Developing spatial prioritisation strategies to maximise conservation impact

PhD thesis submitted by

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BSc (Hons)

July 2019

For the degree of Doctor of Philosophy

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Acknowledgements

First and foremost, I would like to thank my advisory panel. Bob, the passion and dedication you have for conservation has been a tremendous inspiration for me to complete this thesis and to continue working in the field of conservation in the future. Throughout our time together you have endured personal hardships that would have defeated many, yet you have continued, unwavered, to support me and continue on the path towards making this world a better place. For that I am very grateful. Bec, from the very beginning you have been a fantastic advisor. The speed and attention to detail you have provided in feedback on my manuscripts has been exceptional, and none of this research would have been possible without your help. Thank you also for facilitating my trip to Chuuk Lagoon with The Nature Conservancy, which was an unforgettable experience. Mike, your contribution to these manuscripts has been invaluable. I am very glad that I decided to ask you to join my advisory panel, because the perspective and knowledge you have to offer is something that doesn't come around too often.

I would also like to thank the various members of the conservation planning group, Jorge, Danielle, Jeremy Horowitz, Jeremy Raynal, Jon Day, Georgie, Pat, Jess, and Steph, for the helpful feedback and fascinating discussions we have had. Keep up the good fight.

To the staff at ARC CoE, I am eternally grateful. Olga, Janet, Viv, and Jenny, thank you for all the hard work you put in to facilitating the research at the centre, and for always being so positive. You have contributed greatly to making the atmosphere at the centre such a nice place to work. I am sure that the everyday tasks you do often go underappreciated, but please know that I am very appreciative and thankful for everything you have done for me and for other students. Alana, thank you for all the advice you have given me related to my candidature, and for instilling just enough fear of failure into me to push me over the finish line.

Finally, I would like to thank my friends and family who have supported me throughout my PhD. To my parents, Sandy and Gary, for always supporting me no matter what direction I choose to take with my life, and for always being there for me when I need to discuss anything. To my wonderful partner Olivia, the best thing to come out of moving to Townsville and completing my PhD has been that it lead me on a path towards meeting you. For always providing me with inspiration and motivation when it was lacking, I am very thankful. To Olivia's parents, Nigel and Lena, I am also incredibly thankful. Without the support you have provided to me during my time in Sweden, none of this would have been possible.

General abstract

Despite exponential increases in the size, number, and coverage of protected areas (PAs), biodiversity continues to decline worldwide. Additionally, emerging evidence shows that PAs are often located in 'residual' areas, locations with minimal value for extractive activities, such as agriculture, development, mining and fishing. Over recent decades, systematic conservation planning (SCP) has developed new and sophisticated methods for ensuring that protected areas are complementary and representative, so that PA networks avoid redundancy and maximise biodiversity within their bounds. However, the SCP literature has few analyses that aim to maximise conservation impact. Impact is measured as the difference in biodiversity outcomes that occur when a given conservation intervention is applied, compared to when it is not (referred to as a 'counterfactual' scenario). As a result, many modern approaches to SCP have questionable impact, and might do little to counteract residual biases and ongoing biodiversity declines.

The goal of my thesis is develop methods for estimating impact in SCP, and to use these methods to compare alternative spatial prioritisation strategies. To achieve this goal I set three objectives:

1. Establish a framework for using counterfactual-based impact estimation in conservation planning
2. Estimate and compare the impact of currently widespread conservation prioritisation strategies
3. Develop evidence-based spatial prioritisation strategies (i.e. 'rules of thumb') for cost effectively maximising impact in conservation planning

In the first chapter, I introduce the concept of systematic conservation planning, and discuss modern approaches to conservation impact evaluation. I then identify four key knowledge gaps with respect to incorporating impact evaluation into conservation planning using counterfactual methods: (1) What methods can be used to implement counterfactual scenarios and estimate impact in spatial conservation prioritisation? (2) How effective are modern approaches to spatial conservation prioritisation at achieving impact? (3) What is the spatial relationship between threats and costs, and how does this affect conservation prioritisation to maximise impact? (4) How should we prioritise areas for conservation based on spatial patterns of costs, biodiversity, and threats?

In the second chapter, I first address Objective 1 by developing a theoretical model to explore how the impact of alternative prioritisation strategies, compared to a counterfactual, can vary according to various factors. I compare two alternative

prioritisation strategies: protecting high-threat frontier areas, or low-threat wilderness areas. I explore how the relative efficacy of either strategy compared to the counterfactual scenario varies depending on spatial patterns of threats, biodiversity values, conservation costs, timeframes within which impacts are measured, rates of biodiversity recovery, and temporal changes in threats. In doing so, this chapter also contributes to Objective 3, by identifying circumstances under which either frontier prioritisation, wilderness prioritisation, or a combination of both are likely to be most effective.

In the third chapter, I further contribute to Objective 3 by aiming to quantify the spatial relationship between acquisition costs and threats to biodiversity using empirical data in a conservation landscape. As I show in the prior chapter, this spatial distribution has a large influence on the cost-efficiency of any given prioritisation strategy. In this chapter, I use high-resolution datasets of rates of vegetation clearance in Queensland, Australia. I then combine this data with land sales transactions, land valuations, and agricultural profitability to examine the spatial relationship. I then use a classic economic model to explore the potential drivers behind this relationship. I found that counter to what is widely assumed in conservation science, there is no clear spatial relationship between rates of land clearing and acquisition costs, and the relationship displays enormous variability. As a result, the landscape appears to contain a large number of sites with relatively low cost and potential for high impact.

In the fourth chapter, I address all three objectives by implementing an *ex post* method to measure counterfactual outcomes and estimate impacts for several alternative prioritisation strategies. This chapter also uses the case study of Queensland, Australia. With the *ex post* method, the counterfactual scenario is measured using historical changes in vegetation in a landscape with no protected areas. I then retrospectively implement alternative prioritisation strategies and predict how outcomes might have differed compared to the counterfactual. Specifically, I compare four alternative prioritisation strategies: cost minimisation; threat prioritisation and cost minimisation; representation and cost minimisation; and representation, threat prioritisation and cost minimisation. These alternative strategies represent the extremes of how much importance should be placed on costs, threats and biodiversity when aiming to maximise impact. I find that the most effective strategy to maximise impact is to prioritise high-threat locations, and that aiming to achieve representation targets, a widely adopted practice in conservation planning, can be counter-productive to achieving impact.

In the fifth chapter, I provide an alternative method to estimating impacts, which is to use *ex ante* predictions of expected outcomes in counterfactual scenarios and when alternative strategies are implemented. In this chapter, I estimate the impact of several strategies on the coral reefs of Micronesia: frontier prioritisation; wilderness prioritisation; representation; and representation with connectivity. This chapter complements the previous chapter by providing a method for estimating impacts when historical data on changes in biodiversity are unavailable, and when aiming to estimate impacts over long timeframes. Importantly, this chapter incorporates an additional component to measuring impact, which is to compare all strategies to a 'best-case' scenario, where biodiversity outcomes are known and impact can be optimised. Comparing strategies to a counterfactual and best-case allow absolute impacts to be measured. In this chapter I also find that the most effective strategy is generally to prioritise high-threat frontier areas, and that representation targets can be counter-productive to maximising impact.

In achieving the above objectives and addressing the respective knowledge gaps, my thesis provides an important contribution towards incorporating counterfactual-based impact estimation in conservation planning. The global protected area network is expanding at an exponential rate, yet little is known about how well the strategies to spatially allocate these protected areas achieve positive conservation impacts. Given the severity and imminence of global biodiversity declines, it is essential that we develop an evidence base from which conservation policy and practice can draw upon to ensure that future conservation efforts can efficiently maximise impact and prevent further declines.

Statement of contribution of others

Research funding

Australian Postgraduate Award (stipend for 3.5 years)	$90,000 AUD
Grant from Prof. Robert Pressey (ARC CoE funding allowance)	$4,500 AUD
ARC CoE Higher Degree Research Enhancement Scheme	$2,000 AUD

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Distinguished Professor Rober L. Pressey, Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Australia

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Editorial support

Chapter 1: Robert Pressey, Rebecca Weeks

Chapter 2: Robert Pressey, Michael Bode, Rebecca Weeks

Chapter 3: Robert Pressey, Michael Bode

Chapter 4: Robert Pressey, Michael Bode, Rebecca Weeks

Chapter 5: Robert Pressey, Rebecca Weeks, Alastair Harborne

Chapter 6: Robert Pressey, Rebecca Weeks

Outputs related to thesis

Published articles

Sacre, E., Bode, M., Weeks, R. & Pressey, R.L. (2019). The context dependence of frontier versus wilderness conservation priorities. *Conservation Letters*, 12, e12632. (Publication associated with Chapter 2)

Sacre, E., Pressey, R.L. & Bode, M. (2019). Costs are not necessarily correlated with threats in conservation landscapes. *Conservation Letters*, e12663. (Publication associated with Chapter 3)

Articles in preparation

Sacre, E., Weeks, R., Bode, M., Pressey, R. (in preparation). An empirical, counterfactual-based impact assessment of alternative conservation prioritisation strategies. *Conservation Science and Practice*.

Sacre, E., Weeks, R., Pressey, R. (in preparation). Developing a systematic conservation planning framework to maximize the impact of marine protected areas. *Frontiers in Ecology and the Environment*.

Other outputs throughout candidature

Published articles

Toon, A.*, Sacre, E.*, Fensham, R.J. & Cook, L.G. (2018). Immigrant and native? The case of the swamp foxtail *Cenchrus purpurascens* in Australia. *Diversity and Distributions*, 24, 1169–1181.

*A. Toon and E. Sacre should be considered as joint first authors

Conference presentations

Sacre, E., Weeks, R., Pressey, R. (2017). Protect the far and safe or the near and threatened? Measuring the impact of reactive and proactive conservation strategies on the coral reefs of Micronesia. *Australian Coral Reef Society Conference 2017*.

Chapter 1

General introduction

1 General introduction

The earth is currently in a state of rapid biodiversity loss (Dirzo & Raven 2003; Hoekstra et al. 2005; Butchart et al. 2010; Ceballos et al. 2015). Such biodiversity loss occurs when the rate of biodiversity decline (e.g. through extinction or population declines) exceeds the rate of biodiversity creation (e.g. through speciation or population expansion). When over 75% of the species on Earth are lost within short geological timeframes (i.e. over several million years), the event is referred to as a "mass extinction". The earth is generally considered to have suffered five mass extinction events, and many scientists argue that we are currently undergoing a sixth (Wake & Vredenburg 2008; Barnosky et al. 2011). Although one might contend that such extinction events are natural processes, the current crisis is particularly alarming because it appears to be occurring at a rate beyond that of prior extinction events (Barnosky et al. 2011), and might therefore have unexpected and irreversible consequences for Earth's biodiversity. As such, the widespread loss of Earth's natural ecosystems represents a serious existential threat, not only for the living creatures that comprise these ecosystems, but also for humans that depend on them.

The current biodiversity crisis appears to have begun approximately 40,000 years ago, coinciding with the range expansion of *Homo sapiens* to new continents, and the invention of sophisticated hunting tools and techniques (Dirzo & Raven 2003). The range and population of *Homo sapiens* has continued to expand to this day, and along with unprecedented advances in technology and continued exploitation of natural resources, has caused accelerating declines in biodiversity worldwide (Pimm et al. 2006; Dirzo et al. 2014). Today, declines in biodiversity are generally attributed to habitat destruction and fragmentation, climate change, pollution, invasive species and pathogens, and the harvesting of natural resources.

Because we cannot feasibly create biodiversity, and biodiversity creation will only naturally occur over evolutionary timeframes, the most practical solution to the imminent biodiversity crisis is to prevent the loss of biodiversity. The goal of conservation is to do exactly that by minimising the negative impacts of human activities on biodiversity.

1.1 Conservation policy and protected areas

Origins and adoption of conservation policy

Conservation is not a modern invention, but dates back many centuries. Some of the earliest conservation practices existed in Africa and Asia, serving to protect sacred habitats of spiritual and religious importance (Chandrashekara & Sankar 1998). Other early conservation actions had pragmatic objectives, such as preventing the overharvesting of game, timber, or wild food plants, and the minimisation of erosion. One of the earliest examples of conservation policy with such objectives is that of the French in Mauritius in the early 18th century, who designated forest reserves to prevent erosion and overharvesting of timber, along with other conservation measures, such as reforestation programmes and the control of invasive goat populations (Grove 1992, 1993). It is clear, therefore, that humans have had a good understanding of the importance of conserving natural habitats for some time, whether for the sake of self-preservation, or for ethical reasons.

Protected areas

A myriad of conservation techniques have been developed to stem the loss of biodiversity caused by human activities. These include, but are not limited to: protected areas (PAs), where activities that might threaten biodiversity are legally restricted or prohibited within their bounds; regulation, whereby activities that might threaten biodiversity are legally constrained (e.g. vegetation clearing limits, carbon emissions quotas, fishing gear restrictions and catch quotas); restoration programmes (e.g. revegetation, population rehabilitation); and pest control (e.g. eradication of invasive species).

The most extensively adopted conservation technique is the establishment of protected areas (PAs). The International Union for Conservation of Nature (IUCN) defines a protected area as "a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (UNEP-WCMC et al. 2018).

Today, PA targets are an integral part of international and national policy (Barrett 1994, 1997; Finus et al. 2017). Many bilateral and multilateral environmental agreements exist between most of the major countries in the world, and PA targets are often explicit in these agreements. The Convention on Biological Diversity, for example, is a multilateral treaty containing 168 signatories across the world. One of the widely cited strategic goals of this plan, Aichi Biodiversity Target 11, is that "by 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes" (Secretariat of the Convention on Biological Diversity & United Nations Environment Programme 2014).

In accordance with national and international conservation policies, the number and size of PAs has increased exponentially (Figure 1.1). As of 2018, the number of PAs on Earth is estimated to be 238,563 (UNEP-WCMC et al. 2018). These PAs cover an estimated 14.9% of land, approximately 20 million square kilometres, and 7.3% of the world's oceans, approximately 26 million square kilometres (UNEP-WCMC et al. 2018).

For the purposes of this thesis, I focus particularly on PAs as a tool for conservation. Specifically, I focus on PAs for the following reasons: (1) as I describe above, the use of, and funding towards, the implementation of PAs has increased dramatically over recent years (Figure 1.1); (2) PA targets are an integral part of international and national conservation policy (Secretariat of the Convention on Biological Diversity & United Nations Environment Programme 2014); and (3) there is now widespread evidence to suggest that PAs are an effective tool to mitigate biodiversity losses within their borders (Halpern & Warner 2002), assist in the recovery of degraded natural resources (Roberts 2001; Russ et al. 2004), and improve the welfare of nearby human populations (Naughton-Treves et al. 2005; Naidoo et al. 2019).

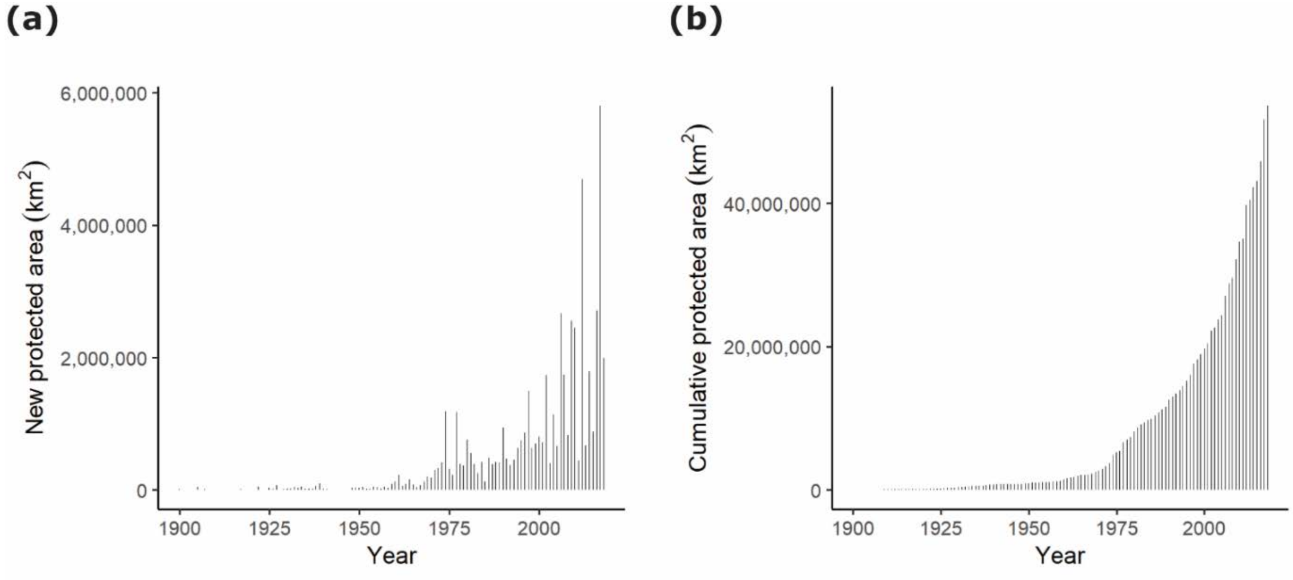

Figure 1.1 The global coverage of protected areas from the years 1900-2018. Panel (a) represents the total area covered by newly implemented protected areas each year. Panel (b) represents the cumulative area protected.

1.2 The modern conservation process and the systematic design of protected area networks

The conservation process

The modern conservation process contains multiple stages (Figure 1.2). In Figure 1.2, I provide a simplified framework of the general conservation process, adapted from (Pressey et al. 2015). The first stage is the formulation of policy goals, objectives and targets. This stage is the most influential, because it dictates the procedure of all subsequent stages. The second stage is the planning stage, which involves developing an action plan based on the stated goals and objectives, and identifying priority areas for conservation action. This stage also involves consultation with stakeholders, such as members of the local community, landowners, and representatives of economic sectors that might be affected by the conservation intervention. The conservation plan might then be modified according to input from these stakeholders. The third stage is the implementation stage, in which the conservation plan is enacted. This stage might involve ratification of international treaties, legislation by state and/or federal governments, or formal agreements with landowners or communities with resource tenure. A key part of this stage involves ongoing management and monitoring of conservation actions (e.g. patrolling of protected areas, policing of fish catch quotas, pest control). The final phase of the conservation process is the evaluation phase, in which conservation outcomes are measured and the contribution of interventions to conservation objectives is assessed.

As I describe in Figure 1.2, *a priori* assumptions about how conservation goals, objectives and targets lead to conservation actions must be made prior to the initiation of the conservation process. This should ideally then initiate an adaptive loop, in which conservation outcomes are assessed, and conservation goals are redefined according to *a posteriori* knowledge of conservation outcomes. Failure to re-formulate objectives according to this adaptive loop ensures that the conservation process will continue to be constrained by *a priori* belief systems, rather than evidence, and could lead to conservation actions that make little difference to desired outcomes (Pressey et al. 2017).

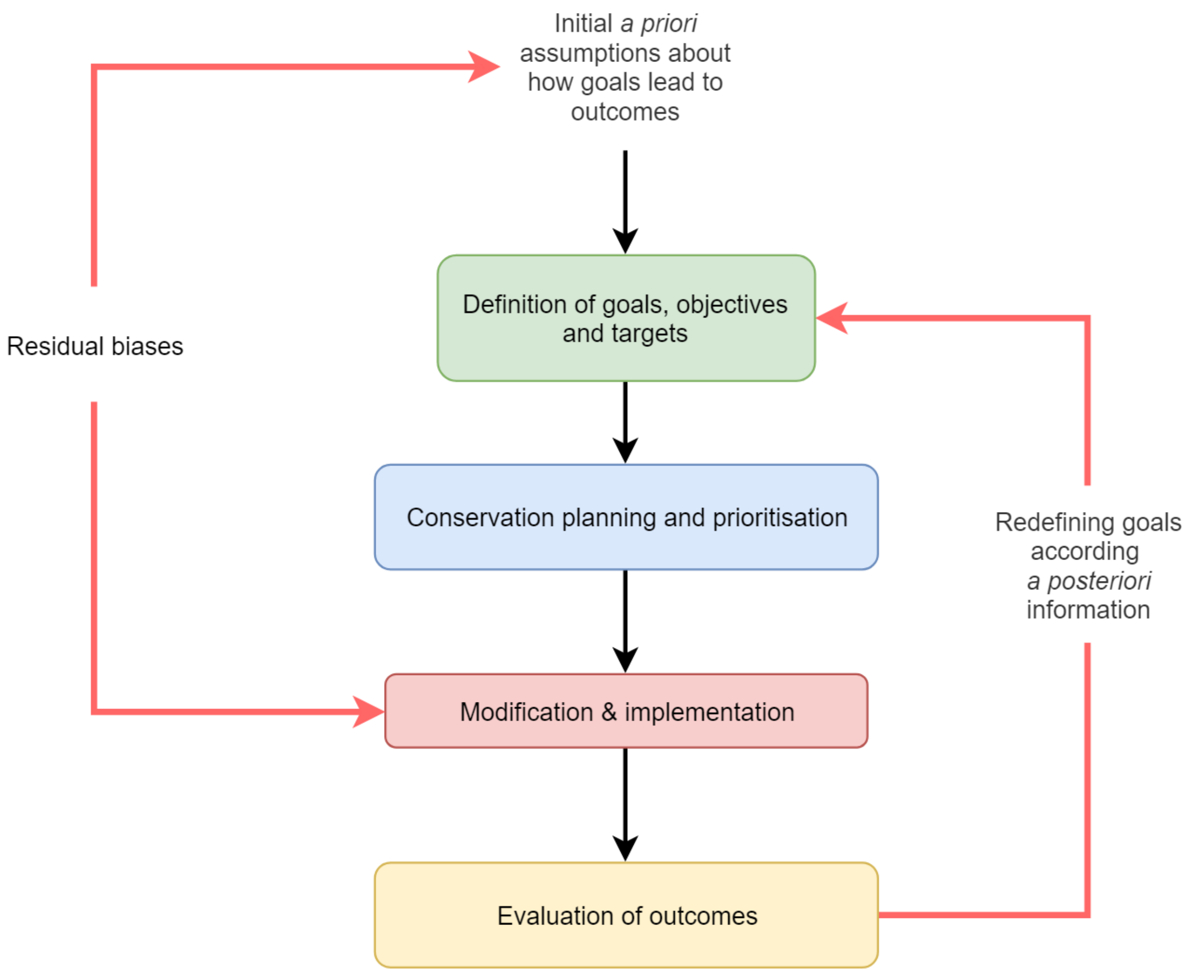

Figure 1.2 Flow chart of the conservation process.

Systematic conservation planning

With widespread adoption of broad-scale conservation policies across the planet has come rapid evolution of the second stage of the conservation process: planning. Prior to the 21st century, conservation planning was predominantly *ad hoc* in nature (Pressey et al. 1993). That is, conservation strategies were typically devised in response to local biodiversity concerns (e.g. declines in game populations, degradation of popular tourist sites), without consideration of the contribution of these interventions to broader or strategic conservation objectives. Over recent decades, a new approach referred to as systematic conservation planning (SCP) has come to fruition, with the aim of developing methods to more efficiently achieve broad conservation objectives (Margules & Pressey 2000; Pressey & Bottrill 2009; Kukkala & Moilanen 2013).

In their seminal paper, Margules & Pressey (2000) describe the steps involved in SCP, which was subsequently adapted by Pressey & Bottrill (2009):

1. Scoping and costing the planning process
2. Identifying and involving stakeholders
3. Describing the context for conservation areas
4. Identifying conservation goals
5. Collecting data on socio-economic variables and threats
6. Collecting data on biodiversity and other natural features
7. Setting conservation objectives
8. Reviewing current achievement of objectives
9. Selecting additional conservation areas
10. Applying conservation actions
11. Maintaining and monitoring conservation areas

A systematic approach resolves many inefficiencies that arise from an *ad hoc* approach. For example, a systematic approach ensures that additional conservation interventions focus on protecting biodiversity features that are under-represented in an existing reserve network, and avoids the redundant protection of features that are already well represented. This concept, referred to as 'complementarity' is one of many attributes that SCP considers when designing reserve networks. Other attributes typically considered in SCP include efficiency, adequacy, representativeness, comprehensiveness, vulnerability, threat, irreplaceability, and persistence (Kukkala & Moilanen 2013). In Table 1.1, I define each of these attributes. For a more detailed history and summary of the attributes and concepts of SCP, see Kukkala & Moilanen (2013).

