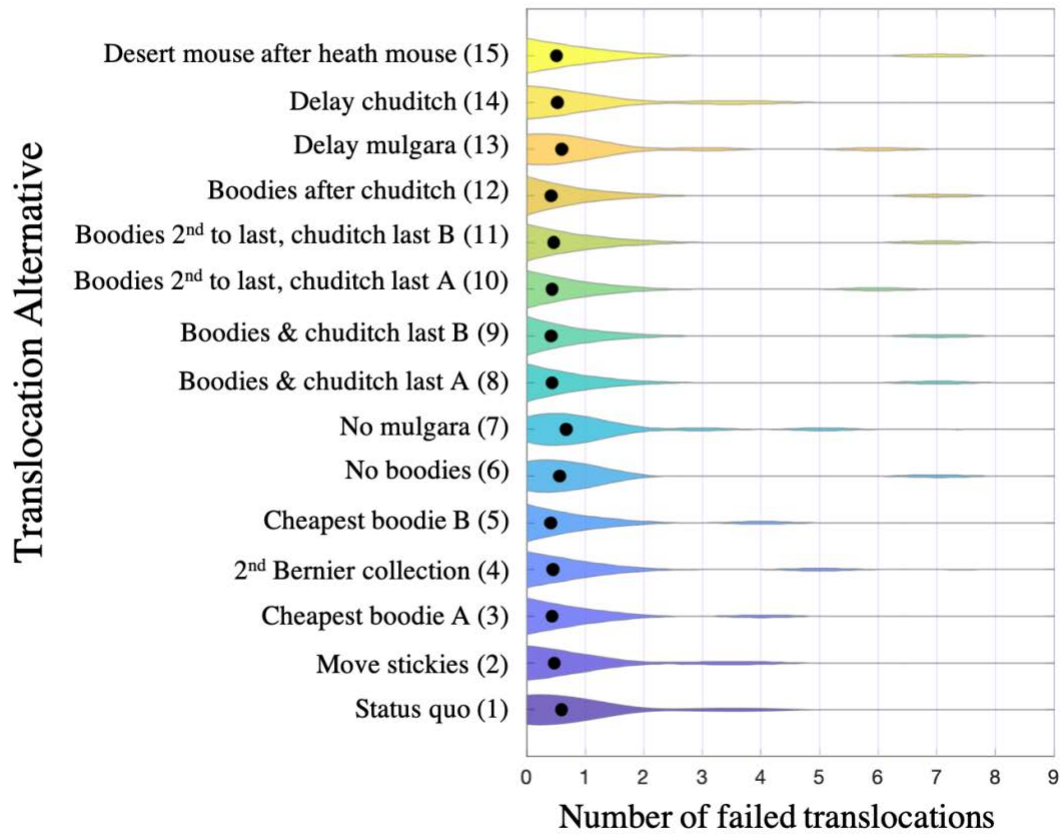


Figure A2.4: The number of local extinctions for each Translocation Alternative using Interaction Matrix 2. The Translocation Alternatives have approximately the same outcome, with Translocation Alternative 7 being slightly worse.

Matrix 3 (Saul 3)