It should be noted that this thesis is concerned primarily with the spatial 'prioritisation' component of conservation planning. Spatial prioritisation is the part of the conservation planning process concerned with the identification of priority areas for conservation based on socioeconomic, ecological, biological and geographic data.

Table 1.1 Definitions of the attributes typically considered in systematic conservation planning and prioritisation, adapted from Kukkala & Moilanen (2013). Throughout this thesis I refer to these attributes according to the definitions below.

Attribute	Description
Cost	Costs represent any undesirable outcome from a conservation intervention. These are typically considered in financial terms, such as the acquisition costs of land, opportunity costs through forgone profits (e.g. lost agricultural areas), or transaction costs involved in the establishment of protected areas. The types of economic costs of conservation are summarised by Naidoo et al. (2006). Costs need not always be financial in conservation planning. For example, conservation plans might also consider the socio-political costs of conservation interventions, such as the recreational, traditional, or spiritual values of locations to stakeholder groups.
Efficiency	Efficiency relates to cost-effectiveness, which is calculated as conservation returns divided by conservation costs. More efficient plans achieve the same objectives at lower costs.
Comprehensiveness	The comprehensiveness of a reserve network is typically defined as the degree to which broadly defined features such as ecoregions or bioregions are sampled.
Representativeness	The representativeness of a reserve network is typically defined as the degree to which all biodiversity features of interest within broadly defined features are protected within the network. If we expect our targeted biodiversity features to be a true representation of biodiversity, then we expect both comprehensiveness and representativeness to be achieved.
Complementarity	Complementarity refers to the extent to which parts of a reserve network complement, rather than unnecessarily duplicate, one another in the features they contain. The concept of complementarity is closely related to representativeness and comprehensiveness and to cost and efficiency. Reserve networks based on complementarity can maximise representativeness for a given cost or minimise the cost of representing all features.
Threat	Threats are any processes that cause the loss of biodiversity.
Vulnerability	Vulnerability has been defined in terms of three dimensions related to threats: exposure, or the likelihood of threats operating over some time frame; intensity of threats when they occur; and the variable responses of biodiversity features. The terms threat and vulnerability are often used interchangeably in the conservation literature.
Irreplaceability	Irreplaceability is the likelihood that a particular area will be required to achieve biodiversity targets. Highly irreplaceable areas will contribute greatly to representativeness or connectivity because they contain rare features and/or large amounts of less rare features.
Persistence	Persistence is the maintenance of biodiversity in protected areas. The persistence of biodiversity within protected areas might be affected by various factors, such as population size, management effectiveness (e.g. preventing illegal activities within protected areas, eradication of invasive species), connectivity between protected areas, and other external factors (e.g. climate change).
Adequacy	Adequacy is the degree to which biodiversity targets are sufficient to maintain the persistence of biodiversity. If targets are inadequate, biodiversity features, even if protected, might fail to persist.
Impact	Impact is the causal effect of conservation action. Measuring conservation impact requires comparing outcomes to a counterfactual scenario in which no intervention is applied. Impacts are typically measured as biodiversity outcomes, such as changes in species richness or biomass. Achieving targets for any of the above attributes does not necessarily equate to achieving impact. However, particular conservation strategies that achieve certain targets for the above objectives might lead to positive (or negative) impacts.

1.3 Residual biases in conservation

Despite the efforts of modern conservation, there exists a strong bias in the global PA network towards protecting areas that are remote and have little value for extractive uses (Scott et al. 2001; Joppa & Pfaff 2009; Devillers et al. 2015; Venter et al. 2017). Such areas are often referred to as "residual" areas (Devillers et al. 2015; Vieira et al. 2019) - areas that have minimal economic value. Residual PAs typically arise when organisations seek to avoid placing PAs in locations that might adversely affect stakeholder groups, such as fishers, farmers, or extractive industries (mining, oil & gas, etc.). When PAs are established in areas from which these stakeholders gain economic value, they incur an opportunity cost, both to the stakeholders themselves and, consequently, to the politics and economy of the state or country (Naidoo et al. 2006).

Establishing PAs in areas that will not have adverse economic consequences is, of course, desirable (i.e. maximising efficiency). However, a paradox arises when one seeks to minimise economic opportunity costs while also conserving biodiversity features. Namely, the economic activities to which we seek to minimise opportunity costs are often the same activities that threaten biodiversity, and the very activities we seek to prevent by establishing PAs. Therefore, when developing cost-efficient plans, residual PA systems can arise when too much importance is placed on biodiversity-centred attributes (e.g. representation, comprehensiveness, connectivity) and too little importance is placed on threat-centred attributes (e.g. vulnerability, persistence).

This paradox highlights an important and highly consequential dilemma that exists in conservation. How can we cost-effectively prevent the loss of biodiversity? It also highlights many gaps that exist in the conservation science literature. Much of the literature has thus far focussed on how to systematically design cost-effective PA networks that maximise the attributes described in Table 1.1. The literature, however, contains very few analyses focussing on how we can design cost-effective PA networks that maximise impact, which is the primary goal of conservation.

1.4 Conservation impact and evidence-based conservation planning

Evidence-based impact evaluation

With recognition of the residual bias in conservation has come calls for more rigorous methods to inform conservation policy, planning and practice (Ferraro & Pattanayak 2006; Ferraro 2009; Ferraro & Pressey 2015; Pressey et al. 2015). In other scientific fields, causal inference relies on comparing outcomes of treatment groups to control groups, to which no treatment programme is applied. In the field of medicine, for example, drug treatments are considered effective only if it can be demonstrated through clinical trials that the desired outcomes (e.g. remission from disease) are statistically greater in treatment groups than in control groups. In impact evaluations, the equivalent of a control group is referred to as the 'counterfactual' scenario, which can be defined as the outcomes that occur when no intervention is applied (Ferraro 2009).

Such counterfactual-based impact evaluations have hitherto been rare in conservation science due to the far greater challenges involved compared to other fields. Conservation is typically concerned with outcomes over large scales, long time periods, and in contexts where interventions can be highly consequential, such as those involving declining fisheries that support local livelihoods. As a result, experimental impact evaluations in conservation are typically small in scale and short in timeframe (e.g. Wiik et al. 2019). However, quasi-experimental techniques are now gaining traction in the conservation literature to allow impact evaluations of conservation interventions over large scales (e.g. Naidoo et al. 2019). When estimating the impact of PAs, these typically involve matching techniques, which match PAs to counterfactual areas based on the similarity of various attributes that might affect outcomes, such as elevation, soil type, and distance to human centres (Andam et al. 2008; Joppa & Pfaff 2011; Ahmadia et al. 2015; Jones & Lewis 2015).

Evidence-based conservation planning

While counterfactual-based impact evaluation is useful for identifying residual biases and measuring the efficacy of conservation interventions, it is not in itself a solution to the residual problem. Instead, the solution lies in framing conservation goals and objectives in terms of conservation impact prior to the implementation and evaluation phases of the conservation process, so that residual biases do not carry over to subsequent phases (Figure 1.2; Ferraro & Pressey 2015; Pressey et al. 2015; Visconti et al. 2015). However, rarely are objectives in conservation planning set with the aim of maximising impact. Instead, plans typically set objectives that are tangential to maximising impact, such as achieving arbitrary targets for the attributes defined in Table 1.1.

Incorporating counterfactual methods in conservation planning presents a unique challenge beyond that of impact evaluation: conservation planners attempting to maximise conservation impact must predict the impact of PA networks prior to their implementation. This can only be achieved using predictive methods (as opposed to descriptive methods; Figure 1.3). Descriptive methods for measuring impact include the experimental and matching procedures I describe above. Predictive methods, on the other hand, seek to estimate the impact of spatial prioritisation strategies using models of changes in biodiversity in response to conservation action. Although these methods are accompanied by the assumptions involved in predictive modelling (Figure 1.3), they overcome many of the limitations of descriptive methods. A predictive modelling approach has two uses for conservation planning. First, in data rich regions, it can be used to estimate the impact of protecting specific areas, and can be used to directly inform spatial prioritisation within a region. Second, it can be used to establish 'rules of thumb' for spatial prioritisation in other regions where impacts have yet to be estimated, or where the datasets necessary to do so are unavailable. Rules of thumb might include strategies that attempt to achieve targets for any of the objectives described in Table 1.1. Importantly, planners working in data-poor regions can draw upon these analyses to develop evidence-based plans with the objective of maximising impact.

Strategies for impact maximisation

A large part of the SCP literature has focussed on the debate over what level of relative importance should be placed on the attributes in Table 1.1 (Kukkala & Moilanen 2013). Those attributes can be grouped into the three broad groups: cost-centred, biodiversity-centred, and threat-centred. In recent years it has become apparent that threat-centred attributes have received little attention compared to those related to both cost and biodiversity. However, threat is an important component of conservation planning and one that is clearly necessary to avoid residual conservation. As a result, research has emerged that aims to quantify threats for use in spatial prioritisation, and develop strategies for their incorporation into SCP (Wilson et al. 2005; Visconti et al. 2010b; Kuempel et al. 2019). Although we should clearly prioritise sites of low cost and high biodiversity value, the best strategy to prioritise locations based on threat is less clear. Should we prioritise low-threat wilderness areas, or high-threat frontier areas? As I describe above, cost and threat objectives might be antagonistic. As such, there are likely to be trade-offs between cost, biodiversity and threat. An important knowledge gap, therefore, exists in the literature concerning how areas should be prioritised based on spatial patterns of cost, biodiversity and threat to maximise impact.

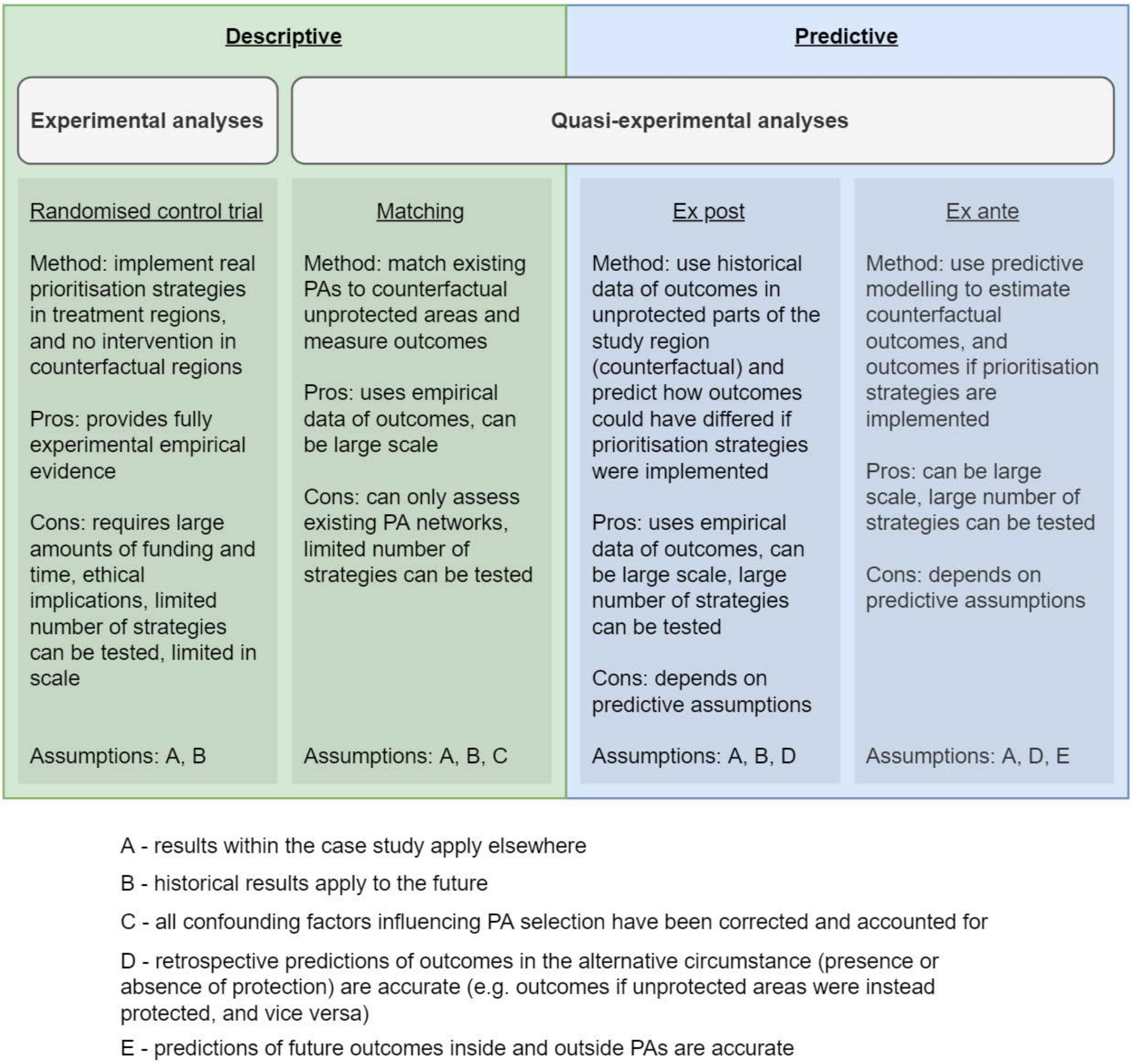

Figure 1.3 Alternative methods to implement counterfactual scenarios in conservation impact evaluation. The descriptive methods are useful for impact evaluation after the fact, to measure real outcomes. However, descriptive methods are limited in their ability to compare and estimate impacts of several alternative large-scale conservation prioritisation strategies. In conservation planning, with the goal of designing and comparing strategies, predictive methods are more useful.

1.5 Thesis goal and objectives

The primary goal of this thesis is to develop methods for estimating counterfactual outcomes and impact in spatial conservation prioritisation, and to use these methods to develop prioritisation strategies to maximise impact. To achieve this goal, I have set three objectives (Figure 1.4):

1. Establish a framework for using counterfactual-based impact estimation in conservation planning
2. Estimate and compare the impact of currently widespread conservation prioritisation strategies
3. Develop evidence-based spatial prioritisation strategies (i.e. 'rules of thumb') for cost-effectively maximising impact in conservation planning

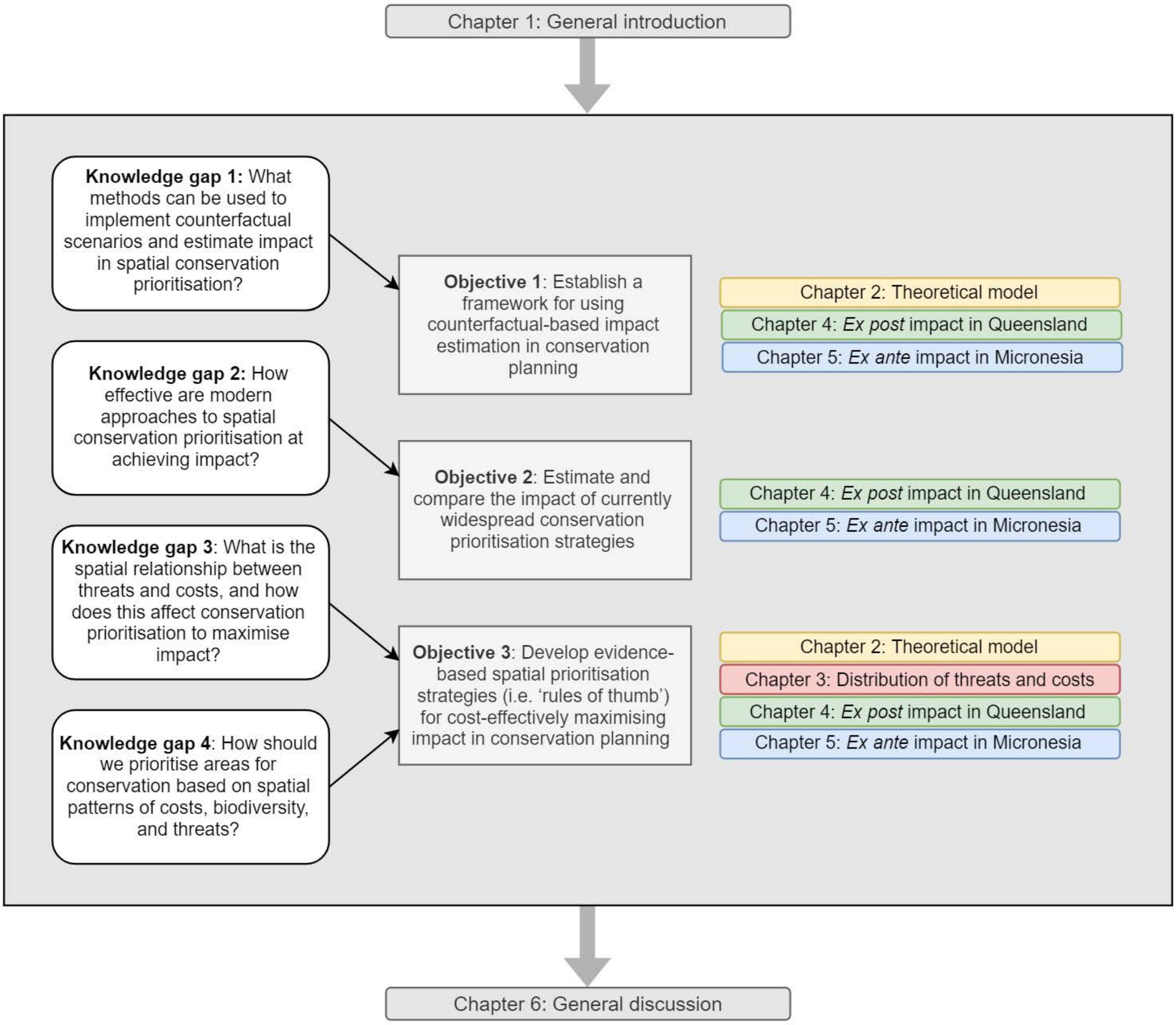

Figure 1.4 A schematic diagram of knowledge gaps and objectives addressed in this thesis, and which chapters contribute to achieving each objective.

1.6 Thesis outline

This thesis contains five chapters that aim to meet the objectives specified in the section above. Below I provide a summary of each chapter and how it addresses each of the relevant objectives.

Chapter 1: Introduction (present chapter)

In Chapter 1, I outline four important knowledge gaps present in the conservation science literature that this thesis aims to address (Figure 1.4): (1) What methods can be used to implement counterfactual scenarios and estimate impact in spatial conservation prioritisation? (2) How effective are modern approaches to spatial conservation prioritisation at achieving impact? (3) What is the spatial relationship between threats and costs, and how does this affect conservation prioritisation to maximise impact? (4) How should we prioritise areas for conservation based on spatial patterns of costs, biodiversity, and threats?

Chapter 2: The context-dependence of frontier versus wilderness conservation priorities

Chapter 2 first contributes to achieving Objective 1 by providing a theoretical foundation for the subsequent chapters. In Chapter 2, I formulate a basic model in which planners must allocate conservation funding between two regions: high-threat frontier areas or low-threat wilderness areas. The impact of protecting either region is determined by several factors, including costs, the severity of threats, initial biodiversity values, rates of biodiversity recovery after protection, and the timeframe within which impacts are measured. The impact of each is strategy is then compared to a counterfactual strategy in which neither location is protected. Chapter 2 also addresses Objective 3, which sets out to determine effective prioritisation strategies to maximise impact. In Chapter 2, I explore how variation in costs, threats, and aspects of biodiversity can affect which strategy has the greatest impact. In doing so, I aim to identify scenarios in which a given prioritisation strategy is generally most effective, to assist planners in determining which strategy is likely to achieve the greatest impact under a given set of circumstances.

Chapter 3: The spatial relationship between conservation costs and threats to biodiversity

Chapter 3 builds on the theoretical analysis of Chapter 2 by utilising empirical data to quantify the spatial relationship between costs and threats. As I explain in the sections above, our understanding of spatial patterns of threats and how these correlate with costs and biodiversity is key to determining which locations should be prioritised. It is often assumed in conservation prioritisation that locations facing high levels of threat are also more costly to protect. However, there is little empirical evidence to support this assumption. Understanding the spatial relationship between costs and threats is essential to Objective 3: if high-threat locations are disproportionately expensive to protect, spatial prioritisation should seek out low-threat areas. I explore this relationship using high-resolution data on land parcel sales prices and valuations in Queensland, Australia. I then analyse the correlation between these land costs and rates of land clearing subsequent to parcel sales. I also utilise a classic economic model, combined with spatial data on habitats and land use type, to explore what underlying factors might drive spatial patterns of costs and threat. This chapter addresses key knowledge gaps concerning how to prioritise areas based on threat (i.e. frontier versus wilderness) and how to use data on costs, threats and biodiversity to determine which areas efficiently maximise conservation impact.

Chapter 4: A retrospective, counterfactual-based impact assessment of alternative conservation prioritisation strategies

Chapter 4 first addresses Objective 1 by developing a counterfactual-based method for estimating the impact of alternative conservation prioritisation strategies. In this chapter, I implement an *ex post* approach to measuring conservation impact (Figure 1.3), whereby a counterfactual scenario is measured by using empirical data of historical changes in biodiversity in an unprotected region. Specifically, I use data on land clearing and vegetation type to measure changes in biodiversity in Queensland, between 2006 and 2016. I then retrospectively implement several alternative prioritisation strategies and explore how outcomes might have differed if each strategy had been implemented. This chapter also addresses Objective 2, by estimating the impact of the standard approach to conservation prioritisation, which is to achieve representation targets for biodiversity features. Then, I compare this approach to three alternative prioritisation strategies: cost minimisation, threat prioritisation, and representation combined with threat prioritisation. These alternative strategies represent the extremes of how areas can be prioritised based on costs, threats, and biodiversity. This chapter also contributes to Objective 3, which is to determine 'rules of thumb' for which general prioritisation strategies should be advocated or avoided to maximise impact.

Chapter 5: Developing a systematic planning framework to maximise the impact of marine protected areas

Chapter 5 further contributes to Objective 1 by developing an alternative method to estimate counterfactual outcomes and impacts. In Chapter 5, I implement an *ex ante* method for measuring impacts, which uses predictive modelling to estimate how biodiversity changes will occur in the future in a counterfactual scenario and when prioritisation strategies are implemented. I do so using models of fish biomass on the coral reefs of Micronesia. I compare how biomass is expected to change over a period of 50 years when four different strategies are implemented: representation, representation and connectivity, frontier prioritisation, and wilderness prioritisation. Importantly, this chapter incorporates an optimal or 'best-case' strategy, which is an important component of estimating impacts. When both counterfactual and optimal strategies are implemented, each prioritisation strategy can be compared in terms of how much improvement it offered over the counterfactual, and how close it was to achieving optimal impacts. This chapter also contributes to Objective 2 by estimating the impact of the widely adopted representation approach, and to Objective 3 by assessing how well the alternative strategies come to achieving 'best-case' impacts.

Chapter 2

The context-dependence of frontier versus wilderness conservation priorities

Associated publication: Sacre, E., Bode, M., Weeks, R. & Pressey, R.L. (2019). The context dependence of frontier versus wilderness conservation priorities. *Conservation Letters*, 12, e12632.

2 The context-dependence of frontier versus wilderness conservation priorities

2.1 Abstract

Much of conservation planning has focused on how we should prioritise areas for protection based on biodiversity and cost, but less is known about how we should prioritise areas based upon the level of threat they face. In this chapter, I discuss two opposing threat prioritisation strategies: frontier conservation (prioritising high-threat areas) and wilderness conservation (prioritising low-threat areas). Using a temporally-explicit model, I demonstrate that the best strategy depends on a variety of factors, including protection costs, heterogeneity in biodiversity, biodiversity-area relationships, the rate of biodiversity recovery, the rate of change in threats through time, and the timeframe within which we measure conservation outcomes. By quantitatively comparing the impact of these strategies, I aim to shift the debate away from a simple dichotomy of frontier versus wilderness, towards an understanding of the context-specific benefits of each option, and a discussion of how threat combines with other factors to determine spatial conservation priorities.

2.2 Introduction

Systematic conservation planning aims to protect biodiversity features from threats that might compromise their persistence, so that overall biodiversity value is maximised within a planning region (Margules & Pressey 2000). Despite these aims, many approaches to conservation prioritisation consider only biodiversity value and/or conservation costs, without considering threats (e.g. UNEP-WCMC 2008). When threats are not considered, areas unlikely to lose biodiversity might be protected, leading to "residual" protected areas (PAs; Joppa & Pfaff 2009; Devillers et al. 2015). To avoid residual outcomes, sites should be prioritised for protection based upon three key factors: their biodiversity value, the costs of protection, and the imminence and/or severity of threats they face (Pressey & Taffs 2001; Newburn et al. 2006; Wilson et al. 2006; Merenlender et al. 2009; Visconti et al. 2010b).

It is intuitive and widely accepted that sites with high biodiversity value and low cost should be prioritised. However, a serious and fundamental debate remains about whether conservation investment should seek out or avoid sites facing high levels of threat. Some approaches advocate the protection of sites imminently facing high levels of threat (henceforth referred to as "frontier" areas; Hoekstra et al. 2005; Ricketts et al.

2005; Venter et al. 2014). Others advocate the protection of sites facing lower levels of threat, and sites likely to become threatened in the more distant future (henceforth referred to as "wilderness" areas; Mittermeier et al. 2003; Klein et al. 2009; Graham & McClanahan 2013; Watson et al. 2018). Each strategy is supported by cogent arguments: frontier conservation avoids immediate biodiversity losses, while a wilderness strategy can secure large intact areas and pre-empt future threats. All conservation prioritisation frameworks exist on a continuum between frontier and wilderness (Brooks et al. 2006), either explicitly or implicitly, and millions of dollars of conservation funding are allocated accordingly.

In this chapter, my goal is to explore the range of factors (e.g. threats, costs, and biodiversity values) that might influence the relative impact of frontier and wilderness conservation strategies. Several recent analyses have used real conservation landscapes to show how conservation impacts depend upon a suite of factors, including the spatial relationship between threats and costs (Visconti et al. 2010b), the species-area relationship within a region (Spring et al. 2007), and decision-makers' time preferences (Armsworth 2018). However, the size and complexity of these landscapes allow for only one or two factors to be explored. Here I present a theoretical planning landscape in which it is possible to systematically vary and control a range of factors. My aim with this general model is not to provide specific recommendations for particular conservation landscapes, but instead to offer a clearer picture of how multiple factors interact to determine the relative impact of frontier and wilderness strategies. Crucially, I show that both frontier and wilderness strategies can deliver the greatest conservation impact under different conditions, and that in some cases a combination of both strategies is most effective. In doing so, I hope to progress the debate beyond a simple dichotomy, towards an understanding of the conditions that determine which strategy delivers the greatest impacts.

2.3 General conservation model

I integrated the suite of factors that determine conservation impact using a deterministic two-patch landscape, where the objective was to maximise biodiversity value across both patches. In this formulation, one patch faces high levels of threat (frontier patch), while the other faces low levels of threat (wilderness patch). Managers allocate a proportion (0 – 100%) of their conservation budget to each patch, which is then immediately used to purchase and protect land.

For the two-patch system, I quantitatively defined a set of key factors that affect conservation decisions, each of which is commonly discussed in the context of the frontier/wilderness debate (Spring et al. 2007; Visconti et al. 2010b; Armsworth 2018).

These are: the biodiversity value of each patch, the cost of protection (e.g. acquisition, transaction and opportunity costs; Naidoo et al. 2006), the biodiversity-area relationship (i.e. the species-area relationship; Wilson & MacArthur 1967), the proportion of biodiversity unique to each patch, the rate at which biodiversity recovers following protection, the rate of change in threats (static or dynamic), and the timeframe over which conservation benefits are measured. In the discussion below, I use the model to test the effect of each factor, and then draw on examples from the literature to discuss how each factor is likely to influence frontier and wilderness conservation priorities.

Model description

At time t the total extant biodiversity value of the system, S_t, is given by the equation:

$$S_t = s_F\left[\frac{b_F}{c_F} + \left((1-q_F)^t\left(1-\frac{b_F}{c_F}\right)\right)\right]^z + s_W\left[\frac{b_W}{c_W} + \left((1-q_W)^t\left(1-\frac{b_W}{c_W}\right)\right)\right]^z$$

Equation 2.1

where the subscripts F and W denote the frontier and wilderness patches respectively, and s_x is the amount of biodiversity value present in patch x at $t = 0$. The model contains three components: $\frac{b_x}{c_x}$ specifies the proportion of each patch that can be protected, given the budget allocated to each patch (b_x) and the cost of protecting each patch (c_x); $(1 - q_F)^t$ specifies the proportion of unprotected biodiversity remaining in each patch after t years, given the annual loss rate (q_x); and $\left(1-\frac{b_x}{c_x}\right)$ specifies the proportion of this biodiversity loss that occurs according to the proportion of biodiversity that is protected. Protected patches experience no loss of biodiversity value (see Appendix 1 for alternative scenarios). I denote the total budget as $B = b_F + b_W$. The parameter z accounts for the non-linear relationship between area and biodiversity (Murdoch et al. 2007). For consistency with other conservation prioritization analyses, I assumed a value of $z = 0.25$ (Spring et al. 2007; see Appendix 1 for alternative values). To measure relative impact, all strategies were compared to a counterfactual scenario, where neither patch is protected (i.e. $B = 0$).

Analyses

I measured impact across the full range of allocation decisions, ranging from total frontier protection ($b_F = 100$, $b_W = 0$) to total wilderness protection ($b_F = 0$, $b_W = 100$). I then calculated the relative impact of strategies when the key factors were varied in both isolation and combination, while other parameters were kept at their default values (Table A1.1). I focused particularly on changes in the ratio of costs and threats, since frontier areas are often characterised as high-threat/high-cost, and wilderness areas as low-threat/low-cost (e.g. Armsworth 2018). I also considered how strategies performed when the relative biodiversity value of the frontier and wilderness patches changed.

I also considered three structural variations of my base model. In the first, protection allowed biodiversity value to recover in degraded sites. I considered a scenario where the frontier patch was significantly degraded (25% of the default value) but could asymptotically regain its biodiversity value, as reported in analyses of post-disturbance recovery (Liebsch et al. 2008; but see Appendix 1 for alternative scenarios). In the second, I considered how threats might change over time. One proposed benefit of a wilderness strategy is that it can secure large, low-threat areas that might become highly threatened in the future (Watson et al. 2018). Thus, I allowed biodiversity loss in the wilderness patch (q_W) to increase over a period of 100 years until it was equal to that of the frontier patch. This modification assumed a sigmoidal transition from wilderness to frontier, as observed in empirical analyses of forest clearing (Etter et al. 2006). The third structural variant considered the degree of biodiversity complementarity between patches. For this variation, I explicitly defined the proportion of biodiversity value that was endemic to each patch. Full details of all structural variations of the model are provided in Appendix 1.

The parameter and model explorations described in this chapter are only a small subset of the dynamics that can be produced by the conservation model. To facilitate further exploration, I have published an online interactive version of the model, available at https://edmondsacre.shinyapps.io/Patch/, where all parameters can be manipulated, and the impact of alternative prioritisation strategies are graphed accordingly.

2.4 Factors that influence the wilderness versus frontier decision

Costs

Majority protection of the frontier patch generally had the greatest impact on biodiversity value, regardless of costs (Figure 2.1a and 2.1b). However, as the cost of the frontier patch increased, allocating a larger proportion of the budget towards wilderness increased impact, particularly over longer timeframes and when threats were dynamic (Figure 2.1a and 2.1b).

In many real-world contexts, conservation costs are unlikely to be homogeneous between frontier and wilderness areas. Instead, when threats are driven by economically profitable activities, conservation costs and threats might be positively correlated (Merenlender et al. 2009; Boyd et al. 2015). For land clearing in California, for example, Newburn et al. (2006) found that land with a high probability of being converted had high acquisition costs. Similarly, Venter et al. (2014) found that threatened terrestrial vertebrate species were more common in areas with high agricultural land value. While these analyses hint that conservation costs and threats might be linked, there is a paucity of empirical analyses examining this relationship across a range of conservation landscapes (but see Chapter 3; Sacre et al. 2019b). My results suggest that the more positive this relationship, the more resources should be allocated towards wilderness areas.

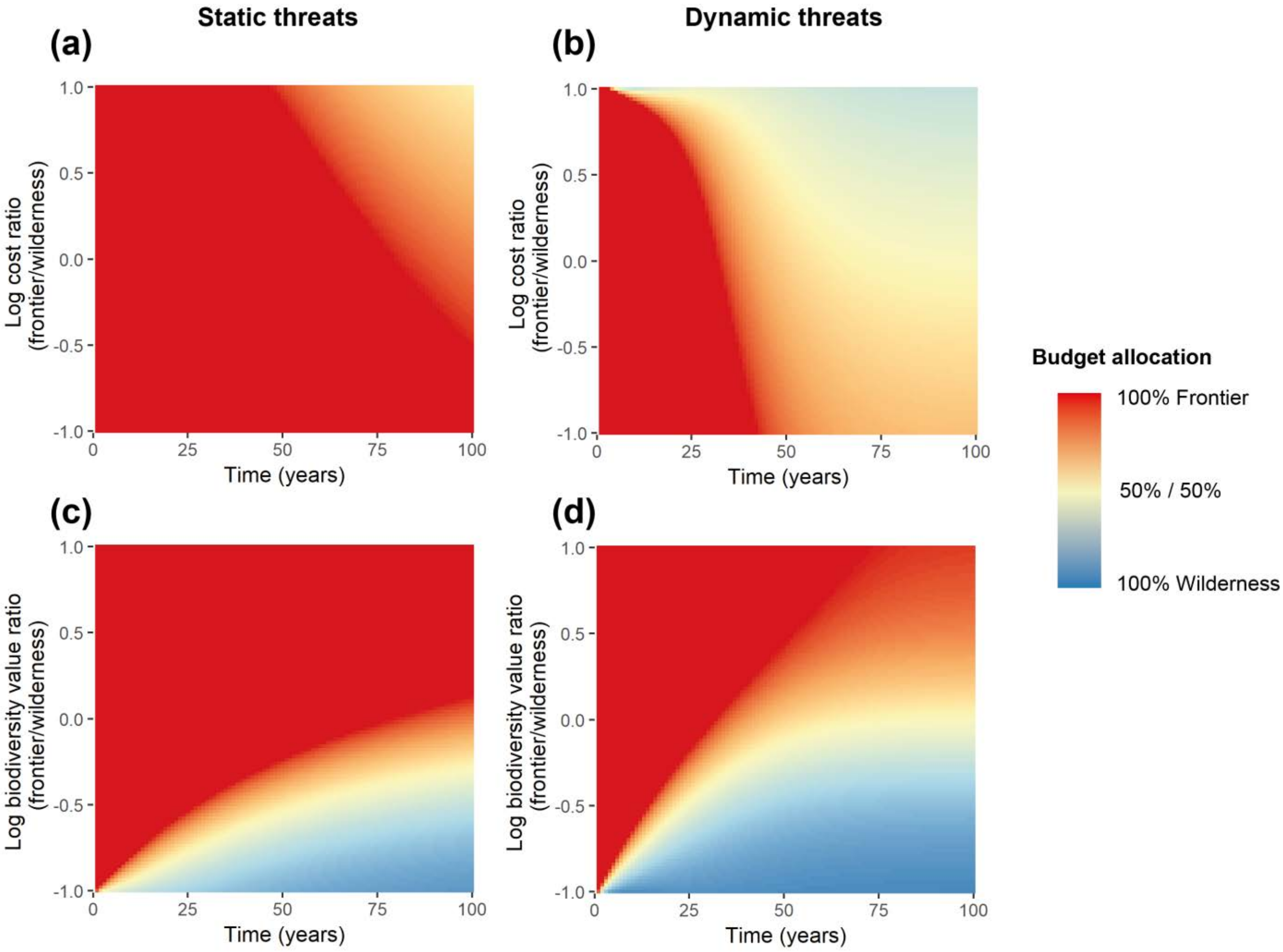

Figure 2.1 Variation in the most effective budget allocation across different time frames. Panels A and B show how the most effective strategy varies according to the ratio of cost between frontier and wilderness patches ($c_F/\ c_W$). The maximum and minimum cost ratios represented on the y-axis of panels A and B is where costs were ten times higher in the frontier patch ($c_F = 1000,\ c_W = 100$) and ten times higher in the wilderness patch ($c_F = 100,\ c_W = 1000$), respectively. Panels C and D show how the most effective strategy varied according to the ratio of biodiversity value between frontier and wilderness patches ($s_F/\ s_W$). The maximum and minimum biodiversity value ratio represented on the y-axis of panels C and D is where biodiversity values were ten times higher in the frontier patch ($s_F = 1000, s_W = 100$) and ten times higher in the wilderness patch ($s_F = 100,\ s_W = 1000$), respectively. Panels A and C represent the most effective strategies when threats were static. In the static threats scenarios, the rate of biodiversity loss in the frontier patch (q_F) and the wilderness patch (q_W) was 10% per year and 1% per year, respectively. Panels B and D represent the most effective strategies when threats were dynamic. In the dynamic threats scenarios, the rate of biodiversity loss in the wilderness patch increased sigmoidally from 1% to 10% over 100 years, while threats remained static in the frontier patch. For all scenarios, untested factors were left at their default values (Table A1.1). Full details of model parameters are available in Appendix 1.

Aspects of biodiversity value

Frontier prioritisation had a greater impact when biodiversity values were equal or higher in the frontier patch (Figure 2.1c and 2.1d). Over shorter timeframes, majority frontier protection was most effective unless the wilderness patch had significantly higher biodiversity value (i.e. more than 5 times greater, Figure 2.1c and 2.1d). However, over longer timeframes, majority wilderness protection became beneficial if the wilderness patch had moderately higher biodiversity value (~2 times higher; Figure 2.1c and 2.1d). The amount of biodiversity overlap between patches had no qualitative effect on conservation impact, but reduced the relative difference between strategies overall (Figure A1.1). When the biodiversity-area relationship was linear ($z = 1$), the same effects occurred, but it became always beneficial to fully protect either frontier or wilderness, while partial protection was always suboptimal (see Appendix 1 for further details).

If we consider anthropogenic threats (e.g. land clearing for agriculture, harvesting of natural resources, pollution) over large extents, then we expect frontier landscapes to have high levels of both threat and biodiversity value (Luck 2007). This is because human populations tend to inhabit productive landscapes that foster high levels of biodiversity (Chown et al. 2003). There is also evidence to suggest that global wilderness areas – because they are often ecologically homogeneous – are relatively species poor (Mittermeier et al. 2003). However, across smaller spatial extents, a negative relationship is often observed, particularly where anthropogenic threats have been present long enough to cause local declines in biodiversity value (e.g. Turner et al. 2004). This scale-dependence adds another dimension to the choice between frontier and wilderness: planners working at regional or national scales (e.g. ecoregions) could justifiably prioritise frontier areas, while planners working at smaller local scales might justifiably focus on areas with greater wilderness value.

The rate of biodiversity recovery

When the frontier patch had a low initial biodiversity value, but could recover following protection, frontier prioritisation had an increased impact (Figures 2.2b and 2.2d). Interestingly, this effect was more pronounced with lower initial biodiversity values of the frontier patch (Figure A1.3), because more degraded patches had higher recovery potential. Thus, frontier prioritisation can produce large gains in biodiversity value, relative to initial conditions, when the frontier patch is substantially degraded but can recover. Furthermore, when the frontier patch had substantial recovery potential, changes to cost had minimal effect on the relative impact of each strategy (Figure A1.4).

Wilderness areas, by definition, are closer to their pristine state and, therefore, are likely to have minimal recovery potential. More degraded frontier areas, on the other hand, might have significant recovery potential. However, such areas might have been degraded to a point that trophic cascades and ecosystem shifts could inhibit recolonisation and habitat recovery after protection. The recovery potential of degraded areas will depend highly upon the proximity and connectivity of degraded and intact habits, and the particular characteristics of habitats within a planning region (Jones & Schmitz 2009). For example, differences in dispersal capabilities between marine and terrestrial species might mean that frontier marine systems have greater recovery potential than terrestrial ones (Carr et al. 2003).

In regions where recovery is unlikely to contribute towards conservation objectives (e.g. the return of extirpated species) or to occur only over long timeframes (e.g. habitats containing slow-growing species), protecting some wilderness areas might be beneficial. In regions where biodiversity is likely to substantially recover within the required timeframes (e.g. habitats containing fast-growing species), frontier prioritisation is likely to have a greater impact.

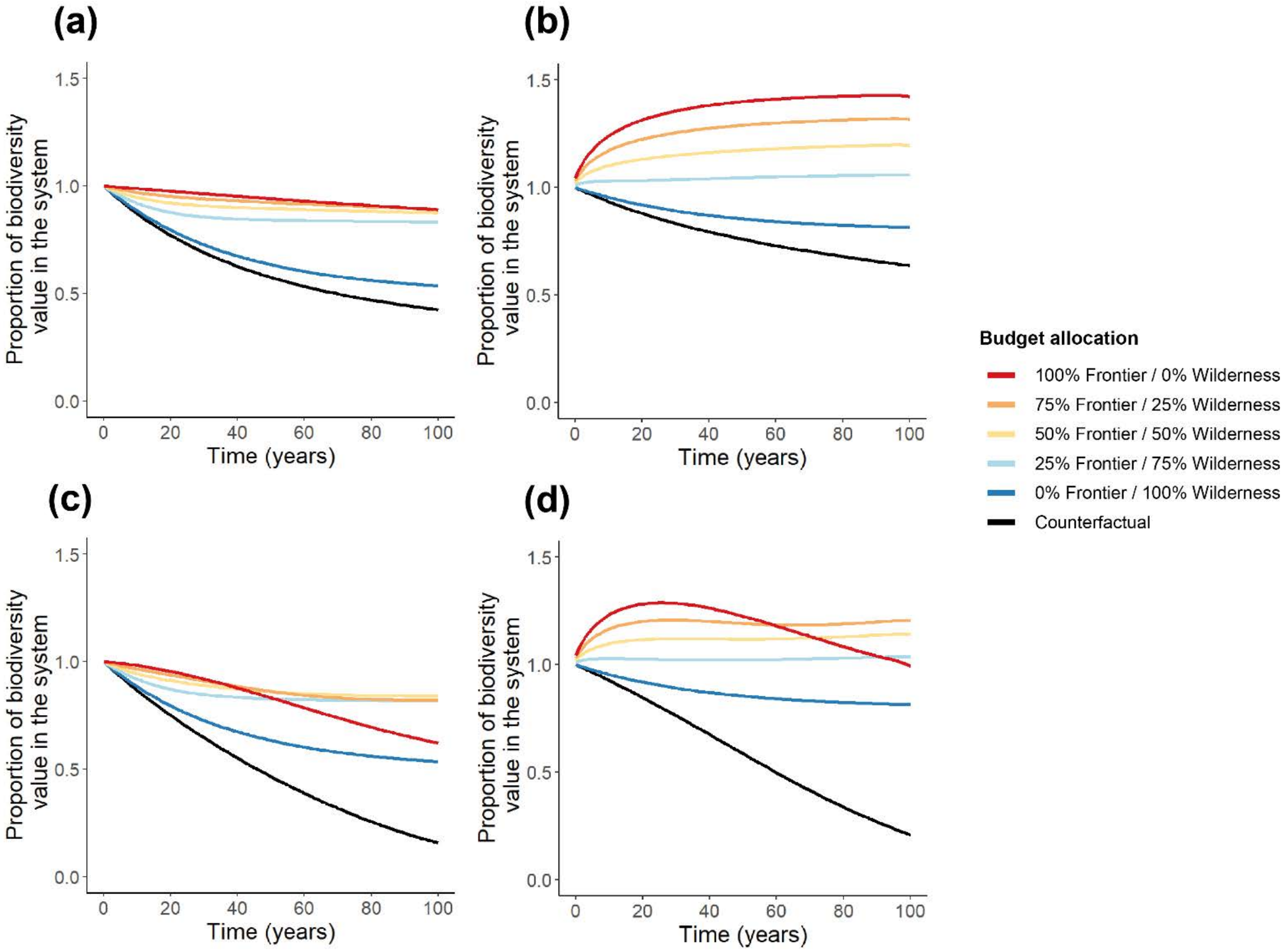

Figure 2.2 The proportion of biodiversity value remaining when different proportions of the budget were allocated to the frontier and wilderness patches. Panel (a) shows the base scenario where all factors were at their default values (Table A1.1). Panel (b) shows a scenario where biodiversity value in the frontier patch was degraded to 25% of its potential value ($s_F = 25$), but could recover to potential levels if protected (see Appendix 1 for more details). Panel (c) shows a scenario where the rate of biodiversity loss was dynamic in the wilderness patch. Panel (d) shows a scenario where biodiveristy value could recover in the frontier patch, and the rate of biodiversity loss was dynamic in the wilderness patch. In the dynamic threats scenarios, the rate of biodiversity loss in the wilderness patch increased sigmoidally from 1% to 10% over 100 years, while threats remained static in the frontier patch. The black line represents a counterfactual scenario in which neither patch was protected. Full details of model parameters and default values for all factors are available in Appendix 1.

Temporal change in threats

When threats increased over time in the wilderness patch, the relative impact of wilderness prioritisation increased (Figure 2.1b, 2.1d and 2.2c). This effect was amplified over time, as the wilderness patch transitioned into a frontier patch. When threats were dynamic, partial protection of both patches also became more effective relative to total frontier or wilderness protection (Figure 2.1b, 2.1d and 2.2c). This is because the biodiversity-area relationship dictated that there were diminishing returns on investment in each patch, and a split protection approach cost-effectively mitigated short-term losses in the frontier patch, and long-term losses in the wilderness patch. This effect was amplified when there was a greater difference in initial threat levels between frontier and wilderness patches (Figure A1.6).

Threat dynamics are important to consider, given extensive evidence that threats change over time (e.g. Sabbadin et al. 2007; Spring et al. 2010). The threat of land development, for example, often follows a "contagion" process, where forested areas that are close to development are cleared, making more distant sites accessible and threatened. Both terrestrial and marine ecosystems exhibit the sigmoidal degradation trajectories that are characteristic of contagion dynamics (Etter et al. 2006; Worm et al. 2009). Such contagion dynamics are a common motivation for wilderness conservation: by undertaking conservation actions before threats arrive, large amounts of future biodiversity loss can be avoided at a relatively low cost. However, because these benefits will be realised in the future, the timeframe over which biodiversity impacts are measured plays a critical role in this scenario, as I explain in the next section.

Timeframe to reach conservation objectives

Wilderness conservation delivered benefits over longer timeframes, at the cost of immediate frontier losses. Conversely, frontier prioritisation performed better over shorter timeframes (Figures 2.1 and 2.2), but became less effective over longer timeframes. When threats were dynamic, losses in the wilderness occurred sooner, reducing the time required until which it became beneficial to prioritise wilderness (Figures 2.1 and 2.2).

The effect of timeframe on frontier and wilderness prioritisation is particularly important because different conservation actors often pursue goals over different timeframes. In Australia, for example, government timeframes range from years (e.g. State of New South Wales and Office of Environment and Heritage 2018) to decades (e.g. Natural Resource Management Ministerial Council 2010). For nongovernmental conservation actors, in contrast, timeframes can extend to centuries (e.g. Pressey et al. 2004). This variation may arise from different political and funding cycles, or from differing objectives. For example, short-term impacts will be most important when conserving endangered species or habitats that face imminent extinction. Similarly, where livelihoods and ecosystem service objectives are concerned, standard economic discount rates, where short-term benefits are favoured over long-term benefits, might be most appropriate (Armsworth 2018). In such cases, frontier prioritisation is likely to have a greater impact. In contrast, where practitioners are working towards long-term goals, wilderness prioritisation might have a greater impact.