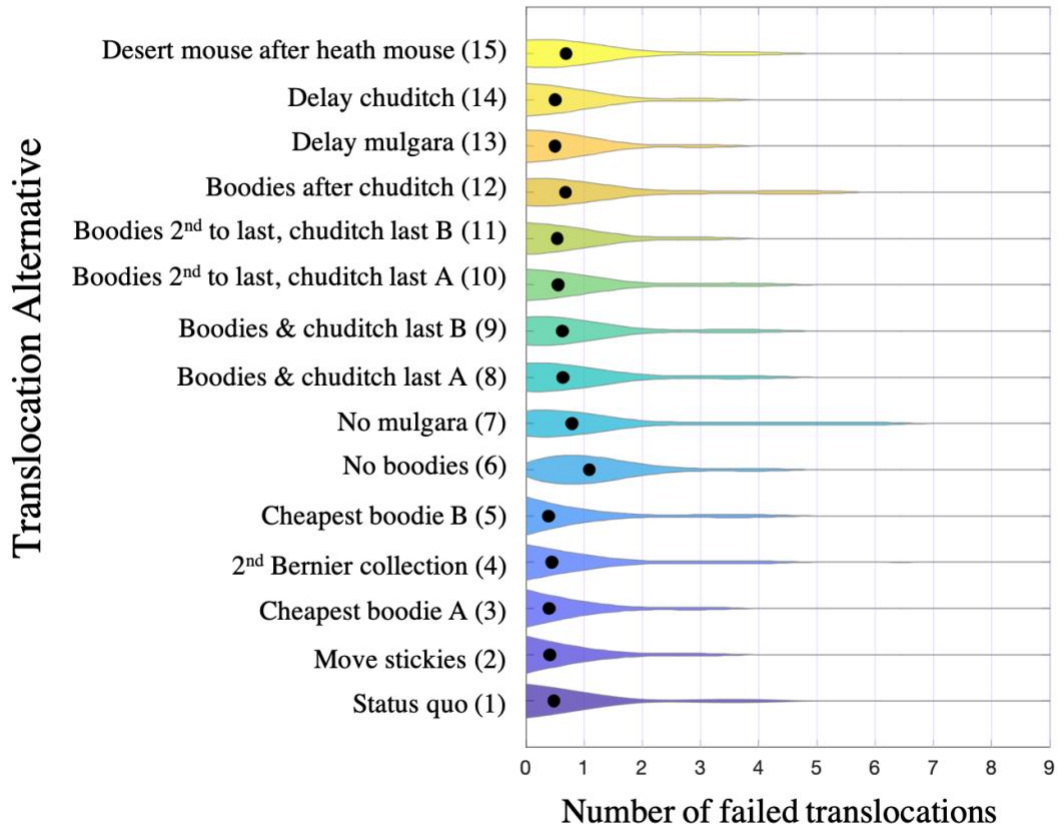


Figure A2.5: The number of local extinctions for each Translocation Alternative using Interaction Matrix 3. Translocation Alternative 6 is slightly worse among the options with an average number of one failed translocation. This interaction matrix assumed that boodies function as ecosystem engineers and have a positive effect on other species.

Matrix 4 (Lesley 1)

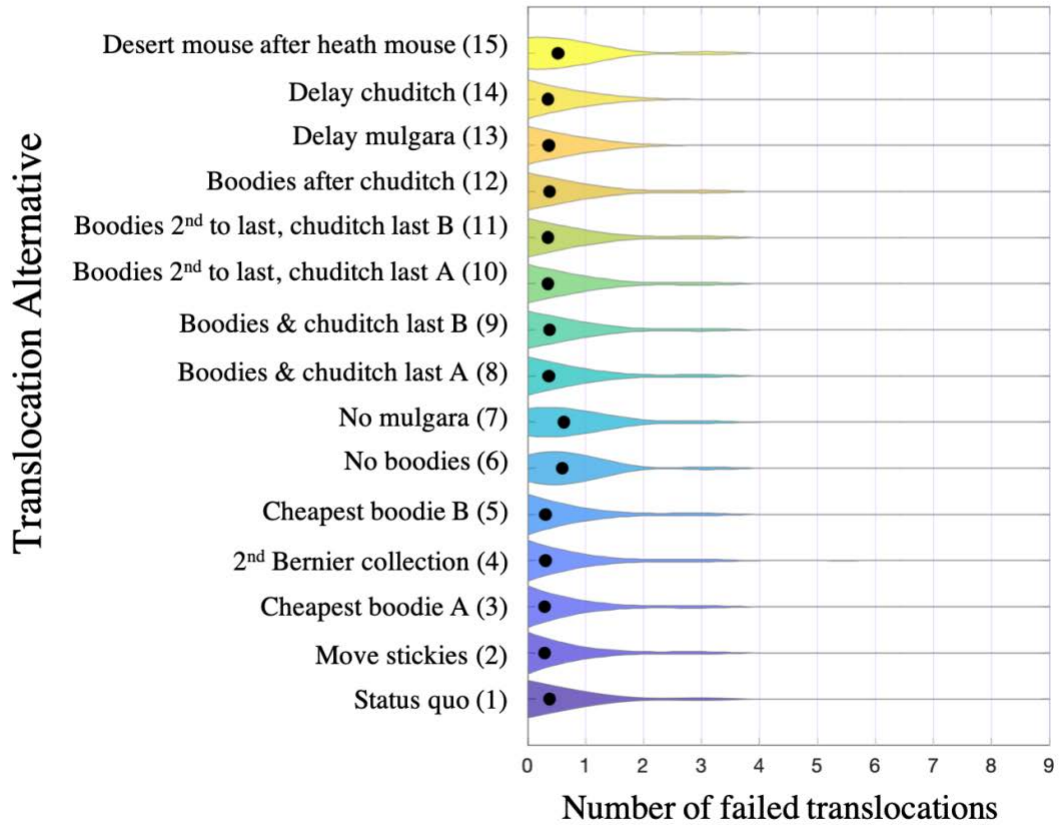


Figure A2.6: The number of local extinctions for each Translocation Alternative using Interaction Matrix 5. The Translocation Alternatives have approximately the same outcome. This interaction matrix was considered a “conservative” estimate of dynamics by Expert 2.