2.5 Conclusion

My results demonstrate that the impact of different threat prioritisation strategies can vary dramatically depending on how threats relate to other factors. Furthermore, I have shown that interactions between key factors can amplify or supress the effects of others. For example, costs can heavily influence frontier and wilderness impacts, but this influence is suppressed if frontier areas are degraded and have significant recovery potential, and amplified if threats are dynamic (Figures 2.1a, 2.1b, 2.2b and 2.2d). It is essential, therefore, that conservation practitioners consider these relationships when developing conservation prioritisations. Much of the data required to quantify these processes are readily available. Information on biodiversity values and costs is widespread and commonly used across a variety of conservation contexts, although there are concerns about its accuracy for conservation planning purposes (Adams et al. 2010; Armsworth 2014). Data on recovery potential have been collated in both terrestrial (Liebsch et al. 2008) and marine environments (McClanahan et al. 2016). Even models of threat dynamics are available for some terrestrial habitats (Etter et al. 2006), and could feasibly be constructed for others. To incorporate timeframes, planners need only explicitly state their objectives, or identify relevant discount rates (Armsworth 2018).

My general model identifies and isolates factors that are likely to be influential within particular planning regions. However, a two-patch model does not account for the potentially complex spatial distribution of frontier and wilderness areas, or how this distribution might affect important spatial processes, such as species' dispersal. For specific conservation contexts, more extensive analyses that account for the characteristics of habitats within the planning region are required. In addition to the factors discussed above, further analyses should consider rates of biodiversity loss within protected areas (explored partially in Appendix 1), the displacement of threats from protected to unprotected areas (i.e. leakage; Ewers & Rodrigues 2008), species persistence in relation to fragmentation and connectivity (see Visconti et al. 2010b), and rates of protected area downgrading, downsizing and degazettement.

Importantly, my results do not support the use of either frontier or wilderness strategies. Instead, they stress the importance of context in deciding which approach will deliver the greatest benefits from limited conservation resources. My results also clearly show that failure to quantify, or at least consider, all relevant factors might produce prioritisations that have a much lower impact than expected. Specifically, wilderness-focused conservation efforts that neglect to consider heterogeneity in recovery potential, and the specific timeframes to reach objectives, will likely have sub-optimal conservation impacts. Likewise, frontier-focused conservation efforts that neglect to consider heterogeneity in costs, threat dynamics, and biodiversity values will likely have sub-optimal impacts.

Chapter 3

Quantifying the spatial relationship between conservation costs and threats

Associated publication: Sacre, E., Pressey, R.L. & Bode, M. (2019). Costs are not necessarily correlated with threats in conservation landscapes. *Conservation Letters*, e12663.

3 Quantifying the spatial relationship between conservation costs and threats

3.1 Abstract

The priority of an area for conservation is determined by three primary factors: its biodiversity value, the level of threat it is facing, and its cost. While much attention has been paid to the spatial relationship between biodiversity value and threats, and between biodiversity value and costs, little is known about how costs and threats are spatially correlated. The orthodox assumption in conservation science is that costs and threats are positively correlated. Here, I adapt a classic economic theory of land use to explain how conservation scientists came to expect a positive correlation between costs and threats. I then use high-resolution, ground-truthed datasets of land sales and habitat clearance to show that this assumption is false in the state of Queensland, Australia. My results provide an empirical counter-argument to a widespread assumption in conservation science, and illustrate why spatial prioritisation needs to include independent measures of costs and threats.

3.2 Introduction

In systematic conservation planning, three primary factors combine to determine the relative priority of a particular location: its biodiversity value, the degree of threats to biodiversity, and the costs of conservation action. To date, much of the conservation literature has focussed on understanding the spatial relationship between biodiversity value and conservation costs (Naidoo et al. 2006; Bode et al. 2008; Armsworth 2014). With increased understanding of this relationship has come a large body of conservation research that seeks maximise biodiversity benefits using limited conservation funds by securing areas that offer the greatest return on investment (Strange et al. 2006; Murdoch et al. 2007; Naidoo & Iwamura 2007; Bode et al. 2008; Carwardine et al. 2008). Similarly, the spatial relationship between biodiversity value and threats has received considerable empirical attention (the irreplaceability-vulnerability framework; Margules and Pressey 2000; Pressey and Taffs 2001). However, relatively little attention has been paid to how threats might be spatially co-distributed with conservation costs, and how this might affect spatial conservation priorities.

It is frequently assumed that conservation costs are positively correlated with threats (Table A2.1). This assumption is often explicitly stated (e.g. Moore *et al.* 2004; Costello and Polasky 2004; Newburn *et al.* 2005; Merenlender *et al.* 2009; Visconti *et al.* 2010;

Butsic *et al.* 2013; Boyd *et al.* 2015; Devillers *et al.* 2015), based on the argument that anthropogenic habitat transformation is most rapid and intense in economically profitable areas, such as those containing valuable natural resources (Costello & Polasky 2004; Newburn et al. 2005; Visconti et al. 2010b). Based on this assumption, many conservation planning exercises use metrics of threat as surrogates for conservation costs, thereby assuming that costs and threats have the same spatial distribution (Sala et al. 2002; Klein et al. 2008; Murdoch et al. 2010; Venegas-Li et al. 2018). The assumption that costs are positively correlated with threats also influences important debates in conservation theory. For example, it is often claimed that attempts to minimise conservation costs will lead to "residual reserves" (Arponen et al. 2010; Boyd et al. 2015; Devillers et al. 2015), because the cheapest locations are also the least threatened.

The intuition that conservation costs and threats are positively correlated relies on the assumption that the economic value of land and threats to biodiversity are driven by the same underlying processes. However, the profitability of a given economic activity at a particular location is likely to be affected by a range of factors that might be unrelated to threats, such as agricultural labour costs, political regulations and incentives (e.g. subsidies), and non-economic land use decisions (e.g. tradition or social perception; Vanclay and Lawrence 1994). These same factors might have minimal influence on the degree of habitat modification required to utilise land for a given economic activity. Instead, threats to biodiversity posed by habitat modification at each respective location might depend on a range of independent factors, such as the degree of modification required to utilise land, and technological advancements in the modification of particular habitats. Furthermore, each of these factors are likely to form complex interactions through space and time, and across spatial scales (Seabrook et al. 2006; Cattarino et al. 2014). If these potentially separate drivers of costs and threats are sufficiently influential, then it is expected that the spatial co-distribution of cost and threats might exhibit a more complex relationship than is widely assumed in the conservation literature.

Here, I explore the spatial co-distribution of costs and threats in conservation landscapes. To do so, I first use a classic economic model to examine the expected relationship. I then use data on historical land acquisition costs and rates of vegetation clearing in the state of Queensland, Australia, to offer empirical insights into this same relationship. In doing so, I hope to highlight the importance of verifying the theoretical assumptions we make in conservation prioritisation.

3.3 Methods

Definitions of cost and threat

In my analysis, I focussed particularly on the costs incurred by conservation organisations when acquiring land for the establishment of protected areas, and the threats to biodiversity caused by habitat clearance. I chose to focus on the acquisition costs of purchasing land for protection because it is one of the most widespread methods of conservation action, and because it is typically the focus of spatial conservation prioritisation. I note, however that (1) acquisition costs are not the sole cost incurred when establishing protected areas, which also involve management costs, and opportunity costs to stakeholders (Naidoo *et al.* 2006); and (2) biodiversity is threatened by processes other than habitat clearance, such as climate change, invasive species, and pollution (Allek et al. 2018).

Theoretical analysis

To explore the theoretical relationship between acquisition costs and rates of habitat loss, I adapted von Thünen's classic "isolated state" model (Thünen 1826), which describes how different economic activities arrange themselves in space, and how these patterns affect the cost of land. In the von Thünen model, land quality is homogeneous, distributed radially around a central marketplace. Each location is amenable to the same economic activities (in the original model, these were types of agriculture). Each activity i generates commodities that can be sold at constant price p_i net their production cost c_i. Commodities have different transport costs τ_i, which accrue at a constant rate with distance. The profit generated by an activity at a distance r from the market is therefore a declining linear function of distance:

$$\pi_i(r) = p_i - c_i - \tau_i r.$$

Equation 3.1

To maximise their net profits, all parties compete to secure the land that is closest to the market, since this minimises transportation costs. The rent $P(r)$ generated by an area of land is defined by the most profitable land use at that distance:

$$P(r) = \max_i [p_i - c_i - \tau_i r].$$

Equation 3.2

These rents can be considered proportional to acquisition costs. Note that all economic activity – and in my model, all threat – will cease at distances $r > (p_i - c_i)/\,\tau_i$ (for all values of i). Beyond this distance high transport costs make all activities unprofitable.

Threats to biodiversity were incorporated into von Thünen's model using a simple model of habitat degradation. I assumed that each activity i threatens a particular proportion λ_i of the habitat at that location with degradation or loss. The most profitable land use in each location therefore determines both the local acquisition cost and the magnitude of the threat to biodiversity.

I analysed both a deterministic and a stochastic version of the extended von Thünen model to explore the relationship between acquisition costs and threats. For the deterministic model, values for τ_i, λ_i, p_i and c_i were chosen at random from uniform distributions $U(0,1)$ for four different land use types, and assumed these parameters were constant in space. For the stochastic model, economic heterogeneity was included by adding normally distributed random noise to production costs at each discrete radial distance from the market. Ecological heterogeneity was included by adding similar noise to the degradation caused by each activity. Specifically, I defined $c_i(r_x) = \overline{c_i} + \epsilon_x$, and $\lambda_i(r_x) = \overline{\lambda_i} + \delta_x$, where $\epsilon_x, \delta_x \sim N(0, \sigma)$ and $\overline{c_i}$ and $\overline{\lambda_i}$ are the mean values for each activity.

Empirical analysis

For my empirical analysis, I examined the spatial co-distribution of surrogates for conservation acquisition costs, and rates of habitat loss, on land parcels in Queensland, Australia (Figure 3.1). Queensland is a large state, covering 185 million hectares and containing a broad range of ecosystems, ranging from tropical and subtropical ecosystems along the east coast, to arid assemblages west of the Great Dividing Range. Queensland is divided into private and state land parcels, each of which represents a legal property. Because these parcels are the resolution at which most conservation action takes place, they were used as replicates in my analysis.

For my primary analysis, I used a dataset of property sales that occurred between 2000 and 2008 (Adams et al. 2011b). Because these record real market transactions, they are likely to accurately reflect acquisition costs. However, I note that actual acquisition costs for conservation might vary from standard land transactions, because of differing objectives and negotiation dynamics (Armsworth 2014). All sale prices were adjusted to 2008 Australian dollars (AUD), based on annual inflation rates (Australian Bureau of Statistics 2017). My primary analyses assumed that it would be necessary for a conservation organisation to purchase entire parcels. Thus, the mean cost per hectare of vegetation on each parcel was calculated as the total price of the parcel divided by the number of hectares of vegetation on the parcel. In Appendix 2, I also provide analyses assuming that vegetated sub-sections of each parcel can be purchased, which might affect the relative cost-effectiveness of purchases depending on what proportion of each parcel is vegetated (Adams et al. 2011b).

To estimate threats to biodiversity, I measured the amount of anthropogenic vegetation clearing that occurred on each parcel between 2009 and 2018. This measure of threat, therefore, reflects the amount of vegetation clearing that could have been prevented by purchasing and protecting vegetation in 2008. I chose to measure clearing between 2009 and 2018 because: (1) measuring clearing after the land was sold avoids the possibility that clearing affected the sale price; (2) cost data were available immediately before this period; (3) threat data were available up until the year 2018; and (4) this period spans different phases of land clearing policy (discussed below in *Supporting analyses*). For each parcel, I divided the area of vegetation cleared by the area of remnant vegetation in 2008, to give the mean proportion of remnant vegetation that was cleared. In Appendix 2, I also provide results when vegetation clearing was standardised by total parcel size.

Land clearing was estimated from the Statewide Landcover and Trees Study (SLATS; Queensland Department of Science, Information Technology and Innovation 2017), which uses Landsat satellite imagery to measure woody vegetation clearing in Queensland, and is verified by extensive field surveys. All clearing is classified according to the economic or natural process responsible (e.g. mining, pasture, natural disaster). I included only direct, anthropogenic clearing in my analysis. I excluded all parcels within 1 km of present-day protected areas to avoid the possibility that clearance rates were affected by protection. I also restricted my analyses to rural land parcels with remnant vegetation in 2008, under the assumption that urban areas and parcels without vegetation are unlikely candidates for conservation acquisition. Finally, because the SLATS dataset detects only woody vegetation clearing, I removed parcels that contained any non-woody vegetation types. The amount of remnant vegetation on each parcel at the time of purchase was calculated by combining the SLATS dataset with data from the National Vegetation Information System (NVIS Technical Working Group 2017).

To explore how the relationship between my estimates of conservation acquisition cost and threat might vary according to ecological and economic variation, I intersected parcels with layers of bioregions and land use types (see Appendix 2 for further details). For all analyses, I used Kendall's rank correlation coefficient to measure associations between cost and threat. Kendall's coefficient is useful when datasets contain many zero values, such as parcels that experienced no vegetation clearing.

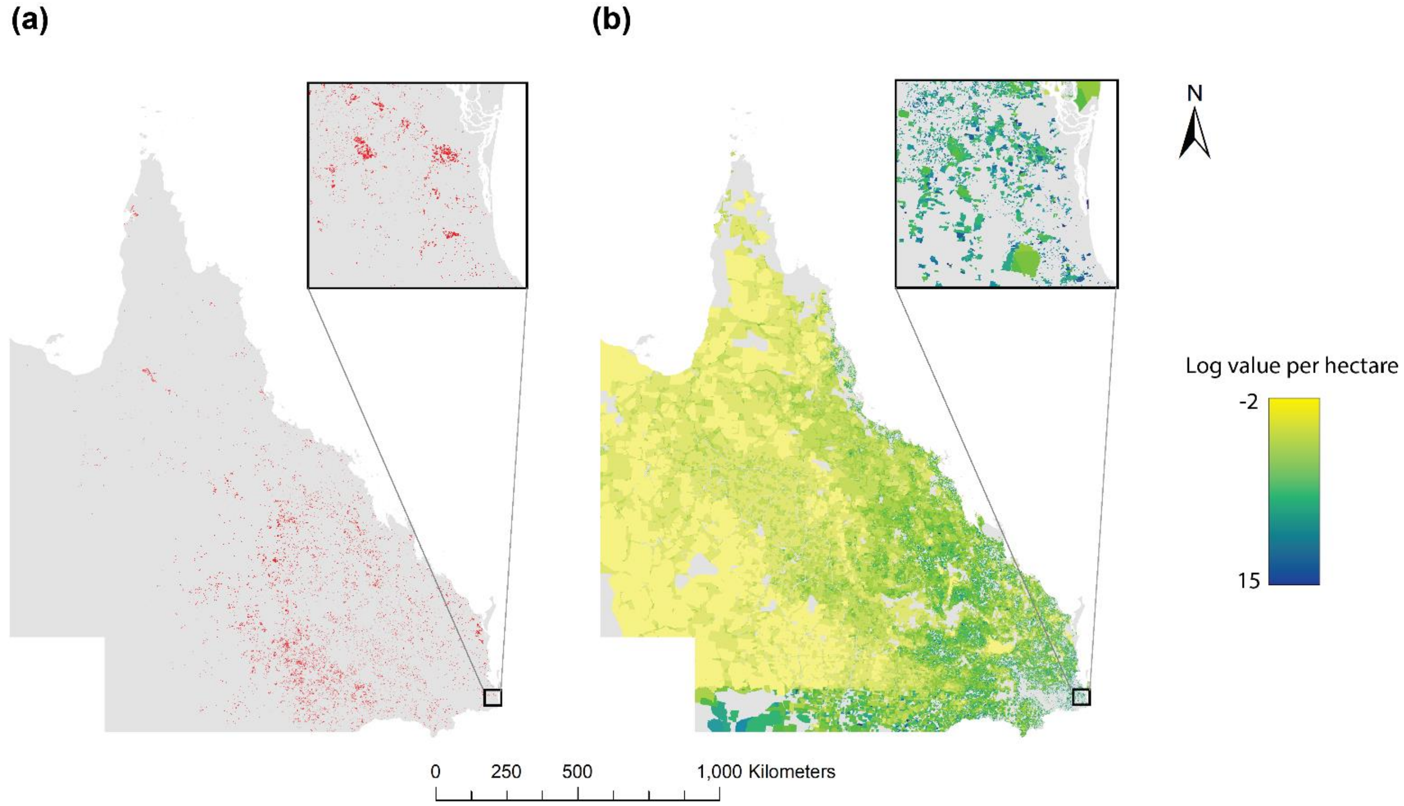

Figure 3.1 The spatial distribution of land valuation and threats from land clearing in Queensland, Australia. Panel (a) shows anthropogenic land clearing (red) that has occurred in Queensland from mid-2007 to mid-2018 derived from the Statewide Landcover and Trees Study (SLATS). Panels (b) shows unimproved land valuation in log 2006 AUD per hectare of vegetation derived from valuations collected by the Queensland Valuer-General. Grey areas represent parcels where land valuations were not performed (e.g. on public land), or parcels where no remnant vegetation was present in the year 2006. Only land valuations, and not sales prices, were used for production of the above map due the low number of property sales in the dataset.

Supporting analyses

I performed several supporting analyses to test the robustness of my results. I repeated my analyses using two alternative surrogates for conservation acquisition costs. The first was unimproved land values as estimated by the Queensland Valuer-General between 2002 and 2006 (Carwardine et al. 2010), converted to 2006 AUD (Australian Bureau of Statistics 2017). For the analysis using land valuations, I measured land clearing between 2007 and 2018. Our second surrogate was the agricultural profitability of land in 2006, modelled by Marinoni *et al.* (2012). Agricultural profitability is a useful alternative measure because it might better reflect the opportunity costs of conservation (forgone economic profits) as well as acquisition costs.

I repeated my correlation test for two separate phases of land clearing policy in Queensland to test whether my results varied across regulatory regimes. I also stratified my analyses across each of Queensland's 13 bioregions, to see if my results were sensitive to changes in geographic location, extent, or government jurisdiction. Finally, because land prices can exhibit efficiencies of scale, with larger parcels having lower per-hectare costs, I stratified my analysis according to parcel size (0-1 ha, 1-10 ha, 10-100 ha, and over 100 ha). Outputs from these analyses are available in Appendix 2.

3.4 Results

Theoretical analysis

If only a single economic activity occurs in a region, the von Thünen model predicts that land cost will decline linearly with distance to market, as net profitability is reduced by transport costs (Figure 3.2a). Land cost declines to zero at distances $r > (p_1 - c_1)/\tau_1$, once the single activity becomes unprofitable. This simple, single-activity case supports the intuition that cost and threat are correlated (Figure 3.2b): with low cost (unprofitable) land experiencing low degradation (wilderness), and high cost (profitable) land experiencing greater degradation (λ_1).

With multiple economic activities, a positive correlation between costs and threats can no longer be assumed. Land cost still declines with distance to market, although following a piecewise linear relationship as a sequence of different economic activities maximise net profits (Figure 3.2c). Habitat degradation remains lowest in land with the lowest cost (wilderness), but is otherwise unrelated to net profitability (Figure 3.2d). Unless the most profitable activities are also the most ecologically degrading, high-cost land will not face the greatest threats. The result is an uncertain correlation between land costs and threats.

Figure 3.2e shows how the optimal land use changes through space as a consequence of varying production costs, and Figure 3.2f shows the consequences for the relationship between costs and threats when ecological heterogeneity adds further noise. The resulting relationship is complex, and unlikely to produce a simple positive correlation between costs and threats.

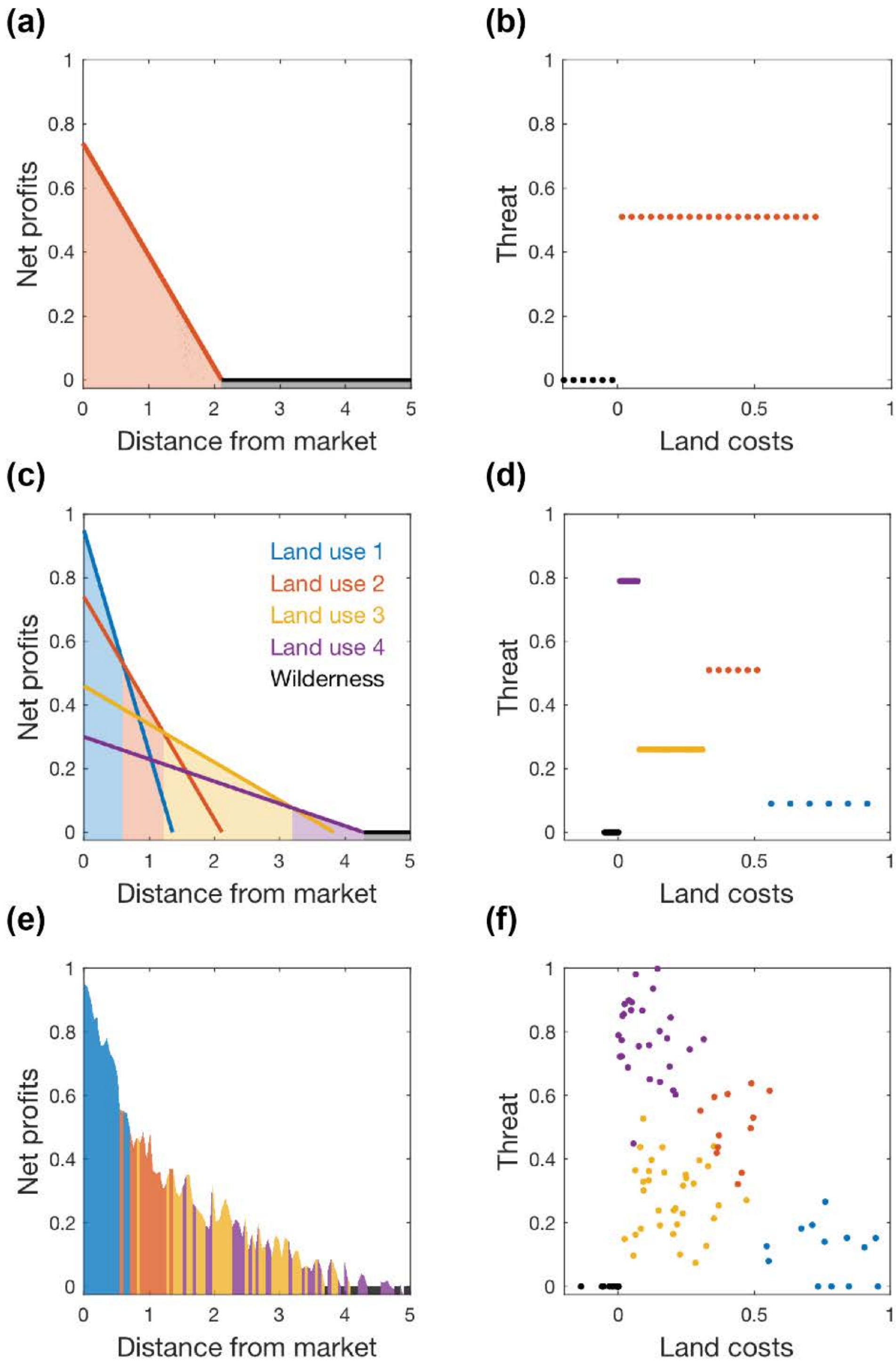
(a)
(b)
(c)
(d)
(e)
(f)
Net profits
Distance from market
Threat
Land costs
Land use 1
Land use 2
Land use 3
Land use 4
Wilderness

Figure 3.2 The relationship between land costs (net profits) and threat from of land clearing as predicted by the von Thünen model. Panels (a,c,e) show the relationship between distance from market, optimal economic activity, and net profits on land. Different colours denote different economic activities, with black denoting wilderness areas where no economic activity is profitable. Each activity produces commodities that can be sold at market for a net profit indicated by the y-intercept. As distance to market increases, transport costs make each activity less profitable at a rate described by the slope of each line. Panels (b,d,f) show scatter plots of the relationship between cost and threat according to the same model. Each point represents a discrete distance from the market. Panels (a-b) show a positive correlation between cost and threat according to the predictions of a deterministic, single-sector version of the model. Panels (c-d) show that the presence of multiple economic sectors can invalidate this assumption. Panels (e-f) show that the presence of ecological and economic variation further complicates the relationship. See Appendix 2 for further details of parameter values.

Empirical analysis

I observed no apparent structure in the co-distribution of acquisition costs and land clearance rates in Queensland (Figure 3.3). Both sales price and land valuation were weakly negatively correlated with clearance rates (sales price, Figure 3.3a, Kendall's rank correlation τ = -0.14, p = <0.01, n = 7,620; land valuation, Figure 3.3b, τ = -0.02, p = <0.01, n = 104,273). There was also no correlation between agricultural profitability and the rate of land clearing (Figure A2.1, τ = ~0.00, p = 0.16, n = 62,402). These results were consistent regardless of whether it was necessary to purchase entire parcels or if vegetated subsections could be purchased, and whether or not clearance rates were standardised by vegetation area or parcel area (Table A2.2). The relationship was unaffected by changes in land clearing policy (Figure A2.2, Table A2.2). These results were also generally consistent across all of Queensland's bioregions, with the exception of the Mulga Lands (τ = 0.20, p = <0.01, n = 2,142) and South East Queensland (τ = 0.04, p = <0.01, n = 46,181), which were weakly positively correlated. Among parcels of similar size, the relationship became slightly positive, (up to τ = 0.18; Table A2.2). However, the relationship was still weak and highly variable (Figure A2.3).

Some portion of the observed variation appears to be driven by economic and ecological variation among parcels (Figure 3.3c and 3.3d). For example, I found that particular bioregions cluster at different locations along the cost axis (Figure 3.3c). As a consequence, parcels in two different bioregions that face the same level of threat can have very different acquisition costs. There appeared to be similar clustering with economic land use (Figure 3.3d), but to a lesser extent.

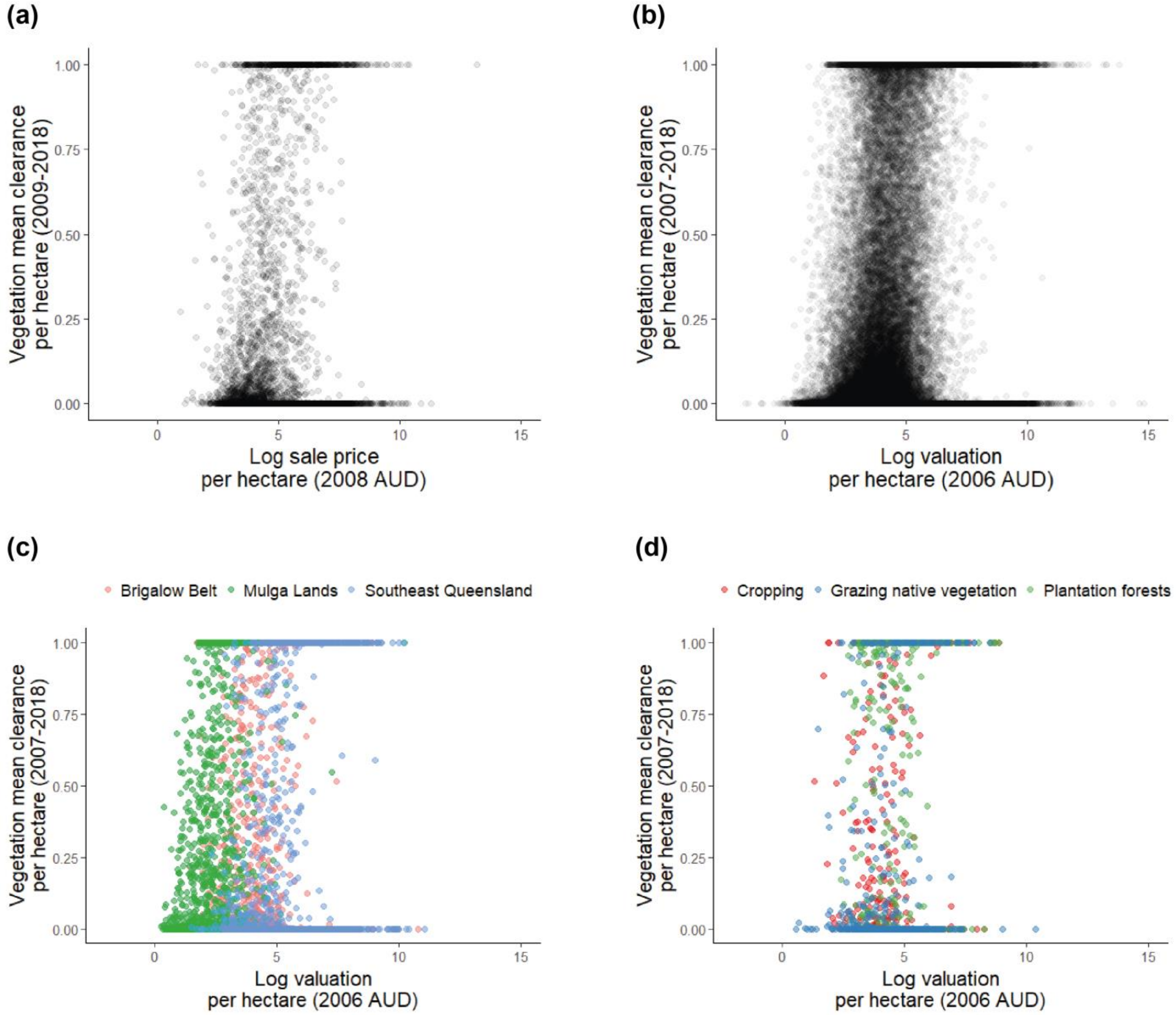

Figure 3.3 Scatter plots of the relationship between land sales and valuations, and rates of land clearing in Queensland. Panel (a) shows the log sale price of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2009 and mid-2018 on each parcel. Panel (b) shows the log unimproved land value of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2007 and mid-2018 on each parcel. Panel (c) shows log unimproved land values of parcels and rates of land clearing in three different bioregions: the Brigalow Belt (red), Mulga Lands (green), and Southeast Queensland (blue) bioregions. For this panel a random subset of parcels within each bioregion were taken for visual clarity. Panel (d) shows log unimproved land values of parcels and rates of land clearing on land used predominantly for three different economic activities: cropping (red), grazing on native vegetation (blue), and plantation forests (green).

3.5 Discussion

My results offer a counterpoint to the widespread assumption that costs and threats have a simple positive relationship in conservation landscapes. Instead, the relationship appears to be complex and highly variable. Both my theoretical and empirical results show how at least some of this variation appears to occur according to economic and ecological spatial heterogeneity. It is beyond the scope of this study to empirically determine whether economic and ecological variation itself is driving some of this variation, or whether processes that underlie or co-vary with this heterogeneity are responsible. However, it is clear that in Queensland, spatial variation in acquisition costs is being driven to a large extent by factors that are at least partially independent of the factors driving spatial patterns of vegetation clearing. These observations are consistent with those from the land economics literature, in which it is well understood that the profitability of land is typically only one of many drivers of spatial patterns in land-use change, which can form complex interactions across spatial extents and scales (Ellis et al. 2010; Cattarino et al. 2014). In Queensland, for example, farmers' decisions to clear vegetation are motivated not only by potential profits, but also a variety of other factors, such as the perceived attractiveness of native vegetation types (Seabrook et al. 2008).

There are several caveats to my analyses that require consideration. First, in some cases, the relationship became weakly positive among parcels of similar size (Table A2.2). One possible explanation for this is that parcels of similar size are likely to have similar land use types and ecological characteristics. For example, in Queensland, very large parcels are likely to be used predominantly for cattle grazing in semi-arid regions. Nonetheless, even among parcels of similar size, the relationship was weak (up to τ = 0.18), and highly variable (Figure A2.3). Furthermore, there is no reason to suspect that conservation organisations would be restricted to purchasing parcels of similar size. Second, Queensland is only a single case study; empirical findings might differ for other conservation regions. However, my empirical observations are consistent with my theoretical analysis, indicating that that these patterns are likely to apply to any conservation landscape containing economic and ecological variability. These results are of particular relevance to conservation planning, because the spatial extent of planning regions are often deliberately chosen to encompass ecologically diverse areas, both because the goal is to represent a comprehensive range of ecological features (Margules & Pressey 2000; Kukkala & Moilanen 2013), and because larger planning regions offer efficiencies of scale (McDonald 2009). Third, I considered only one aspect of threats to biodiversity – habitat clearance. Queensland's biodiversity is also threatened by a variety of other processes, such as pollution, climate change, and invasive species (Allek et al. 2018). However, these other measures of threat are less likely to be linked to land costs than land clearing. Finally, my analyses do not consider all types of conservation costs. Management costs, in particular, can dominate conservation expenditures in other contexts, such as in marine conservation, where acquisition costs are less relevant (Adams et al. 2011a; Hunt 2013).

My findings have several important implications for conservation prioritisation and practice. The belief that costs and threats are strongly and positively correlated in conservation landscapes is still broadly held and stated in conservation science (Table A2.1). However, my results show that threats cannot be assumed to be a good proxy for conservation acquisition costs. Rather than simply using threats as a proxy for costs (e.g. Sala *et al.* 2002; Klein *et al.* 2008; Murdoch *et al.* 2010; Venegas-Li *et al.* 2018), future conservation planning exercises should measure costs independently, or devise more sophisticated statistical models that explain the factors driving the spatial distribution of both costs and threats. My results also show that most parcels experienced relatively low rates of land clearing, regardless of acquisition cost (Figure A2.4). As a result, any conservation plan that does not explicitly consider threat levels when prioritising locations could be inadvertently biased towards low-threat, residual areas (Joppa and Pfaff 2009; Devillers *et al.* 2015). Finally, my results show that landscapes are likely to contain a substantial number of highly cost-effective conservation opportunities. In Queensland in 2008, there was a large amount of vegetation that faced large, imminent threats, but which could have been acquired at relatively low cost. Thus, conservation prioritisations that consider the actual relationship between threats and costs are likely to find a landscape full of relative bargains: locations facing serious threat from relatively unprofitable activities.

Chapter 4

A retrospective, counterfactual-based impact assessment of alternative conservation prioritisation strategies

4 A retrospective, counterfactual-based impact assessment of alternative conservation prioritisation strategies

4.1 Abstract

Despite exponential increases in the coverage of protected areas (PAs) over recent decades, global biodiversity continues to decline. Evidence that PAs are often biased toward 'residual' locations with minimal socioeconomic value provides some explanation for the lack of efficacy of modern conservation efforts. Central to avoiding residual conservation is measuring and estimating the conservation impact of proposed PA networks compared to a counterfactual scenario in which no intervention is applied. This approach contrasts with measuring efficacy in terms of tangential targets, such as total biodiversity value, representativeness, and adequacy, which do not necessarily lead to impact. However, implementing an experimental counterfactual scenario is difficult because of time, funding, and ethical constraints. Here, I provide an alternative and complementary approach that has yet to be utilised in conservation planning: an *ex post* analysis with counterfactual outcomes measured using historical empirical data on changes in biodiversity in unprotected landscapes. I retrospectively predict the impact of several alternative PA prioritisation strategies in Queensland, Australia, using high-resolution datasets of vegetation clearing, habitat type, and land acquisition cost. My results show that achieving conventional conservation targets does not equate to achieving impact, and that alternative, and relatively simple, prioritisation strategies can achieve far greater impacts.

4.2 Introduction

Since the inception of systematic conservation planning (Margules & Pressey 2000; Pressey 2002; Moilanen et al. 2009), a myriad of spatial prioritisation methods have been developed and implemented, each with the ultimate goal of maximising the persistence of biodiversity using limited conservation funds. Today, the predominant approach to conservation planning involves designing a network of complementary protected areas (PAs) that contains a representative sample of biodiversity. Other methods focus on designing PA networks that also, or alternatively, maximise other attributes, such as connectivity between PAs (e.g. Beger et al. 2010), or the inclusion of rare or vulnerable biodiversity types (e.g. Pressey & Taffs 2001). Representation targets are widespread in conservation policy and practice (UNEP-WCMC 2008), often serving as the primary objective of national and multi-national reserve systems supported by millions of dollars of public and private conservation funding (e.g. Fernandes et al. 2005). However, evidence of continuing declines in global biodiversity, despite increasing conservation efforts (Butchart et al. 2010; Hoffmann et al. 2010; Tittensor et al. 2014), along with evidence of protection biases towards "residual" areas (Joppa & Pfaff 2009; Devillers et al. 2015), has called into question the efficacy of current conservation prioritisation methods (Carwardine et al. 2009; Pressey et al. 2017).

The lack of progress in developing more effective prioritisation strategies can be attributed largely to two factors: the failure to frame conservation goals and objectives in terms of impact (Pressey et al. 2017), and the difficulty of empirically measuring conservation impact as a guide to setting priorities. Conservation impact can be measured by comparing outcomes from an intervention to outcomes from no intervention (referred to as a "counterfactual" in the conservation literature, *sensu* Ferraro 2009). However, the rigorous experimental procedures standard in other scientific fields, involving control (i.e. counterfactual) and treatment groups, are impractical in conservation science and, in many cases, impossible. Experimental procedures of the same calibre in conservation science would require conservation interventions across many replicate planning regions. This would not only require vast amounts of time and funding, but would also be an ethically questionable procedure, because counterfactual planning regions would receive no conservation intervention when it might be urgently needed.

To overcome this problem, sophisticated quasi-experimental matching techniques have been developed, whereby existing PAs are matched to unprotected areas with similar biophysical and socioeconomic characteristics to correct for the non-random allocation of PAs (Andam et al. 2008; Joppa & Pfaff 2011; Ahmadia et al. 2015; Jones & Lewis 2015). These matched unprotected areas serve as a pseudo-counterfactual to which the outcomes of PAs can be compared. However, matching techniques have limited use in conservation planning, because they can be used only to assess the effects of existing PAs, and not to compare and estimate the impacts of a range of alternative prioritisation strategies. An alternative approach that is more useful for comparing alternative prioritization strategies is *ex ante* modelling of future landscapes to predict counterfactual outcomes (Newburn et al. 2005; Monteiro et al. 2018). These are particularly useful for identifying areas for potential protection. However, predicting impacts with an *ex ante* approach relies upon a range of assumptions and uncertainties about spatial and temporal changes in threats and biodiversity in the absence of, and in response to, protection.

The aim of this chapter is to develop and utilise a method for estimating the impact of alternative conservation prioritisation strategies that overcomes the shortfalls of the above mentioned approaches. In this chapter, I utilise an *ex post* approach to predicting conservation impacts, whereby impacts are measured retrospectively using historical data of vegetation clearing to predict what impacts each prioritisation strategy might have had if they were implemented prior to the period of vegetation clearing. An *ex post* approach is particularly useful for conservation planning because it provides a real, empirical, counterfactual to which predicted outcomes from proposed strategies can be compared. For my analysis, I use empirical data on historical changes in vegetation cover across a range of vegetation types in Queensland, Australia, between 2006 and 2016. The strategies I compare are: (1) prioritising low-cost areas for protection, (2) maximising the representation of biodiversity features in protected areas, (3) prioritising areas facing high threat from land clearing for protection, and, (4) maximising the representation of biodiversity features within protected areas while also prioritising areas facing high threat from land clearing. I also use high-resolution datasets of land valuation to explore the cost-efficiency of each strategy, and to explore how impacts vary according to available budgets.

4.3 Methods

Case study

For my analysis, I used the case study of Queensland, Australia. Queensland provides a useful case study because it is a large state (185 million ha) containing a broad range of vegetation types, from semi-arid woodlands to tropical rainforests. Queensland is also the most intensively cleared state in Australia, with most clearing occurring in the last 50 years for the creation of cattle grazing lands (Bradshaw 2012; Evans 2016). Spatial conservation prioritisation is therefore both urgently need and highly consequential in Queensland.

Planning units and the counterfactual

The planning units for my analysis consisted of land property parcels in Queensland. Land parcels in Queensland are variable in size and irregularly shaped. The mean land parcel size in Queensland in 2006 was 86 ha, which is approximately equal to a square 930 m by 930 m. The analysis was restricted to parcels that were outside existing PAs, to ensure that I could obtain a reliable counterfactual measure of land clearing in the absence of protection. All parcels within 1km of PAs were also removed from the analysis to avoid potential confounding differences in vegetation clearing patterns in areas proximal to PAs. The conservation goal was to minimise the loss of woody vegetation using the available budget. I tested how well each prioritisation strategy could achieve the conservation goal over a period of ten years, from 2006 to 2016. Each prioritisation strategy could protect a set of parcels in 2006, after which I assumed that protected parcels would lose no vegetation (but see below for consideration of displacement of land clearing). I measured the realised loss of woody vegetation on unprotected parcels using the Statewide Landcover and Trees Study (SLATS), which uses Landsat satellite imagery and field surveys to measure woody vegetation clearing across Queensland. To estimate the extent of woody vegetation in 2006 and 2016, I combined SLATS data with data on the extent of woody vegetation in 2016 (Queensland Government 2018). I then created a layer of woody vegetation in 2006 under the assumption that all woody vegetation present in 2016 and registered as cleared between 2006 and 2016 was present in 2006.

Prioritisation strategies

I measured the impact of all prioritisation strategies relative to a counterfactual scenario in which no parcels were protected over the period of analysis. All prioritisation strategies were designed with the software Marxan (Watts et al. 2009). All strategies attempted to achieve their respective targets using only the specified budget (see section below). In Marxan, this was implemented by setting a cost threshold that could not be exceeded.

I compared four different strategies. First, the cost-only strategy, which prioritised parcels with the lowest cost per unit area. This strategy was implemented by treating all parcels as a single biodiversity feature, and setting protection targets to 100%. This strategy, therefore, simply maximised the total amount of area protected using the available budget. Second, the threat strategy prioritised parcels that were expected to face high levels of threat. I assigned each parcel a threat score, measured as the extent of land clearing in the 10 years prior to the beginning of the planning period (1995 – 2005) within 20 km of the parcel's centroid. This was then multiplied by the parcel area. This threat score, therefore, assigned conservation value to each parcel based on the amount of land under threat (parcel size) and the intensity of threats in the area. I implemented this strategy by setting threats as a single feature to be maximised (target of 100%) using the available budget. Third, the representation strategy attempted to represent 30% of each of 29 woody broad vegetation groups (BVGs) within Queensland (Neldner et al. 2014). I also tested alternative representation targets (50% and 90%), the results of which are available in Appendix 2. Fourth, the representation and threat strategy attempted to represent all broad vegetation groups while also prioritising areas under high levels of threat from land clearing. For this strategy, I used the same representation objectives as those from the representation-only strategy (including supporting analyses with targets of 50% and 90%), and the same threat objectives as those from the threat-only strategy. Then, in Marxan, I set the vegetation groups and the threat feature as two distinct feature types with equal priority. Full details of the prioritisation methods are provided in Appendix 3.

Budget constraints and analyses

To estimate the conservation acquisition cost of each parcel, I used statutory unimproved land valuations by the Queensland Valuer-General for all rateable land parcels (Queensland Government 2008). This dataset included valuations between 2002 and 2006. To account for inflation, I standardised these land valuations to Australian dollars in 2006 (2006 AUD) using the average annual Australian consumer price index (Australian Bureau of Statistics 2017).

In the primary analysis, I set the total budget to 1 billion 2006 AUD to purchase land in 2006 for protection over the entire period from 2006 to 2016. This is equivalent to 100 million 2006 AUD per year, which is within the range of annual expenditures by Queensland's Environmental Protection Agency in 2006 (Queensland Government 2006). However, I also tested how the impact of each strategy varied according to the available budget by varying the total budget from 200 million to 10 billion 2006 AUD. See Appendix 3 for further details of the budget analyses.

Measures of impact

I compared each prioritisation strategy using three different impact metrics, all relative to the counterfactual scenario. The first metric was the total area of mitigated vegetation loss within each BVG (Neldner et al. 2014). Because some BVGs naturally cover large extents while others are restricted, my second metric was the area of mitigated vegetation loss in each BVG in proportion to its total extent in 2006. My third metric was a relative impact score that weighted more heavily the preservation of BVGs according to their rarity (i.e. higher weighting to groups with smaller extents in 2006) and their historical rate of clearing (i.e. higher weighting to groups that had a lower proportion of their pre-European extent remaining in 2006). Full details and sensitivity analyses for this metric are provided in Appendix 3.

I also measured how evenly impact was distributed across groups. I refer to this as "impact equality", based on Chauvenet et al. (2017)'s protection equality metric. Impact equality was higher if the proportion of avoided loss was more evenly distributed across groups. Notably though, impact equality alone is not a good measure of impact, because it does not consider the total extent of avoided loss. For example, a strategy that saved an equally small proportion of each group would have higher impact equality than a strategy that saved higher, but more variable, proportions of BVGs. Full details and formulas for this metric are available in Appendix 3.

Displacement of land clearing

One of the criticisms of PAs is that their positive effects can be offset by "displacement", also known as "leakage". Displacement occurs when, after protection, threatening processes shift to nearby unprotected areas (Ewers & Rodrigues 2008; Renwick et al. 2015; Moilanen & Laitila 2016). To account for the possibility of displacement after protection, I created a spatial displacement model. In the displacement model, once a parcel was protected by a prioritisation strategy, all land clearing that would have occurred in that parcel between 2006 and 2016 was distributed to unprotected parcels within a 5 km radius. I also investigated alternative displacement distances (1 km, 10 km and 20 km) and report on these in Appendix 3. The spatial model was employed in ArcGIS 10.4.1 using custom python code (available upon request).

4.4 Results

Counterfactual outcomes

The final analysis included 126,232 land parcels, covering 34,996,900 ha in Queensland, of which 19,442,148 ha were remnant woody vegetation in 2006. Between 2006 and 2016, in the counterfactual scenario, these parcels lost 1,014,118 ha of woody vegetation. Vegetation loss was uneven across BVGs, both in terms of area and as a proportion of their extents in 2006 (Table A3.1). The most extensively cleared BVG in terms of area was dry woodlands dominated by *Eucalyptus populnea* (poplar box) or *E. melanophloia* (silver-leaved ironbark), losing 267,895 ha within analysed parcels. *Acacia harpophylla* (brigalow) dominated open forests and woodlands was proportionally the most extensively cleared BVG, losing 27% of its extent between 2006 and 2016.

Prioritisation strategy impacts

In the primary analysis (budget of 1 billion 2006 AUD), the total area protected by the cost, threat, representation, and representation/threat strategies was approximately 19.4 million ha, 13.4 million ha, 11.0 million ha, and 9.7 million ha, respectively (Table 4.1). Spatial overlap between strategies varied from 27% (between the threat and representation/threat strategy) to 57% (between the cost and threat).

When measuring impact in terms of the total area saved, a threat prioritisation strategy was most effective (Figures 4.1a and 4.2a). A threat prioritisation strategy prevented the loss of 633,712 ha of vegetation (380,406 ha not prevented), while a cost prioritisation strategy saved 586,670 ha (427,448 ha not prevented), a representation strategy saved 223,620 ha (790,498 ha not prevented), and a representation/threat strategy saved 218,371 ha (795,747 ha not prevented; Table A3.2). A threat prioritisation strategy was also most effective when measuring impact proportional to the extent of each BVG (Figures 4.1b and 4.2b), and when rare and historically cleared BVGs were weighted more heavily (Figure 4.2c). These results were consistent, regardless of representation targets (Figure A3.3) and when displacement of land clearing was considered (Figure A3.4).

For all three metrics of impact, changing the budget did not affect which strategy was most effective (Figures 4.2a-c). Notably though, the relative difference in impact between strategies increased as the budget increased. There were also diminishing returns on conservation investment for all four prioritisation strategies (Figures 4.2a-c). Although cost and threat strategies had higher overall impacts, representation and representation/threat strategies had higher impact equality, particularly at lower budgets, but this difference narrowed as the budget increased (Figure 4.2d).

Table 4.1 Spatial overlaps between strategies in the primary analysis with a budget of 1 billion 2006 AUD for the 10-year period from 2006 to 2016.