Matrix 5 (Lesley 2)

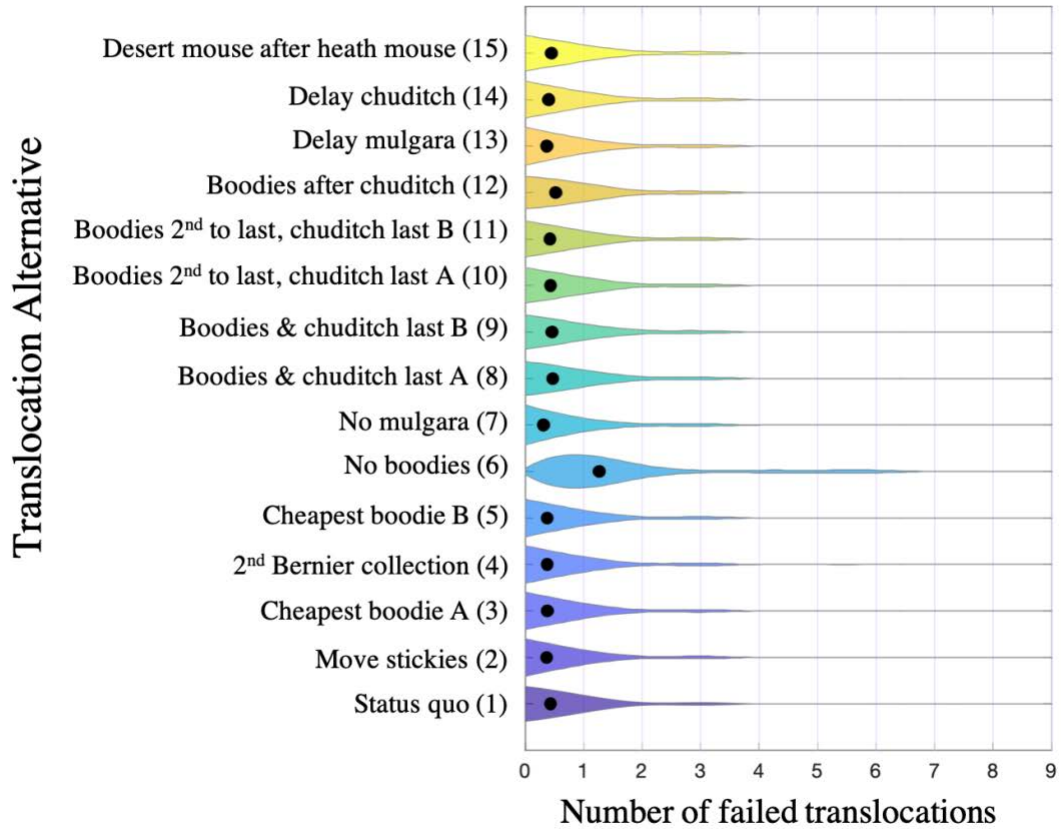


Figure A2.7: *The number of local extinctions for each Translocation Alternative using Interaction Matrix 5. Translocation Alternative 6 is quite worse than the other Translocation Alternative with an average number of 1.25 failed translocations. This interaction matrix assumed that boodies function as ecosystem engineers and have a positive effect on other species.*

Matrix 6 (Colleen)

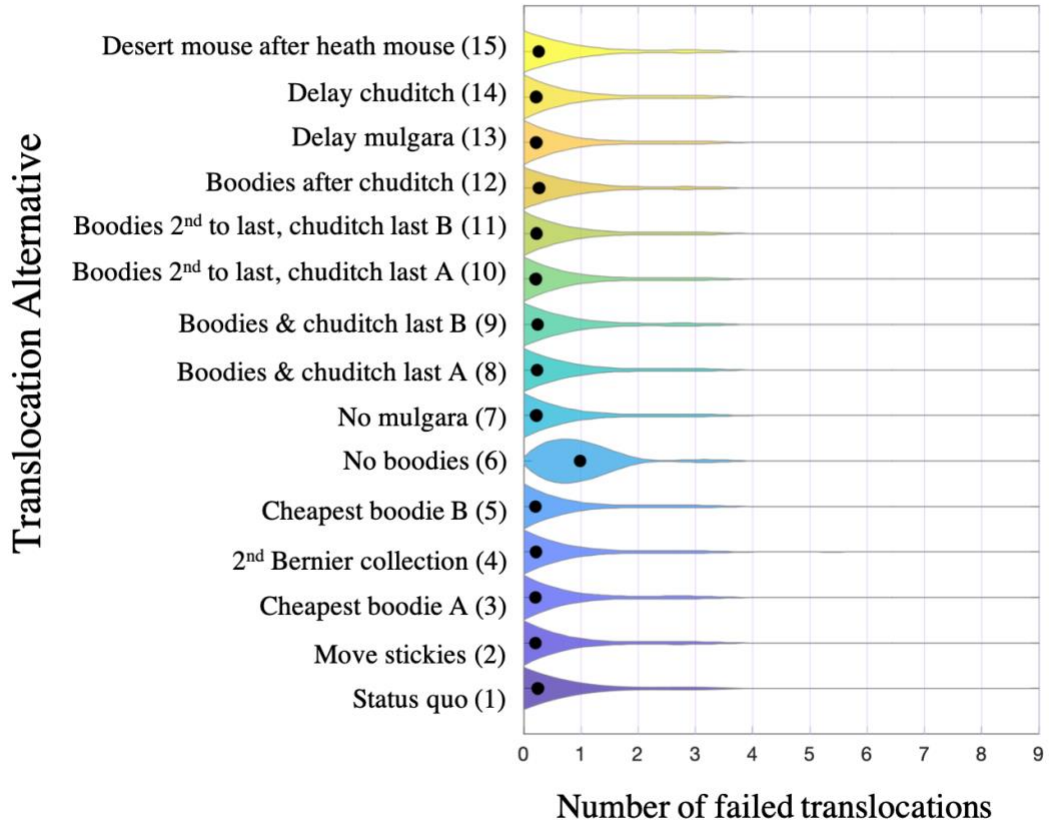


Figure A2.8: The number of local extinctions for each Translocation Alternative using Interaction Matrix 6. Translocation Alternative 6 is worse among the options with an average number of one failed translocation.