		Hectares		
	Cost	Threat	Representation	Representation/Threat
Cost	19,380,662	11,905,338	9,547,457	8,753,898
Threat	11,905,338	13,411,204	6,230,764	4,846,359
Representation	9,547,457	6,230,764	11,015,431	6,738,626
Representation/Threat	8,753,898	4,846,359	6,738,626	9,721,435
		Percentage		
	Cost	Threat	Representation	Representation/Threat
Cost	100%	57%	46%	43%
Threat	57%	100%	34%	27%
Representation	46%	34%	100%	48%
Representation/Threat	43%	27%	48%	100%

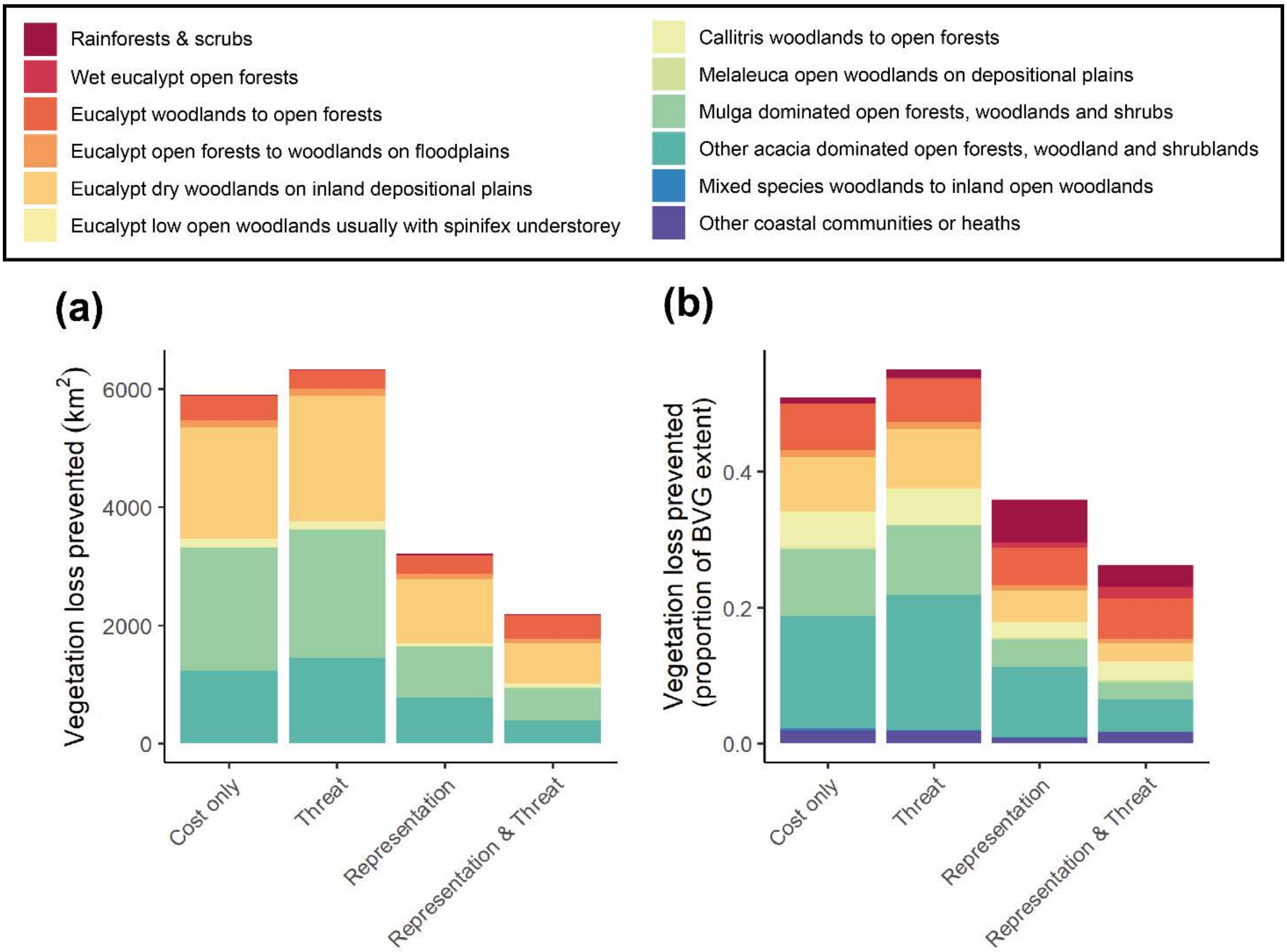

Figure 4.1 The impact of each strategy relative to the counterfactual scenario. Panel (a) shows impact measured as the total area of mitigated woody vegetation loss within each broad vegetation group (BVG). Panel (b) shows impact with mitigated vegetation loss measured in proportion to the extent of each BVG in 2006, such that a score of 1.0 means that all vegetation loss was mitigated. Note that BVGs have been simplified into the above 12 categories (according Neldner et al. 2014) for ease of interpretation. For the primary analysis, all impact metrics considered the 29 woody BVGs present in Queensland. For this analysis, the budget was set to 1 billion 2006 AUD for the 10-year planning period.

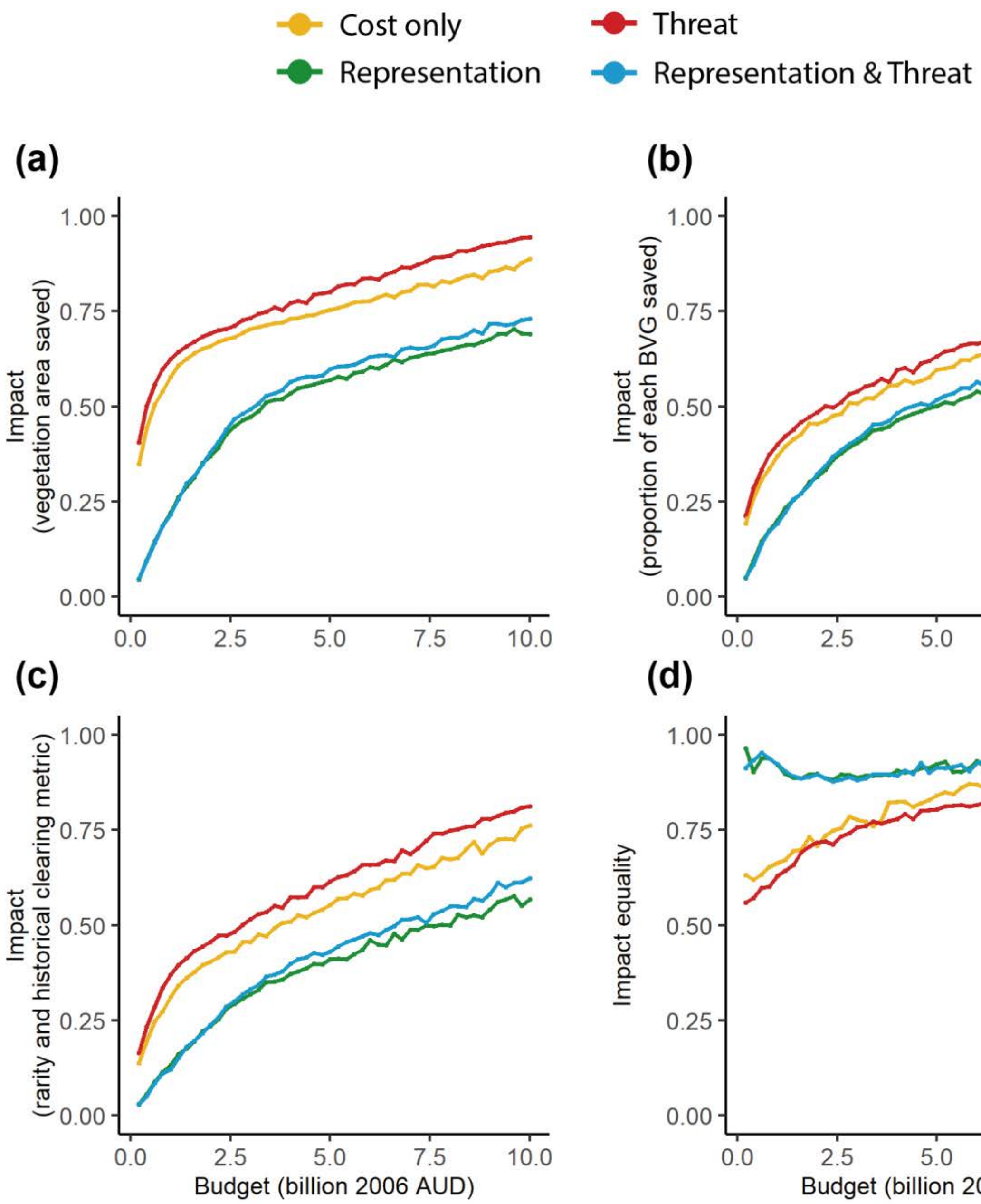

Figure 4.2 The effect of budget on the impact of alternative prioritisation strategies according to different metrics. Panel (a) shows the impact of each strategy, measured as the total area of mitigated woody vegetation loss relative to the counterfactual scenario, such that a score of 1.0 means that all vegetation loss was mitigated. Panel (b) shows impact with mitigated vegetation loss measured as the sum of the proportions of mitigated vegetation loss in each BVG relative to the counterfactual. Panel (c) shows impacts with proportions from panel (b) weighted according to the rarity of each BVG and how extensively it was cleared prior to 2006. Panel (d) shows the impact equality of each prioritisation strategy, based on the "protection equality" metric from Chauvenet et al. (2017). Full details and formulae for each metric are in Appendix 3.

4.5 Discussion

There is an alarming lack of empirical analyses estimating the impact of modern approaches to conservation priority setting (Ferraro & Pattanayak 2006; Pressey et al. 2017). Instead, much of the science and practice of conservation prioritisation has focussed on developing plans that efficiently achieve specific representation targets (IUCN-WCPA 2008; National Reserve System Task Group 2009), while the impacts of achieving such targets are unknown. I offer an empirical *ex post* approach that allows impacts to be estimated by comparing predicted outcomes to a real counterfactual scenario. This approach allows comparison of any number of hypothetical PA systems, rather than being restricted to measuring the impact of existing PA networks, as is the case with matching analyses. Furthermore, this method is easy to replicate across a variety of terrestrial ecosystems, because it can be employed using data available across much of the world, such as satellite imagery or land surveys.

My results offer empirical support for the argument that equal-area representation targets are likely to have suboptimal conservation impacts. They also show that, even when these targets are achieved, the same impact can be achieved with other prioritisation strategies for a fraction of the cost. For example, the budget required by the biodiversity representation strategy to prevent 50% of the vegetation loss that occurred in the counterfactual scenario was ~3.4 billion 2006 AUD, while the same impact was achieved with the threat prioritisation strategy with a budget of only ~600 million 2006 AUD. Representation targets were counterproductive because loss of woody vegetation was unequal across vegetation types (Table A3.1). As a result, setting equal representation objectives forces the protection of vegetation types unlikely to be cleared. Protecting such areas is not only likely to have low impact, it is also an ineffective use of budget resources, which could have been invested in other high-impact locations.

My results show that relatively simple cost-minimisation and threat prioritisation strategies achieve greater impacts than a representation-based approach. Although both the cost and threat strategy achieved similarly high impacts, the partial overlap between strategies (57%) indicates that impacts were achieved in somewhat different places through different means. Cost-minimisation simply protected a large amount of land (Table 4.1), and inadvertently mitigated a large amount of vegetation loss in doing so. Because in Queensland there are a large number of low-cost, high-threat locations (Chapter 3; Sacre et al. 2019b), many of these locations were inadvertently protected. Threat prioritisation, on the other hand, protected less land, but was more effective at targeting land at risk of imminent vegetation loss. Notably, however, protecting a large amount of land as in the cost strategy might become less efficient when considering other conservation costs, such as management costs, which will be higher for larger areas, and transaction costs, which might be significant if it is necessary to purchase a large number of parcels. Nonetheless, my analysis shows that both strategies are viable ways of achieving high impact. My observation that threat prioritisation is an effective way to achieve high impact aligns with those of other analyses that utilise an *ex ante* model-based approach to generate a counterfactual. Visconti et al. (2010), for example, found that a strategy that attempted to prioritise sites most likely to lose biodiversity (i.e. threat prioritisation) was generally more effective than prioritising sites that will contribute to maximising biodiversity within the PA network. Similarly, Monteiro et al. (2018), found that prioritising sites most likely to lose vegetation – from both habitat clearing and climate change – outperformed, in terms of impact, a strategy that attempted to represent all biodiversity features.

There are several limitations to this analysis that must be considered. First, the *ex post* method relies upon the assumption that areas selected for protection would not lose any vegetation. This might not necessarily be true, because some land users might not comply with vegetation clearing restrictions (Taylor 2013). Second, an *ex post* method measures impacts only retrospectively, and the predicted impacts from this method might not apply forward into the future. However, my general observation that threat prioritisation is more effective than a representation- or biodiversity-focussed approach is consistent with *ex ante* predictive methods that estimated future impacts (Chapter 5; Visconti et al. 2010; Monteiro et al. 2018). Finally, this analysis considers only the case study of vegetation clearing in Queensland. Because the impact of any given strategy depends highly upon the spatial distribution of threats, costs, and biodiversity (Chapter 2; Sacre et al. 2019a), results might differ in other planning regions, and when using alternative measures for these factors. For example, impacts might differ substantially in marine planning regions, because the costs associated with conservation in these regions are typically opportunity costs (forgone economic profits) and management costs rather than acquisition costs (Hunt 2013). Similarly, impacts might differ when using other measures of biodiversity, such as species richness or functional diversity, rather than vegetation types. A key knowledge gap to be explored in further analyses is how the relative impact of strategies might change in response to the spatial relationship between these factors, and particularly how results might differ in regions where costs and threats are more tightly linked than in this case study.

These results offer some encouraging insights for conservation prioritisation. The first is that effective threat-based prioritisations can be designed using fairly simple and widely available datasets, such as historical land clearing data. Many other systematic conservation planning approaches require rigorous data and models on species and/or biodiversity feature distributions. Such prioritisations might not be feasible in countries without such datasets. However, I show that rudimentary approaches that consider costs and threats can be highly effective. In my analysis, the threat prioritisation index uses only data on historical clearance rates within a 20 km radius, but more refined indices could be tested, and might prove more effective. Furthermore, these approaches could be improved with more sophisticated spatial models of expected threats (e.g. Newburn et al. 2006; Monteiro et al. 2018). These could consider not only spatial patterns of historical land clearing, but also other factors, such as soil types, land clearing regulations, proximity to urban centres, land-clearing policies, and susceptibility to climate change. However, of paramount importance is that prioritisation strategies are tested within an impact framework. Although it cannot be expected of conservation practitioners to always develop sophisticated models of conservation impact, it can be expected that the strategies they choose to employ are supported by empirical evidence. Failure to do so will inevitably lead to low-impact, residual conservation.

Chapter 5

Developing a systematic conservation planning framework to maximise the impact of marine protected areas

5 Developing a systematic conservation planning framework to maximise the impact of marine protected areas

5.1 Abstract

In recent years, new developments in conservation science have highlighted the importance of measuring conservation outcomes in terms of impact, whereby interventions are compared to a counterfactual in which no intervention is applied. However, much of the literature has focussed on using an impact framework to evaluate past conservation interventions, while relatively little has focussed on developing conservation planning strategies to maximise future impact. Here, I use the case study of Micronesia to estimate the impact of alternative spatial prioritisation strategies at mitigating the loss of coral reef fish biomass over the next 50 years. I also implement an optimal or 'best case' strategy, which, in combination with the counterfactual, can be used to gauge the relative efficacy of each strategy. In doing so, I highlight the importance of using an impact framework within conservation planning, and show that maximising other typical conservation objectives (e.g. representation, connectivity, wilderness value) does not necessarily lead to improved impact.

5.2 Introduction

Despite increasing conservation efforts across the planet, Earth's biodiversity is in a state of crisis (Hoekstra et al. 2005; Butchart et al. 2010). Failure to counteract biodiversity declines has occurred in large part because of the predominantly *ad hoc* nature of conservation prior to the 21st century, when areas were typically selected for protection based on their aesthetic value, or because they had limited economic value (Grove 1992). Recognition of this problem led to the development of more sophisticated approaches to conservation, known as systematic conservation planning (Margules & Pressey 2000). Nevertheless, evidence of 'residual' conservation, whereby protection is biased towards areas unlikely to lose biodiversity, continues to emerge (Joppa & Pfaff 2009; Devillers et al. 2015; Agardy et al. 2016; Mason et al. 2018).

To combat the residual tendencies of conservation, systematic conservation planning should become focused on developing conservation prioritisation strategies that maximise conservation impact (Pressey et al. 2015). Conservation impact can be measured by estimating biodiversity outcomes (e.g. rates of deforestation, changes in fish population size) when an intervention strategy is applied, and comparing these to the outcomes of a 'counterfactual' strategy, in which no intervention is applied (Ferraro

2009). However, much of systematic conservation planning has focussed on developing prioritisation strategies that select areas for protection base on attributes tangential to impact (e.g. area, species richness, complementarity), rather than impact itself, and/or has neglected to measure the success of any proposed prioritisation strategies using counterfactual-based impact measurements (Pressey et al. 2017).

The lack of impact evaluations throughout the conservation planning literature can be attributed to the difficulty involved in estimating impact, both retrospectively and predictively. Because conservation interventions are often large in scale, and can have immediate and serious consequences for both people and nature, it is difficult and potentially unethical to implement counterfactual control groups. Furthermore, vast amounts of funding and time would be required to achieve the number of replicates standard in other scientific fields. As a result, randomised control trials in conservation impact evaluation are rare and small in scale (Wiik et al. 2019).

When the goal is to estimate the impact of existing protected area (PA) networks, quasi-experimental matching techniques can be used (e.g. Andam et al. 2008; Joppa & Pfaff 2011; Ahmadia et al. 2015; Jones & Lewis 2015). With this approach, protected and unprotected areas are compared only when they have similar characteristics for expected confounding factors (e.g. soil type, elevation, distance to urban centres). However, this approach does not allow for the comparison of multiple alternative prioritisation strategies with which to inform future conservation efforts.

When the goal is to estimate the potential future impact of several alternative systematic prioritisation strategies, and to develop 'rules of thumb' for other planning regions, two modelling approaches are applicable. The first is *ex post* observation of recent actual biodiversity loss to measure outcomes in areas that have historically received no conservation interventions - to serve as a counterfactual outcome - and then to estimate how outcomes might have differed if an intervention had taken place (i.e. if areas that were not previously protected had been protected). The benefit of an *ex post* approach is that it provides a real counterfactual outcome to which prioritisation strategies can be compared. The disadvantage is that this approach can be used only in regions where datasets on historical changes in biodiversity (e.g. changes in vegetation cover) are available. A further disadvantage is that it relies on the assumption that conservation interventions applied in the past will have the same effect if they are applied in the future, which might not hold if any of the factors that affect biodiversity outcomes are variable through time (e.g. temporal changes in human population density or climate).

The alternative approach to estimating the potential impact of prioritisation strategies is to use *ex ante* predictive models of biodiversity change in the future under different assumptions about protection (e.g. Monteiro et al. 2018). The benefit of this approach is that it can be used in areas where historical data on changes in biodiversity are unavailable. A further benefit is that it provides decision makers with specific recommendations about the future outcomes of alternative prioritisation strategies, which can then be utilised directly in conservation policy and practice, compared to an *ex post* analysis, where results might not be directly applicable because of changes in the distribution of biodiversity, costs and threats since the period of analysis.

There are now several examples from the literature using the quasi-experimental matching and *ex post* approaches I describe above. There are, however, few analyses that have used an *ex ante* predictive approach (Visconti et al. 2010b; Monteiro et al. 2018), and none in a marine context. In this chapter, I use predictive models of fishing and coral reef fish biomass to estimate the impact of several alternative conservation prioritisation strategies on the coral reefs of Micronesia. In doing so, I have three objectives: (1) to establish a framework for using counterfactual methods to predict the impact of conservation interventions; (2) to contribute to a growing body of literature using counterfactual-based methods to assess the efficacy of alternative conservation strategies; and (3) to provide counterfactual-based impact evaluations of alternative conservation strategies in a marine context. In achieving these objectives, I hope to provide conservation practitioners and policy makers with robust, evidence-based recommendations for which prioritisation strategies are most likely to maximise impact within their respective planning regions.

5.3 Methods

Case study

I estimated the impact of several alternative spatial conservation prioritisation strategies (discussed below) on coral reef fish biomass over 50 years across five jurisdictions in Micronesia: the Federated States of Micronesia (FSM), Guam, the Commonwealth of the Northern Mariana Islands (CNMI), Palau, and the Marshall Islands (MI). In Micronesia, marine conservation has historically been dominated by non-systematic approaches (Isechal et al. 2014). With increasing demand for seafood in foreign countries (e.g. China and Japan) in recent years, commercial fishing pressure on Micronesian coral reefs has increased (Houk et al. 2012). This growing pressure is particularly concerning given the importance of reef fisheries for both food and income for a large portion of the population (Zeller et al. 2007). In recognition of this problem, more systematic PA network designs are beginning to be implemented across the region (The Federated States of Micronesia 2002; Micronesia Conservation Trust 2014). The most notable initiative is the Micronesia Challenge, which aims to protect 30% of marine resources by

2020 (Houk et al. 2015). For these reasons, Micronesia presents a useful case study in which new impact evaluations could prove useful for the implementation of evidence-based systematic conservation planning.

Estimating conservation impact

There were two components to my measure of conservation impact: first, the amount of biomass loss that was mitigated by protection (i.e. the difference in biomass loss between protection and the counterfactual); and second, the amount of biomass recovery that occurred after protection. The conservation impact of each prioritisation strategy was calculated as the sum of these two components. For my analysis, coral reefs in Micronesia were divided into 320,715 one hectare, square planning units. I measured the conservation impact of protecting any given planning unit using models of fish biomass and fishing threat adapted from those produced by The Nature Conservancy's Mapping Ocean Wealth (MOW) project (Harborne et al. 2018). Note that the MOW model of fishing is referred to as 'fishing impact', though throughout this chapter I refer to the model as 'fishing threat' to avoid confusion with 'conservation impact'.

The MOW fishing models used data on mean parrotfish length collected using underwater visual and video surveys from 470 sites across Micronesia. Mean parrotfish length has been shown to be a good proxy for fishing threat (Vallès & Oxenford 2014; Vallès et al. 2015). These data served as the basis of Boosted Regression Tree (BRT) models, which extrapolated values across the region based on a variety of predictor variables, such as distance to ports, human population density per reef area, and reef geomorphology. The MOW fish biomass models used data on the estimated weight of 19 key reef fish species collected from a separate set of underwater surveys at 657 sites across Micronesia. These 19 species were selected because they are present across the entire region, were recorded at each survey site, and represent a broad range of reef fish taxa. Biomass values were also extrapolated using BRT models based on a range of predictor variables, including the extrapolated values of fishing threat. The fishing threat model was used as a predictor variable in the biomass model to produce a separate prediction of potential fish biomass, which adjusted all fishing values to 0, and therefore modelled unfished biomass (Harborne et al. 2018).

In my analysis, to calculate the impact of protecting each planning unit, I used the models of fishing threat, fish biomass, and potential fish biomass to estimate fish biomass recovery (if protected) and decline (if left unprotected). I assumed that any planning units selected for protection would fully recover to potential levels within the 50-year planning period. This assumption was based on evidence that the population recovery times of reef fish species are typically within the range of a few years for small, fast growing species, to a few decades for larger species (Russ & Alcala 1996; McClanahan et al. 2007; Abesamis et al. 2014; MacNeil et al. 2015). Thus, the total amount of recovered biomass in protected planning units was calculated as the potential biomass minus the current standing biomass.

To estimate the loss of fish biomass in unprotected planning units, I assumed that the relationship between fishing threat and loss of biomass each year exhibited a power relationship. This assumption was based on evidence that, as sites undergo ecosystem shifts and trophic cascades, losses to different metrics of biodiversity can accelerate in a non-linear fashion (McClanahan et al. 2011). Thus, I modelled the loss of biomass according to the following function:

$$B_t = B_{t-1} \times \left(1 - (F^a \times M)\right), \text{ for } t = 2,3,4,\dots,50$$

Equation 5.1

where B is the biomass in a planning unit at time t, F is the fishing threat in a planning unit, a is a constant that determines the shape of the power function, and M is the maximum percentage of biomass that can be lost in a cell each year. A default value of 4 was used for a (see Appendix 4 for alternative values). A default value of 20% was used for M, based on studies that suggest areas previously protected from fishing can lose a significant proportion of their fish biomass (e.g. over 50%) in 2 to 5 years (Russ & Alcala 1996). Biomass in each planning unit at $t = 1$ was the current standing biomass from the MOW model.