When Dibbler translocation failed:

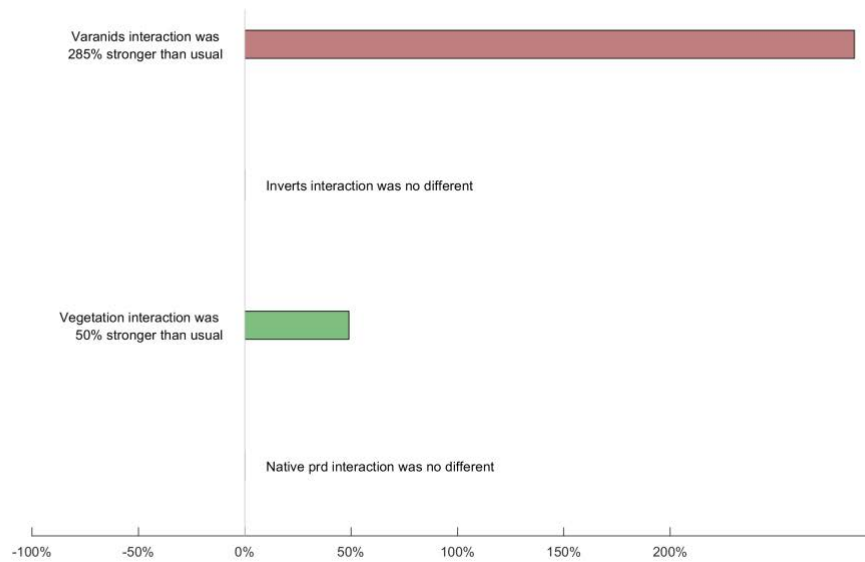


Figure A2.9: *The dibbler translocation failure is associated with a stronger negative interaction with varanids. The interaction with varanids during translocation failure was on average 285% stronger than when translocation was successful.*

When Shark Bay Bandicoot translocation failed:

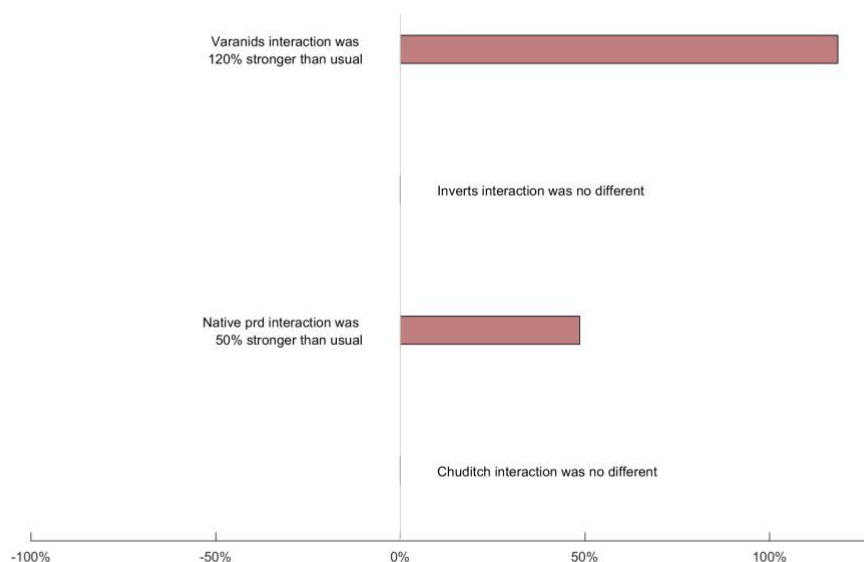


Figure A2.10: *The Shark Bay bandicoot translocation failure is associated with stronger negative interactions with varanids and native predators. The interaction with varanids during translocation failure was on average 120% stronger than when translocation was successful, and the interaction with native predators was 50% stronger.*

When Woylie translocation failed:

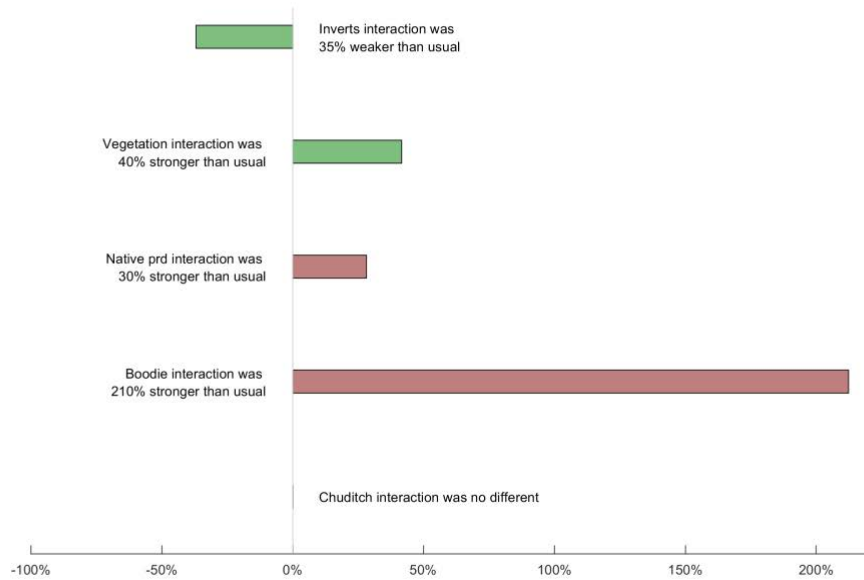


Figure A2.11: *The woylie translocation failure is associated with stronger negative interactions with boodies. The interaction with boodies during translocation failure was on average 210% stronger than when translocation was successful.*



Figure A2.12: The chuditch translocation failure is associated not associated with any interactions at all. Translocation failure of chuditch may be due to another factor.

When Rufous hare-wallaby translocation failed:

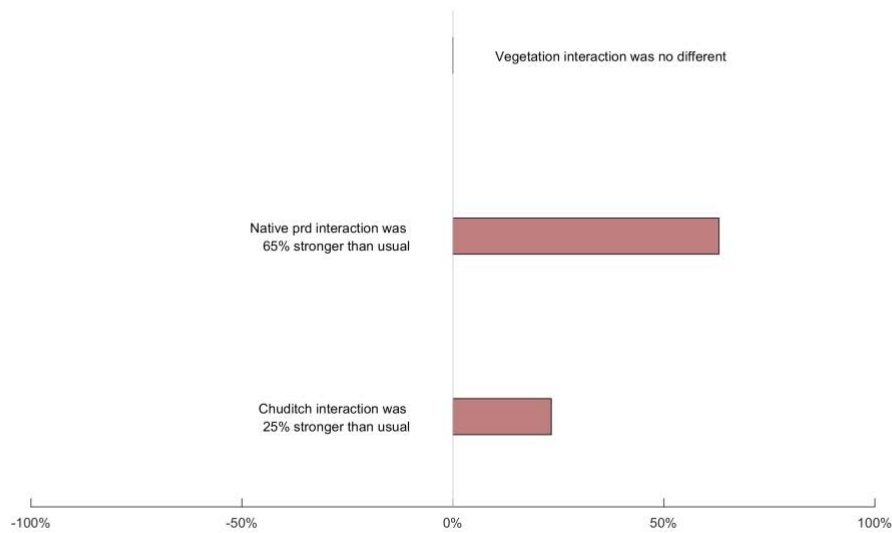


Figure A2.13: *The rufous hare-wallaby translocation failure is associated with stronger negative interactions with native predators and chuditch. The interaction with native predators during translocation failure was on average 65% stronger than when translocation was successful, and the interaction with chuditch was 25% stronger.*

When Banded hare-wallaby translocation failed:

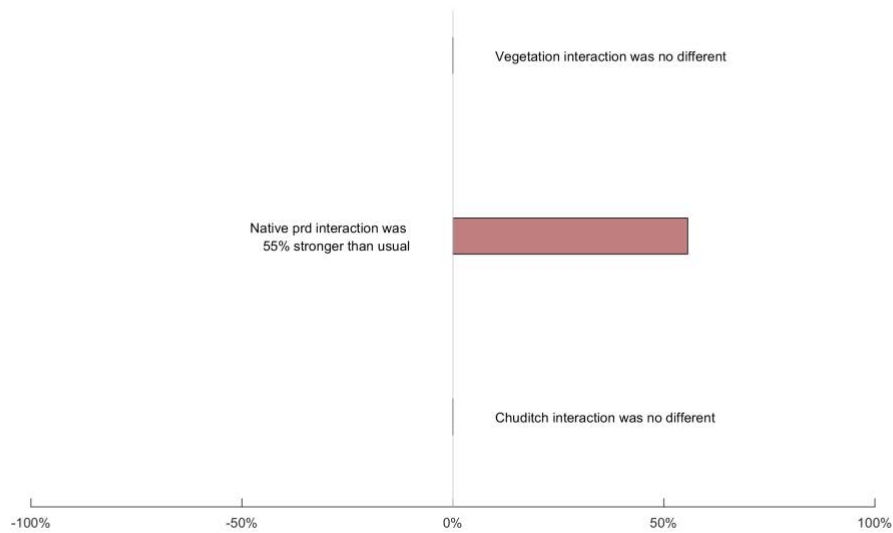


Figure A2.14: The banded hare-wallaby translocation failure is associated with stronger negative interactions with native predators. The interaction with native predators during translocation failure was on average 50% stronger than when translocation was successful