It should be noted that the MOW fishing model produced by Harborne et al. (2018) estimated the historical cumulative results of fishing, which might not necessarily reflect ongoing fishing pressures. Some locations might be significantly degraded from fishing activities, and might have minimal standing biomass. As such, a high cumulative fishing threat could be maintained with relatively low levels of ongoing fishing activity. This possibility is somewhat negated in the model of biomass loss, which estimated losses as a percentage of standing biomass (i.e. areas with low biomass will lose relatively little biomass). However, the model of biomass loss still assumed that historical fishing patterns were indicative of ongoing fishing activities.

Prioritisation strategies

I estimated the impact of four alternative PA network design strategies: (1) representation; (2) representation and connectivity; (3) frontier prioritisation; and (4) wilderness prioritisation. The objectives and implementation procedures for each strategy are detailed in Table 5.1. I assumed that planning units within existing protected areas were unprotected at the beginning of the planning period, were available to be selected for protection, and would lose biomass if left unprotected.

Strategies 1 and 2 utilised a typical representation-based approach to systematic conservation planning, with the goal of representing equally each biodiversity feature within a planning region. I chose to estimate the impact of a representation-based approach because it is the most widespread approach to systematic conservation planning, both in conservation science (Margules et al. 2002; Kukkala & Moilanen 2013) and in conservation policy (e.g. Fernandes et al. 2005), and is central to the systematic approaches currently used in Micronesia (The Federated States of Micronesia 2002; Micronesia Conservation Trust 2014).

Strategies 3 and 4 took alternative approaches to conservation prioritisation, with the aim of prioritising features based on the level of threat they faced. Frontier prioritisation aimed to protect features facing the greatest level of threat (i.e. at the threat frontier). Wilderness prioritisation took the opposite approach, prioritising the least threatened and most pristine features, in order to pre-empt any threats they might face in the future. Although frontier and wilderness strategies have directly opposing objectives, both strategies are advocated in the literature (frontier: Hoekstra et al. 2005; Ricketts et al. 2005; Venter et al. 2014; wilderness: (Mittermeier et al. 2003; Klein et al. 2009; Watson et al. 2018). Which approach should be favoured remains the subject of debate (Brooks et al. 2006; Armsworth 2018; Sacre et al. 2019a; Chapter 2).

Each prioritisation strategy was implemented within each country separately, which is consistent with the scale at which conservation plans are typically implemented in Micronesia (Remengesau et al. 2006; Isechal et al. 2014). Impacts were measured within each country, and across Micronesia as a whole. The amount of fish biomass lost and recovered after the implementation of each strategy was then compared to a counterfactual strategy, in which no planning units were protected. I also formulated an "optimal" strategy as a best-case to which other strategies could be compared. For the optimal strategy, potential biomass loss and recovery, and therefore total potential impact, was known, and planning units with the greatest impact/cost ratios were selected for protection.

Budget and costs of protection

To estimate costs of protection, I created a surrogate for the opportunity cost (i.e. forgone profits from fishing) of protecting each planning unit. Opportunity costs were estimated by multiplying the human population density within 200 km per reef area of each cell by the fish biomass currently estimated within each cell, such that reefs with high biomass and large surrounding populations had high opportunity costs. A distance of 200 km was used for consistency with other analyses (Williams et al. 2015; Harborne et al. 2018), and based on the assumption that both commercial and artisanal fishing activities are unlikely to extend beyond this distance. Population densities were obtained from the MOW models, which sourced data from the Socioeconomic Data and Applications Center database (SEDAC, 2018). This surrogate assumed that protection of sites with most abundant fishing resources, and with the greatest number of people in their vicinity, would cause the greatest losses of food and/or income. I also added a minimum cost of protection to each cell that was equivalent to the average opportunity cost of all planning units, so that none were free to protect. Each strategy was constrained by the same budget, which was equivalent to 20% of the total cost of protecting all planning units within each country.

Scenarios of fishing displacement and human population growth

There is evidence from both terrestrial and marine contexts that threats to biodiversity can be displaced to nearby areas after protection (Ewers & Rodrigues 2008; Moilanen & Laitila 2016). To account for this possibility, I also measured conservation impact under an alternative scenario in which fishing within planning units selected for protection was displaced to nearby planning units. For this scenario, I distributed fishing threat from each protected planning unit equally to all unprotected planning units within a 20 km radius. I chose to estimate displacement within a 20 km radius because artisanal fishers typically travel distances within that range to reach fishing sites (Daw 2008; Metcalfe et al. 2017; Navarrete Forero et al. 2017). However, I also provide analyses in Appendix 4 using displacement distances of 1 km and 5 km. The displacement model was implemented using custom Python code in ArcGIS (available upon request).

To avoid the possibility of some planning units experiencing unrealistically high fishing threat after displacement, I assumed that fishing threat in any one planning unit could not exceed the maximum observed fishing threat (maximum value = 1). The displacement of fishing threat to each planning unit depended on the unique combination of planning units selected for protection within the displacement radius. Therefore, the optimal strategy could not optimise impacts based on fishing displacement, because doing so would require calculating the increased fishing threat to each planning unit for all possible combinations of planning unit protection within the displacement radius of each respective planning unit, which would be computationally impracticable. Thus, the optimal strategy should not be considered truly optimal for the displacement scenarios.

One of the proposed benefits of a wilderness strategy is that it will secure low-cost areas likely to be subject to increased threats in the future. For this reason, I also considered a scenario in which fishing impacts were dynamic throughout the 50-year period, increasing according to human population growth. I assumed that human population density per reef area grew at a rate of 2% per year, which is slightly above the global average rate. I then re-ran the MOW fishing models using the increased population densities and re-calculated biomass decline in each planning unit each year according to changes in the fishing model. For all analyses and all scenarios, the fishing threat metric from the MOW models (a unit-less measure between 0 and 1) was re-scaled such that a value of 1 represented the highest fishing threat observed over the whole 50-year period with population growth incorporated in the model. Thus, the maximum possible value was 1, and the amount of biomass loss that occurred according to a given value of fishing threat was consistent across scenarios. It should be noted that an annual population growth of 2% is likely to be an overestimate for Micronesia; population growth is stagnating in many Micronesian countries (United Nations Population Fund 2018), and so the default scenario of no population growth might better reflect reality.

The impact of each prioritisation strategy was measured across four scenario variations: (1) without displacement and without human population growth; (2) without displacement and with human population growth; (3) with displacement and without human population growth; and (4) with displacement and with human population growth.

5.4 Results

Across the whole of Micronesia, a frontier prioritisation strategy had the greatest impact for all scenarios including and excluding displacement of fishing and human population growth (Figure 5.1, Table 5.2). These results were consistent regardless of whether representation targets were set to 30%, 50% or 100% (Figure A4.1), and were unaffected by variation in the model parameters (Figures A4.4 and A4.6).

Across all scenarios and all countries, a frontier prioritisation strategy achieved 85-90% of the impact of the optimal scenario. Wilderness prioritisation was less effective, achieving 54-63% of the impact of the optimal scenario. Both representation-based strategies were generally less effective than frontier and wilderness strategies, and their results were more variable (Table 5.2). A representation strategy without connectivity achieved 33-49% of the impact of the optimal scenario. A representation strategy with connectivity achieved 16-59% of the impact of the optimal scenario. While the relative efficacy of each strategy varied between countries, in most cases frontier prioritisation was the most effective (Table 5.2). An exception was the Marshall Islands, where a wilderness strategy had the greatest impact when displacement occurred (Table 5.2).

Incorporating displacement of fishing reduced the impact of some strategies. These effects were most notable in Guam, where displacement caused the wilderness and representation-based strategies to have negative impacts (i.e. to perform worse than the counterfactual strategy of no action; Table 5.2). Incorporating human population growth had less dramatic effects than the displacement of fishing, but caused much larger losses of fish biomass overall. Most notably, the impact of the wilderness prioritisation strategy increased when population growth occurred, while frontier and both representation-based strategies were less affected (Figure 5.1, Table 5.2).

Table 5.1 The objectives and implementation procedures for each of the prioritisation strategies.

Strategy	Objective	Implementation
Representation (no connectivity)	Represent 18 different coral reef habitat types. Habitat types were the level four geomorphological classes from the Millennium Coral Reef Mapping Project (Andréfouët et al. 2006).	This strategy was designed using the conservation planning software Marxan (Watts et al. 2009). In the default strategy, representation objectives in Marxan were set to 30% for each habitat type (but see Appendix 4 for strategies using 50% and 100% objectives).
Representation (connectivity)	As above, but also attempting to maximise connectivity between planning units.	For this strategy, representation objectives were set as above, while also progressively increasing the boundary length modifier (BLM) in increments of 10 for each strategy until it could no longer be increased without exceeding the budget.
Frontier	Prioritise planning units under high fishing threat.	For this strategy, planning units were sorted from highest to lowest fishing threat. The top 30% were then taken to the next step of the prioritisation. In the second step, the ratio of biomass to cost was calculated and planning units were sorted from the highest to lowest ratios. Selection for protection then proceeded from the top of the list until the budget was reached. This strategy was implemented using heuristics in R.
Wilderness	Prioritise planning units under low fishing threat.	This strategy used a similar method to the frontier prioritisation, except that, in the initial step, planning units were sorted from lowest to highest fishing threat, and the top 30% were taken to the second step.
Counterfactual	This strategy served as a counterfactual in which no planning units were protected.	No planning units were allocated for protection.
Optimal	This strategy was intended as a best-case, whereby planning units with the highest predicted impact/cost ratio were selected for protection.	For this strategy, models of fish biomass decline and recovery described in the *Methods* were used to determine the total potential impact of protection of each planning unit for the entire 50-year period. The impact/cost ratio was then calculated for each planning unit, and all units were sorted from highest to lowest ratios. Planning units with the highest ratios were then progressively selected for protection until the budget was reached. This strategy was implemented using heuristics in R.

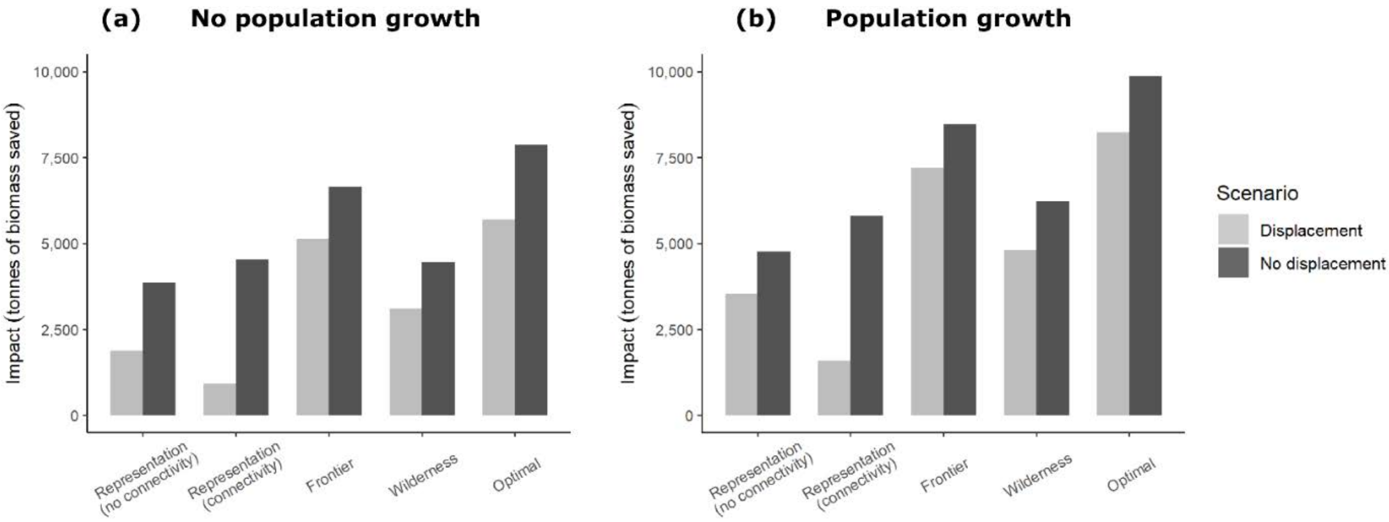

Figure 5.1 The impact of alternative prioritisation strategies measured as the total coral reef fish biomass saved by each strategy relative to the counterfactual strategy. Specifically, impact was measured as $S - C$, where C is the total biomass remaining across the whole of Micronesia over the 50-year planning period when the counterfactual strategy was implemented, and S is the biomass remaining when the corresponding strategy was implemented. Light grey bars indicate impact without displacement of fishing after protection. Dark grey bars indicate impact without displacement of fishing. Panel (a) shows the impact of each strategy without population growth over the 50-year planning period. Panel (b) shows the impact of each strategy with population growth rate of 2% per year.

Table 5.2 The impact of four prioritisation strategies relative to the optimal strategy. Impact was measured as $S - C / O - C$, where S is the total fish biomass remaining after the 50-year planning period when strategy S is implemented, C is the total fish biomass remaining when the counterfactual strategy is implemented, and O is total fish biomass remaining when the optimal strategy is implemented. Impacts are presented under the four different scenario combinations. Impact was measured across the whole of Micronesia, and within each country: the Federated States of Micronesia (FSM), Guam, the Commonwealth of the Northern Mariana Islands (CNMI), Palau, and the Marshall Islands.

Country	Representation (no connectivity)	Representation (connectivity)	Frontier	Wilderness
Impact with no displacement, no human population growth				
FSM	54%	51%	81%	46%
Guam	32%	59%	96%	32%
CNMI	22%	63%	82%	34%
Palau	39%	57%	87%	67%
Marshall Islands	54%	69%	90%	82%
All countries	49%	58%	85%	57%
Impact with displacement, no human population growth				
FSM	29%	34%	93%	34%
Guam	-43%*	-16%*	92%	-62%*
CNMI	4%	29%	79%	25%
Palau	10%	9%	78%	68%
Marshall Islands	79%	-24%*	94%	123%**
All countries	33%	16%	90%	54%
Impact with no displacement, human population growth incorporated				
FSM	44%	51%	81%	45%
Guam	36%	64%	96%	37%
CNMI	27%	68%	85%	48%
Palau	44%	59%	87%	78%
Marshall Islands	60%	68%	92%	88%
All countries	48%	59%	86%	63%
Impact with displacement, human population growth incorporated				
FSM	86%	28%	29%	23%
Guam	94%	-9%*	4%	21%
CNMI	89%	51%	28%	46%
Palau	86%	81%	33%	36%
Marshall Islands	89%	113%**	81%	-2%*
All countries	87%	58%	43%	19%

*In some cases values are negative when a strategy had a lower impact than the counterfactual scenario. This was possible only in scenarios that incorporate displacement, because such strategies can displace fishing to adjacent reefs and cause more biomass decline than would have otherwise occurred at those reefs.

** Because the analysis contained a large number of planning units, the optimal strategy was unable to consider the effects of displacement, so some strategies outperformed the optimal strategy (i.e. impact greater than 100%) when displacement was considered.

5.5 Discussion

My results offer important insights for conservation impact evaluation. While the literature on conservation impact has highlighted the importance of measuring counterfactual outcomes (Ferraro 2009; Jones & Lewis 2015; Jayachandran et al. 2017; Pynegar et al. 2018; Wiik et al. 2019), relatively little attention has been paid to considering optimal outcomes. My analyses allow comparison between both counterfactual and optimal (or "best case") prioritisation strategies. The value of the optimal results is that they indicate the potential range of impact results beyond the counterfactual outcomes of not acting. For example, while the representation strategies improved on the counterfactual (Figure 5.1), they generally achieved less than half the impact of the optimal strategy (Table 5.2). Without the comparison to more effective strategies, it might be concluded that representation strategies achieved notable improvements compared to the counterfactual. Only with an optimal comparison can we see that the frontier strategy not only outperformed other strategies, but also generally had close to optimal impacts (Figure 5.1, Table 5.2).

My results also offer insights for the field of conservation policy and practice. Perhaps the most striking result is the relatively small impact achieved by representation-based prioritisation strategies compared to purely threat-based strategies. This is a particularly important finding given the widespread use of representation targets as objectives and metrics of success in conservation planning and policy (Kukkala & Moilanen 2013). Representation-based strategies might be ineffective for two reasons. First, if the most threatened areas are also the most costly, seeking to represent a particular proportion of each habitat while also minimising costs will lead to the unnecessary protection of the least threatened areas within each habitat type, a tendency observed in the rezoning of the Great Barrier Reef Marine Park (Devillers et al. 2015). Second, threats are likely to be distributed unequally across reef habitat types. For example, shallow fringing reefs, because of their greater accessibility to fishers, are generally exposed to higher fishing pressure than deeper offshore reefs (Lindfield et al. 2016). Therefore, in seeking to equally represent all habitat types, representation-based strategies force the protection of low-threat habitats less likely to lose biodiversity (Harborne 2009). This problem could be exacerbated if the most threatened habitat types also tend to have higher biodiversity values (Sacre et al. 2019a; Chapter 2). This is particularly relevant in this case study, where fishers are likely to target sites with high fish biomass.

Although the literature has long recognised that threats (i.e. vulnerability) need to be incorporated into systematic conservation planning (Pressey et al. 1996; Pressey & Taffs 2001; Wilson et al. 2005; Visconti et al. 2010a), this has happened rarely. The results from this analysis support the use of threat-based prioritisation strategies, particularly those that target high-threat frontier areas. The largest criticism of this approach is that targeting high-threat areas is costly, because protecting such areas incurs high opportunity and/or acquisition costs (Mittermeier et al. 2003). My analyses highlight that these frontier areas can actually be highly cost-efficient when efficiency is measured in terms of impact compared to the counterfactual. Avoiding such areas, as was the objective with the wilderness strategy, did not improve cost-efficiency, even under scenarios of human population growth (Figure 5.1b). Targeting areas closer to the threat frontier, therefore, is likely to be a good 'rule of thumb' for practitioners working in data-poor regions where *ex ante* predictions of impact cannot be implemented.

There are several limitations to my analyses that require consideration. First, I used only an *ex ante* predictive modelling approach to measuring conservation impact. The drawback of this approach is that the models are likely to be a simplification of the factors that affect reef fish biomass. Reef fish biomass is likely to be affected not only by fishing, but also by a synergistic combination of long-term changes in ocean temperature, ocean acidification, and pollution, among other factors (Halpern et al. 2007), some of which might alter the relative impact of strategies. Second, I consider only biomass as a measure of biodiversity value. Outcomes might vary when using alternative measures of biodiversity values, such as ecosystem functioning and services, or functional richness. For example, protecting wilderness areas might have increased efficacy when considering these measures, because such areas are likely to maintain higher levels of ecosystem functioning. Third, in my analysis I assume that threats from fishing completely cease within areas selected for protection. However, in reality, threats might continue in protected, from, for example, illegal fishing activities, and the degree of non-compliance might vary according to differences in fishing pressure and suitability. Finally, in my analysis, only coral reef ecosystems within Micronesia were considered. These results, therefore, might not be directly applicable to other regions containing different ecosystem types. Recovery dynamics, for example, might differ between species in terrestrial ecosystems and marine ecosystems because of differing dispersal mechanisms (Carr et al. 2003).

These results highlight that counterfactual methods are not only an essential component of conservation impact evaluation (Pressey et al. 2017), but should also be central to conservation planning. Further analyses should explore yet more alternative prioritisation strategies, and combinations of strategies, as well as exploring alternative metrics of impact. For example, rather than simply measuring changes in biomass, more sophisticated measures might break down impacts across species and weight these according to the species' vulnerability or rarity (e.g. Pressey et al. 2004). However, the primary objective of this study was to highlight the importance of using counterfactual and optimal-based methods to compare any proposed planning strategies. While all of the strategies I tested would have scored well at achieving each of their respective targets, their ability to reach these targets (i.e. representation, connectivity, cost) said little about their impact. Thus, while it cannot be expected that all conservation plans incorporate estimates of impact, it is important that any planning strategies that are being utilised have been tested within an impact framework, so that conservation science can progress further towards utilising evidence-based assessments to support policy and practice.

Chapter 6

General discussion

6 General discussion

The overarching goal of this thesis is to develop a systematic conservation planning approach to maximise impact, and to identify high-impact strategies for use in conservation policy and practice. To measure and estimate conservation impact, it is essential to consider counterfactual outcomes, which are the outcomes that occur when no intervention takes place. Counterfactual scenarios are currently rare in the field of conservation prioritisation and, as such, the literature has been limited in its ability to provide conservation practitioners with evidence of high-impact strategies. As a result, conservation policy and practice across the globe is dominated by prioritisation strategies that have questionable impact, and evidence of residual reserves continues to emerge.

In addition to the knowledge gap in methodological procedures to estimate impact in conservation planning, a key knowledge gap remains concerning which prioritisation strategies should be favoured or avoided if the objective is to maximise impact (e.g. habitat representation, threat minimisation, or wilderness maximisation). In many cases, conservation practitioners will be unable to develop sophisticated models of projected impacts specific to their respective planning regions, either because of time, funding, or data limitations. As such, it is important that the conservation literature establishes an evidence base from which practitioners can draw to implement high-impact interventions. Of particular importance is the assessment of widely adopted protection strategies, such as equal-area representation, and comparison to promising alternatives, such as those that incorporate threats. Given the millions of dollars of funding that are allocated toward conservation actions every year, and the imminence and severity of current biodiversity declines, these knowledge gaps require immediate attention.

Throughout this thesis, I have addressed these knowledge gaps by aiming to achieve three objectives (Figure 6.1). These knowledge gaps and objectives were detailed in the general introduction (Chapter 1). In the subsequent data chapters (Chapters 2 – 5), I addressed each of these objectives. In the present chapter (Chapter 6), I first describe how each of these data chapters has achieved these objectives. I then discuss limitations of the research conducted throughout this thesis, and suggest directions for future work.

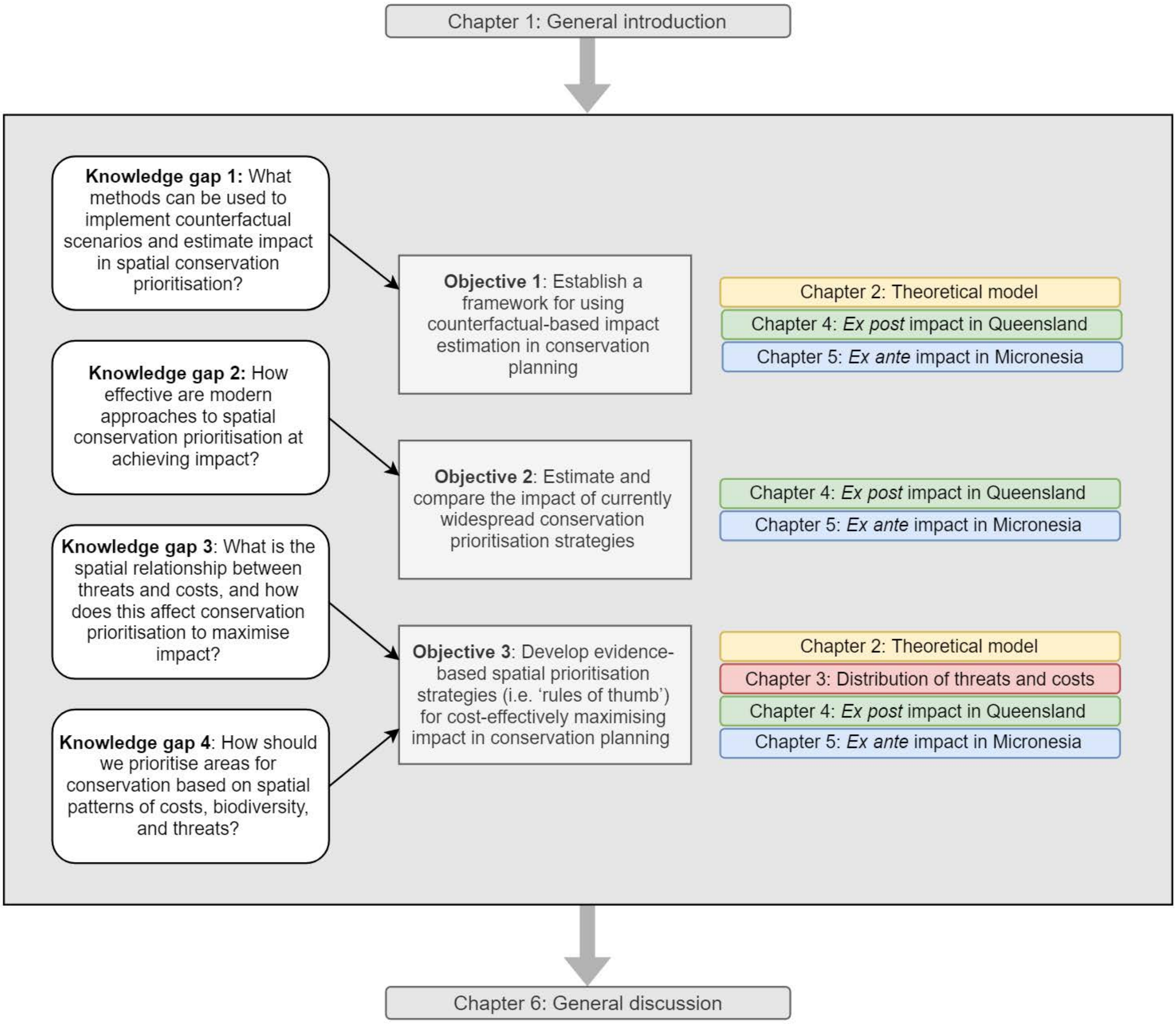

Figure 6.1 A schematic diagram of knowledge gaps and objectives addressed in this thesis, and which chapters contribute to achieving each objective.