When Heath Mouse translocation failed:

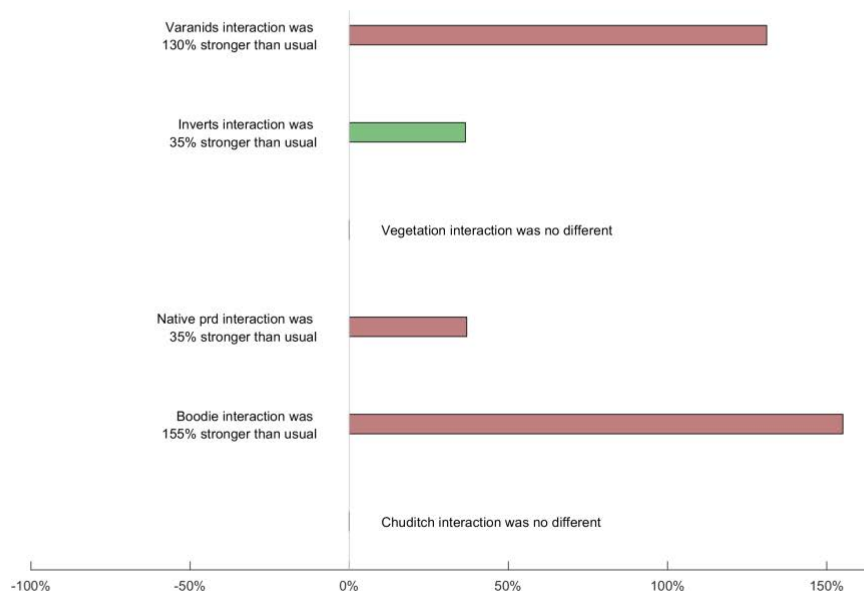


Figure A2.15: *The heath mouse translocation failure is associated with multiple stronger negative interactions, despite having stronger positive interactions with inverts, which are a food source. The interaction with varanids during translocation failure was on average 130% stronger than when translocation was successful, and negative interactions with boodies were 155% stronger. Negative interactions with native predators were also slightly stronger at 35% higher magnitude than usual during translocation failure.*

When Shark Bay mouse translocation failed:

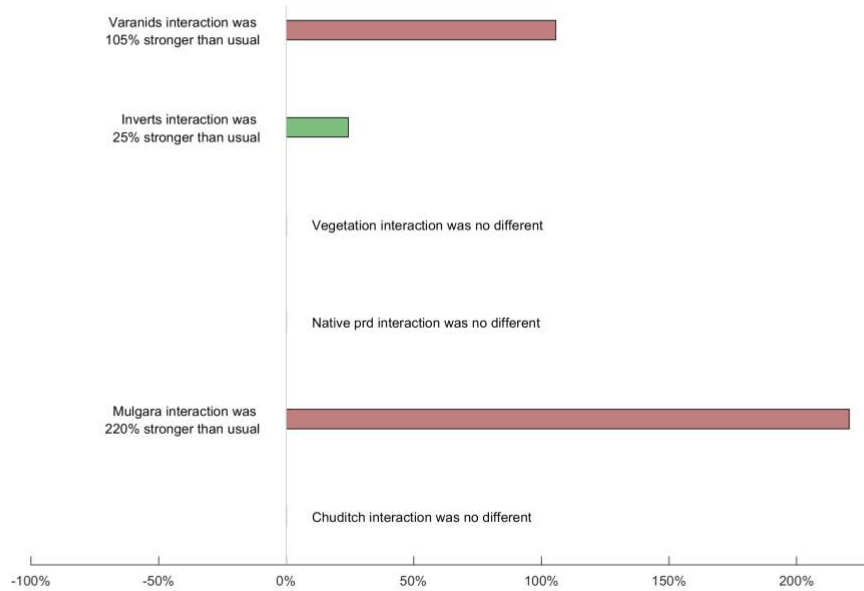


Figure A2.16: *The Shark Bay mouse translocation failure is associated with stronger negative interactions with mulgara and varanids. The interaction with mulgara during translocation failure was on average 220% stronger than when translocation was successful, and the interactions with varanids were 105% stronger.*

When Brush-tailed mulgara translocation failed:

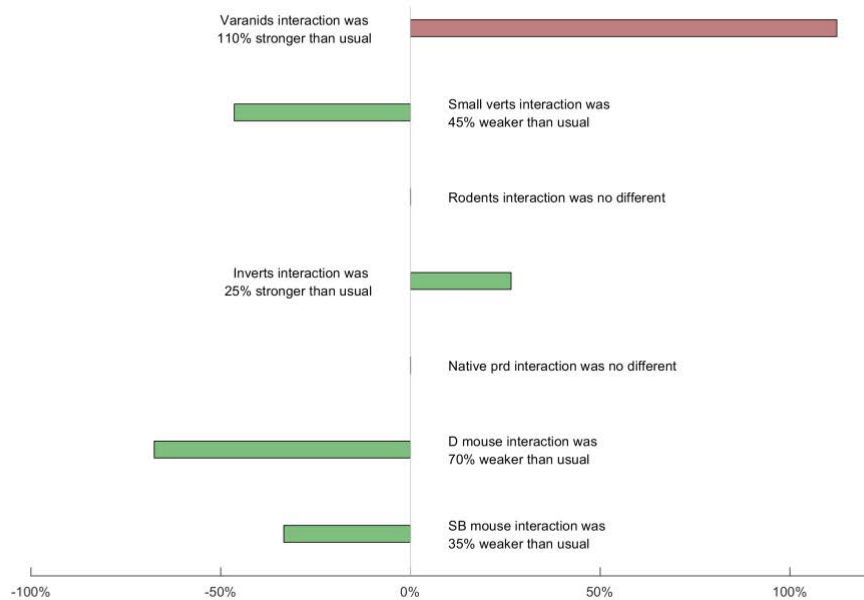


Figure A2.17: *The brush-tailed mulgara translocation failure is associated with stronger negative interactions with varanids, and weaker positive interactions with small vertebrates, the desert mouse and Shark Bay mouse. The interactions with varanids during translocation failure were on average 110% stronger than when translocation was successful. Small vertebrates, the desert mouse, and the Shark Bay mouse are prey for the mulgara. These positive interactions were weaker during translocation failures; small vertebrate interactions were on average 45% weaker, desert mouse interactions were 70% weaker, and Shark Bay mouse interactions were 35% weaker.*

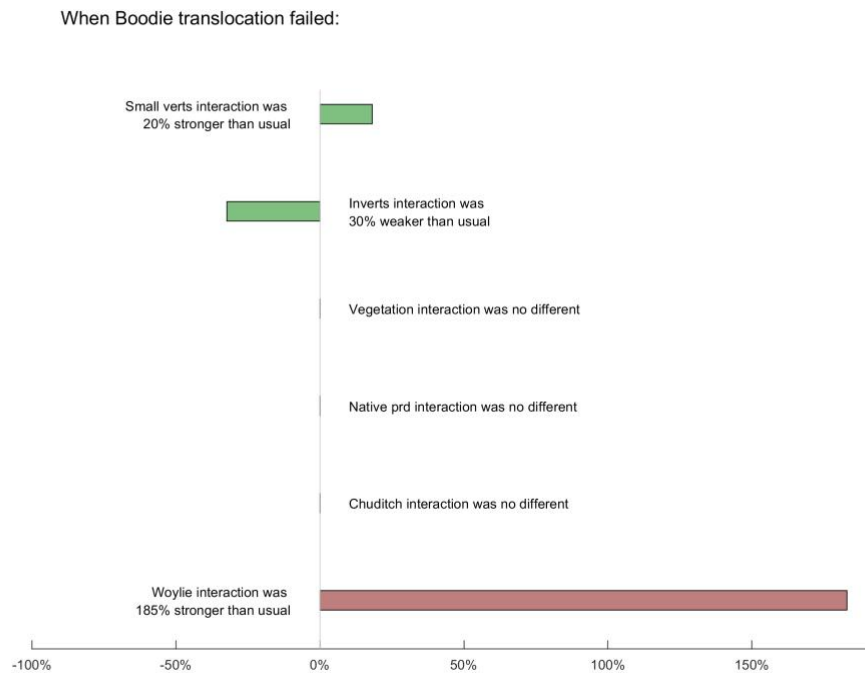


Figure A2.18: *The boodie translocation failure is associated with stronger negative interactions with woylie, and weaker interactions with invertebrates. The interaction with woylie during translocation failure was on average 185% stronger than when translocation was successful. Positive interactions with small vertebrates, a food source, were slightly stronger than usual at 20% on average, but positive interactions with another food source, invertebrates, were 30% weaker on average during translocation failure than during translocation success.*

When Greater stick-nest rat translocation failed:

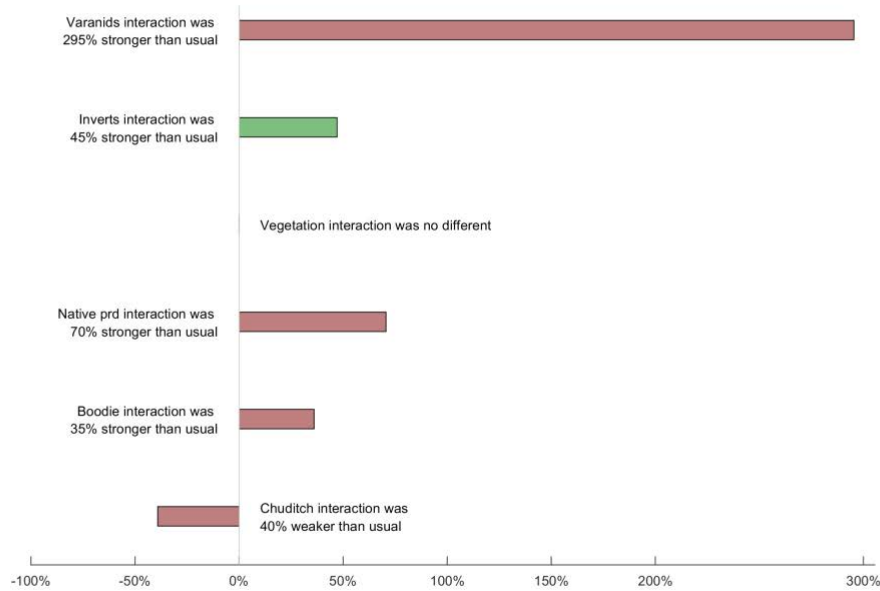


Figure A2.19: *The Greater stick-nest rat translocation failure is associated with stronger negative interactions with varanids, native predators, and boodies. The interaction with varanids during translocation failure was on average 295% stronger than when translocation was successful, and the interactions with native predators were 70% stronger. Negative interactions with boodies were slightly stronger at 35%. Positive interactions with a food source, invertebrates, were 45% stronger on average, and negative interactions with chuditch were on average 40% weaker during translocation failure than during translocation success.*

When Desert mouse translocation failed:

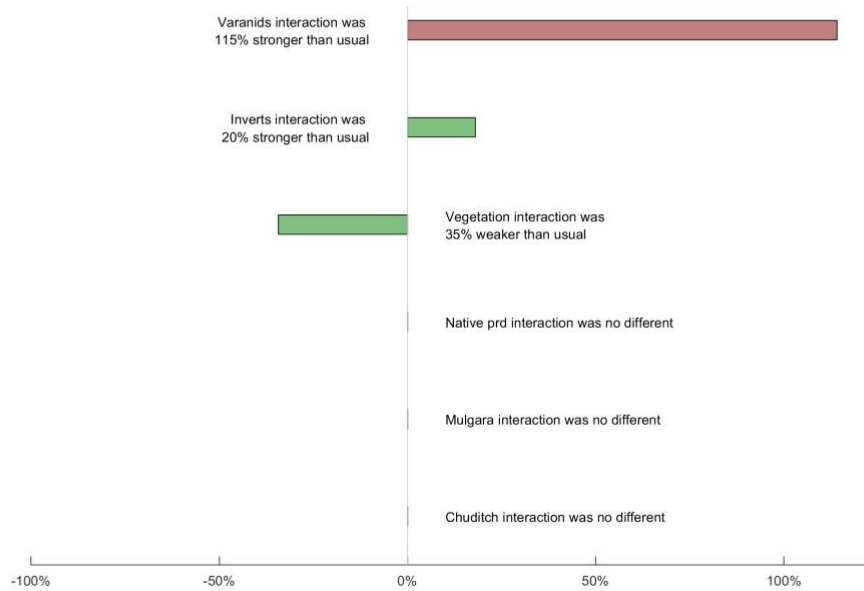


Figure A2.20: *The desert mouse translocation failure is associated with stronger negative interactions with varanids and lack of vegetation. The interaction with mulgara during translocation failure was on average 115% stronger than when translocation was successful. Positive interactions with vegetation, a source of food, were on average 35% weaker during translocation failure.*

When Western grasswren translocation failed:

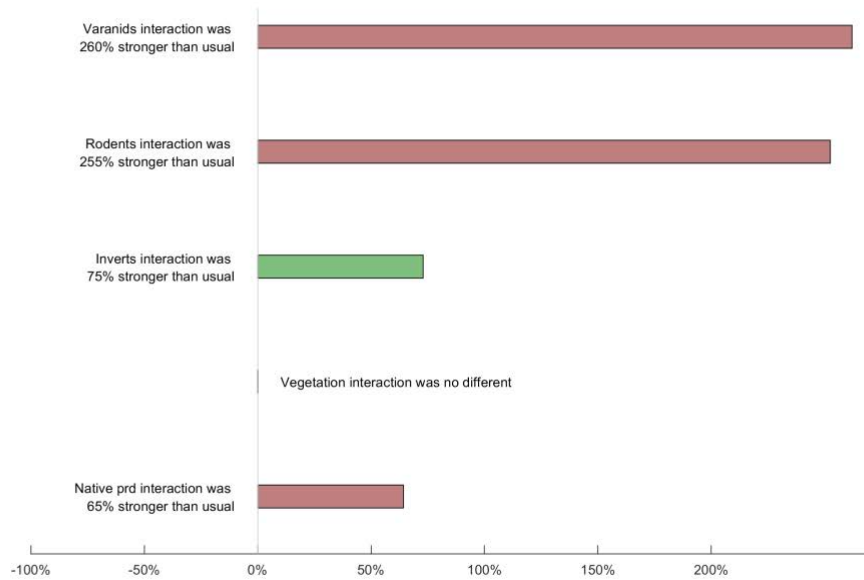


Figure A2.21: *The western grasswren translocation failures are associated with stronger antagonistic interactions. Despite having an increased interaction with a food source, strongly negative interactions from varanids, rodents, and native predators affected the success of the western grasswren in some simulations. Rodents are a source of competition with western grasswren, and it is vulnerable to predation by varanids and native predators such as hawks.*