6.1 Thesis objectives

Objective 1: Establish a framework for using counterfactual-based impact estimation in conservation planning

This objective was addressed in Chapters 2, 4, and 5, where I demonstrated how to design conservation prioritisation strategies that consider a counterfactual scenario. In Chapter 2, I provided a theoretical foundation for measuring the impact of alternative prioritisation strategies, showing that relative impacts can only be measured by comparing outcomes to a counterfactual scenario. In Chapter 4, I built upon this foundation by developing an *ex post* method for retrospectively estimating the impact of conservation strategies using empirical data. I used a high-resolution dataset of land acquisition costs and vegetation clearing in Queensland to demonstrate that counterfactual outcomes can be measured using historical data on changes in biodiversity in unprotected areas, and the impact of alternative prioritisation strategies can be estimated by simulating protection in the same area over the same time period. Using these methods, I found that a prioritisation strategy that prioritised high-threat frontier areas had a greater impact than several alternative strategies, including cost minimisation, and attempting to equally represent a range of vegetation types.

In Chapter 5, I demonstrated an alternative approach to estimating counterfactual outcomes, which is to use *ex ante* predictive models of biodiversity outcomes in the absence of protection. This approach is useful if historical data on biodiversity changes are not available, and is critical for estimating the potential future impact of specific alternative strategies. In this analysis, I modelled changes in coral reef fish biomass over a period of 50 years into the future, comparing several alternative prioritisation strategies to a counterfactual. Using this method, I also found that prioritising high-threat frontier areas had a greater impact than prioritising areas based on representation targets or prioritising low-threat wilderness areas. Importantly, in this chapter I also demonstrated the importance of considering optimal or 'best case' scenarios. While the counterfactual comparison is essential to gauge the relative impact of strategies, an optimal comparison is necessary to gauge the absolute difference in impact between strategies.

These analyses are some of the first to incorporate impact estimation into systematic conservation planning. While other analyses have developed systematic conservation plans that consider counterfactual outcomes in specific case studies (Newburn et al. 2006; Monteiro et al. 2018), the research in this thesis builds substantially on this literature in two ways. First, in this thesis, I compared a range of alternative prioritisation strategies, rather than developing a single strategy to maximise impact. This is useful because, in many cases, conservation practitioners are unlikely to be able to develop sophisticated models to measure impacts. As such, it is necessary to establish an evidence base of the impact of a range of alternative prioritisation strategies that can be used as 'rule of thumb' approaches to conservation prioritisation. Second, in this thesis, I estimated the impact of alternative strategies using both *ex post* and *ex ante* methods, using both terrestrial and marine case studies. The consistency of my results across case studies and methodologies indicates that these results are likely to apply to a broader context.

Objective 2: Estimate and compare the impact of currently widespread conservation prioritisation strategies

Throughout my thesis, I have estimated the impact of a variety of alternative conservation prioritisation strategies. In Chapter 4, I used the case study of Queensland to estimate the impacts of strategies that consider, either alone or combination, costs, threats and biodiversity representation. In Chapter 5, I used the case study of Micronesian coral reefs to compare strategies that aim to prioritise high-threat frontier areas, low-threat wilderness areas, or to achieve representation targets.

Perhaps the most significant finding of these chapters was the consistently poor performance of representation-based strategies at achieving impact. These results are particularly relevant given the prevalence of representation targets in conservation planning and policy worldwide. One of the most notable examples is the Great Barrier Reef Marine Park, which established zones based on objectives to represent at least 20% of the reef area within each of 70 bioregions (Fernandes et al. 2005). Such representation targets also form part of international conservation policy, such as the Aichi Target 11, which aims to ensure that the global protected area networks is "ecologically representative" (Secretariat of the Convention on Biological Diversity & United Nations Environment Programme 2014). However, I showed in Chapters 4 and 5 that pursuing representation objectives was counterproductive to maximising impact, because threats are generally unequally distributed across biodiversity features. In attempting to equally represent all biodiversity features, representation strategies force the protection of low-impact, residual areas unlikely to lose biodiversity.

Another widely utilised approach to spatial prioritisation is wilderness conservation (e.g. Klein et al. 2009). In Chapter 2, I showed that the relative efficacy of wilderness prioritisation depends to a great extent on a variety of factors, such as conservation planning timeframes, and spatio-temporal patterns of biodiversity, costs and threats. In Chapter 5, I showed that wilderness prioritisation generally outperformed representation-based strategies, but generally achieveed lower impacts than strategies that prioritised high-threat frontier areas. In some cases, however, such as in the Marshall Islands, wilderness prioritisation was most effective when threats increased through time and were displaced to surrounding unprotected areas after protection. It might seem intuitive that strategies that attempt to secure areas under low threat are likely to achieve low impacts, but these strategies are widely advocated in the literature under the premise that it is favourable to secure large, pristine, intact landscapes (Klein et al. 2009; Watson et al. 2018). My results indicate that careful consideration of the factors that are likely to affect impacts is necessary when implementing wilderness prioritisation strategies.

Objective 3: Develop evidence-based spatial prioritisation strategies (i.e. 'rules of thumb') for cost effectively maximising conservation impact

The final objective of this thesis was to develop new strategies for conservation prioritisation that progress beyond the conventional and widespread approaches of modern conservation, and that more effectively maximise impact. I detailed in Chapter 1 that a large body of research has established sophisticated methods for efficiently reaching biodiversity targets, and a wide range of software tools have been developed accordingly. However, as I showed in Chapters 4 and 5, these approaches might not necessarily achieve high impacts. What prioritisation methods should, therefore, be utilised to maximise impact?

In Chapter 3, I identified and addressed a significant knowledge gap in the literature that has limited our ability to develop high-impact plans. That gap is our lack of understanding of the spatial relationship between costs and threats. In this analysis, I showed that the spatial correlation between costs and threats is weak, counter to the assumptions often made in the conservation literature. As such, a large number of low-cost, high-threat sites exist, and these areas offer great potential for high-impact conservation planning. Therefore, the widespread assumption that protecting sites under high threat also necessarily incurs high conservation costs is likely to be a poor generalisation. Instead, conservation prioritisation should seek out conservation bargains: high-threat sites with low cost.

This conclusion was supported by my results from Chapter 4, which showed that, in the case study of Queensland, prioritising sites under the greatest threat and with the lowest acquisition costs was an effective way to achieve a high impact. Interestingly, in this case study simply prioritising the cheapest sites was also effective, but prioritising high-threat sites became increasingly effective when larger budgets were available (Figure 4.2). I observed the same result in Chapter 5, where a heuristic ranking of sites from highest to lowest fishing threat achieved close to optimal impact for most countries in Micronesia, under different scenarios of population growth and fishing displacement. The conclusion to draw from these analyses is that conservation planners working in data-poor regions could easily implement a simple strategy prioritising sites facing the highest threat that will likely have high impact. However, as I showed in Chapter 2, planners should account for the various factors, where appropriate data are available, that might affect the best strategy.

6.2 Thesis limitations and directions for further research

Incorporating conservation scheduling

It is well understood from the conservation literature that outcomes can be affected by how actions are scheduled (Pressey & Taffs 2001; Visconti et al. 2010a). For example, protected areas (PAs) might be implemented all at once, or incrementally over several years (Kininmonth et al. 2019). In many cases, conservation funds are allocated periodically, such as for federal and state PAs, for which departments will typically receive annual allowances for the acquisition and management of areas for protection. As such, one key limitation of this thesis is that, in all analyses, I allowed PA systems to be implemented entirely at the beginning of the planning period. Future analyses should explore how PA scheduling might affect impacts. One important consideration is the potential for implementation to be temporally residual. That is, low-impact residual areas might receive protection sooner than other areas where stakeholders from extractive industries (e.g. agriculture, timber, mining) offer resistance to implementation. As such, planning strategies that prioritise areas at the threat frontier might suffer substantially reduced impacts because of modification or delays in the implementation stage. Another concern is the potential for downgrading, downsizing, and degazettement (PADDD) after PAs are implemented, which might offset the benefits of some strategies. Frontier areas, for example, which might be more accessible than wilderness areas if resources are discovered within their bounds, might be more susceptible to PADDD (Symes et al. 2016).

Consideration of timeframes and time discounting

In Chapter 2, I showed that the impact of alternative strategies depends to a large degree on the time frame over which impacts are measured. An additional factor that I did not consider in the analyses of this thesis is that of time discounting (Armsworth 2018). Time discounting describes a process whereby impact or economic benefits are considered more favourable if they are realised sooner in time. For example, in a region where the conservation of food fish resources is desired, surrounding communities are likely to favour near-term recovery over long-term recovery (Smith et al. 2010). The phenomenon of time discounting has been explored in detail in the context and frontier and wilderness priorities by Armsworth (2018), who showed how economic and ecological discounting can affect priorities. Further research should analyse how time discounting might affect the relative impacts of a variety of alternative prioritisation strategies across a range of case studies, and explore how variation in opportunity costs and rates of time discounting might vary across stakeholder groups (e.g. conservation of marine food fish resources versus terrestrial vegetation).

Limitations of case studies and the need for evidence across a range of circumstances

One of the primary objectives of this thesis has been to establish general 'rule of thumb' conservation strategies that can be applied across a broad range of planning regions and conservation circumstances. However, as I showed in Chapter 2, the impact of any given conservation strategy can be highly variable depending on a variety of factors, such as the spatial distribution of threats, biodiversity and costs, the timeframes within which conservation impacts are desired, and temporal changes in threats. These factors will vary according to the unique ecological characteristics of a particular planning region, and according to historical and socioeconomic circumstances. For example, I showed in Chapters 4 and 5 that frontier prioritisation outperforms strategies that focus on protecting wilderness areas, and that threat-based strategies outperform those that focus on representation and connectivity in a terrestrial planning region (Queensland) and a marine planning region (Micronesia). However, similar analyses might not reach the same conclusions in planning regions that have historically been more extensively degraded, such as where coral reef ecosystems have been more severely overfished, and where population pressures and demands for food fish are higher than in Micronesia. In such places frontier conservation might prove less effective because high-threat areas have been degraded to the point where recovery is irreversible, or because historical pressures have caused ecosystem shifts.

Of particular importance in the consideration of different planning regions is the factor of extent, and the possibility of utilising different strategies across different extents. In Chapter 2, I described how spatial patterns of biodiversity could vary over different extents, with biodiversity generally being positively correlated with population density over large extents (i.e. global, national), but inversely correlated across smaller extents. This phenomenon occurs because, generally across large extents, humans tend to settle in locations of high primary productivity, rich soils, and proximal to freshwater resources (Luck 2007). In such locations, biodiversity also tends to flourish. However, over smaller extents, human development negatively impacts the biodiversity of occupied and nearby areas through habitat clearance and degradation. I showed in Chapter 2 that variation in the spatial relationship between biodiversity and threats can have a profound effect on which strategies have the greatest impact. When the relationship is positive, frontier prioritisation becomes more effective, but when the relationship is negative, wilderness prioritisation becomes more effective.

This observation highlights exciting directions for future research. Specifically, further research could explore how well combinations of different strategies across different extents perform. A reasonable hypothesis is that it will be most effective to prioritise high-threat areas at global and national extents, but to utilise wilderness or representation focussed strategies in the smaller jurisdictions within these areas. A key question then also remains: at exactly which extent should priorities switch?

Advanced prioritisation strategies to approximate the optimal

Throughout this thesis, I have assessed the efficacy of relatively simple prioritisation strategies. These typically involved simple ranking procedures, such as those of the 'frontier' strategy which simply ranked sites from highest to lowest threat/cost ratios, and the 'wilderness' strategy, which prioritised low-threat sites. Future exercises should assess more advanced prioritisation strategies so that conservation practice might begin to achieve closer to optimal impacts.

Given the ubiquity of representation targets in conservation practice, and their incorporation into national and international protected area policy, it might prove more expedient to assess the performance of adapted representation strategies. A viable option is to set representation targets according to the degree of threat each biodiversity feature is expected to face (e.g. Burgman et al. 2001; Pressey et al. 2003). For example, in Queensland, the most threatened broad vegetation group (BVG) is the brigalow (*Acacia harpophylla*) dominated woodlands, which lost 27% of their extent between the years of 2006 and 2016. Mulga (*Acacia aneura*) dominated woodlands and semi-evergreen to deciduous microphyll vine thicket habitats are also significantly threatened, having both lost 10% of their extent over the same period. Thus, it is likely to prove more effective to set high protection targets (e.g. 90 or 100%) for these BVGs, while setting lower targets for less threatened BVGs.

The barriers to developing high-impact conservation prioritisation strategies are a failure to use appropriate methods (i.e. without a counterfactual), lack of available data, and inaccuracies and uncertainty surrounding the assumptions made when attempting to predict impact. Therefore, the more these barriers are minimised in future research, the closer prioritisation strategies will come to maximising impacts. Several additional datasets and models that could be added to future analyses include: information on biodiversity persistence in relation to fragmentation and connectivity, higher-resolution datasets of threats and biodiversity, more complex predictive models of threat, and datasets on real costs incurred by conservation organisations (e.g. Armsworth 2014).

Metrics of impact inclusive of multiple threats and measures of biodiversity

In Chapter 3, I used empirical data to quantify the spatial relationship between costs and threats. However, impact is determined not only by these two factors, but also by spatial patterns of biodiversity. In Chapters 4 and 5, I used relatively crude measures of biodiversity: changes in vegetation cover across different vegetation types, and changes in fish biomass, respectively. However, conservationists are typically concerned with much more complex measures of biodiversity, which can be measured in variety of different ways, such as species richness and composition, functional diversity, and genetic diversity, among others. A key question therefore remains to be answered: how does the impact of alternative prioritisation strategies vary according to how biodiversity is measured? In Chapter 4, I implemented some alternative methods of measuring impact, including weighting according to rarity and vulnerability, and measuring the distribution of impacts across biodiversity features. However, one could implement measures of impact that explore changes in more complex measures of biodiversity.

There are a few scenarios under which we might expect incorporation of multiple measures of biodiversity and/or threat to alter our results. Regarding measures of biodiversity, it might be the case that, if more complex measures of biodiversity are considered, the noise surrounding the relationship between costs and threats might be reduced. For example, it might be the case that there is a negative spatial relationship between threats and functional diversity (i.e., low-threat areas have high functional diversity). The return-on-investment of protecting any given area can be calculated as its biodiversity value multiplied by threats, divided by costs. If such is the case, even if costs and threats are uncorrelated, the negative relationship between threats and functional diversity would negate the benefits of protecting high-threat areas. In such circumstances, we would expect frontier prioritisation to have a reduced impact compared to wilderness prioritisation. However, which prioritisation strategy is most effective will depend entirely on the degree and strength of the correlation between threats and biodiversity, and this relationship might vary drastically if different measures of biodiversity value are used.

Additionally, in my analyses I explored only one type of threat at a time – in Chapter 4, land clearing, and in Chapter 5, fishing threat. Future analyses should attempt to incorporate the full variety of threats that affect biodiversity and, therefore, affect impacts. For example, future terrestrial analyses might consider threats from land clearing, invasive species, pollution, and climate change. Future marine analyses might consider threats from fishing, sea temperature change, and habitat destruction. A key question is how PA strategies might vary according to spatial patterns of threats that PAs cannot mitigate, such as the threat of climate change. For example, in a marine context, if threats from fishing and climate change coincide spatially, there is the possibility of synergistic effects; although PAs cannot directly mitigate the effects of climate change, they can potentially mitigate highly detrimental synergistic effects where areas are particularly susceptible to both fishing and climate change. Two sites under equal threat from fishing might have drastically different impacts if one site is more susceptible to the effects of changes in ocean temperature.

Alternative conservation actions and costs

This thesis has been concerned primarily with conservation using protected areas, and in particular, strict no-take PAs. However, a variety of other interventions can be used to achieve conservation impacts, such as partial-take, periodically harvested PAs, multiple use PAs, pest management, and restoration activities, among others. Alternative conservation actions might incur different costs from those associated with the establishment of no-take PAs, and might therefore exhibit different spatial relationships with the other factors that influence impact (biodiversity values and threats). For example, the costs of invasive species management are likely to depend on a variety of factors, such as habitat suitability for pest species and proximity to the point of origin. Acquisition costs are likely to depend on a suite of other factors, such as soil type and proximity to urban centres and roads. As such, the spatial relationship between threats/biodiversity and costs might differ drastically depending on whether a conservation strategy is, for example, prioritising land for invasive species management or for the acquisition of PAs.

Inclusion of socioeconomic and political factors

Planning is only one stage of the conservation process. Even highly effective conservation plans will be modified during the subsequent stages of the process, when stakeholders are consulted and further consideration is given to socioeconomic and political factors. Although throughout this thesis I have incorporated the economic costs of conservation to stakeholder groups (e.g. fishing and land agricultural opportunity costs), there are a variety of socioeconomic factors that are difficult to quantify in dollar terms, such as the traditional, spiritual or aesthetic value of locations. Where possible, these factors should be incorporated into conservation planning, which could be done, for example, using scoring methods to rank sites based on a range of social and economic values.

The more effective conservation planning becomes at incorporating socioeconomic and political factors, the more these factors can be accounted for in the planning stage to maximise impact and the less likely they will be substantially modified at the implementation stage. However, in many cases, considering the full range of socioeconomic factors will not be feasible, and it will be necessary to consider how particular strategies are likely to be modified. For example, although I have shown throughout this thesis that high-threat frontier prioritisation generally offers the greatest return on investment compared to alternative strategies, such a strategy is unlikely to be perceived as favourable to stakeholders causing these threatening processes (e.g. fishing industries). As such, a frontier approach might be particularly susceptible to modification before implementation.

6.3 Conclusion

This thesis has explored how conservation planning can develop strategies to maximise impact. Conservation expenditures are increasing worldwide, with billions of dollars spent annually, yet several fundamental knowledge gaps remain about how to effectively allocate this funding. This thesis addressed these knowledge gaps and provided methods and information that can be used by conservation practitioners to design and implement cost-effective, high-impact conservation strategies. Of utmost importance for conservation policy and practice is framing conservation goals in terms of impact, and initiating a feedback loop that allows objectives to be modified according to evidence of impacts, rather than setting objectives based on belief systems with no empirical support in terms of their paths to impact. Only then will progress be made towards mitigating global biodiversity declines.

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A1 Appendix 1: Supporting information for Chapter 2

A1.1 Model parameters, default values and sensitivity analyses

In Table A1.1 I provide default values for all parameters used in my deterministic two-patch model. When testing the effect of changes to particular parameters on the relative impact of wilderness/frontier strategies, I kept all other parameters at these default values. However, to ensure that my results are robust to changes in these default parameters, I provide supporting analyses below. To facilitate further parameter exploration, I have also published an online interactive version of the model, available at https://edmondsacre.shinyapps.io/Patch/, where all parameter values and functions can be chosen, and the impact of frontier, wilderness, and counterfactual (no protection) strategies are graphed accordingly.

Table A1.1 Descriptions and default values of all parameters in the two-patch model.

Parameter	Description	Default value	Justification
q_F	The proportion of biodiversity value lost in the frontier patch each year.	0.10	Rates of biodiversity loss were chosen to be on a similar order to threat prioritization analyses (e.g. Visconti et al. 2010).
q_W	The proportion of biodiversity value lost in the frontier patch each year.	0.01	As above.
s_F	The biodiversity value of the frontier patch at t = 0.	100	An arbitrary default value of 100 was chosen so that results could be easily interpreted in terms of percentages.
s_W	The biodiversity value of the wilderness patch at t = 0.	100	As above.
z	A constant that defines the shape of the biodiversity-area curve.	0.25	A default value of 0.25 was chosen to be consistent and allow comparability with other analyses in the conservation literature (Spring et al. 2007; Underwood et al. 2008; Underwood, Emma C. et al. 2009)
c_F	The cost of protecting the frontier patch.	100	A value of 100 was chosen so that in the default scenario the entirety of the patch was protected. For the entire patch to be protected costs must equal biodiversity values.
c_W	The cost of protecting the wilderness patch.	100	As above.
B	The total budget available.	100	A default value of 100 was chosen so that the entirety of the patch could be protected, according to the costs and biodiversity values above.
t	The number of years after implementation of wilderness/frontier strategies.	1,2,3...100	A maximum time-frame of 100 years was used as a conservative maximum. Most conservation planning analyses typically consider time-frames less than 100 years.
M_F	The maximum potential biodiversity value of the frontier patch.	100	The default value for this parameter was set to equal s_F, so that this parameter had no influence on other analyses.
M_W	The maximum potential biodiversity value of the wilderness patch.	100	As above.
N	The number of years it takes to recover to the maximum potential biodiversity value (starting from 0).	100	A default recovery time of 100 years was chosen to align approximately with the recovery times observed by Liebsch et al. (2008), which my model of recovery is based on.
a	The number of years required for the wilderness patch to transition into frontier in the scenario of dynamic threats.	100	A conservative default value of 100 was used in line with empirical observations by Etter et al. (2006) that full transition typically occurs over 60 to 100 years.
e_F	The efficacy of protection in the frontier patch. A value of 0 means that protection is completely ineffective, and a value of 1 indicated that protection is completely effective.	1	A default value of 1 was chosen so that this parameter did not influence the primary analyses.
e_W	The efficacy of protection in the wilderness patch. A value of 0 means that protection is completely ineffective, and a value of 1 indicated that protection is completely effective.	1	A default value of 1 was chosen so that this parameter did not influence the primary analyses.

A1.2 Integration of biodiversity complementarity

The base model described in the main text (Equation 2.1) can be simplified to:

$$S_t = s_F[p_F]^z + s_W[p_W]^z$$

where

$$p_F = \frac{b_F}{c_F} + \left((1 - q_F)^t \left(1 - \frac{b_F}{c_F}\right)\right)$$

and

$$p_W = \frac{b_W}{c_W} + \left((1 - q_W)^t \left(1 - \frac{b_W}{c_W}\right)\right)$$

To incorporate biodiversity complementarity, I added a third component, s_C, which specifies the amount of biodiversity value that is common to both the frontier and wilderness patches as follows:

$$S_t = s_F[p_F]^z + s_W[p_W]^z + s_C[\min(1, p_F + p_W)]^z$$

Equation A1.1

Where s_F and s_W now specify the amount of endemic biodiversity value in the frontier and wilderness patches, respectively. We than added the parameter u, which defines the proportion of biodiversity within the 2-patch system that is common to patches. Thus, the total biodiversity value of two-patch system can now be described by the equation

$$S_t = s_F(1 - u)[p_F]^z + s_W(1 - u)[p_W]^z + u(s_F + s_W)[\min(1, p_F + p_W)]^z$$

Equation A1.2

This model assumes that common species require more space to persist. That is, you can guarantee that an endemic frontier species will be protected if all of the frontier is protected. However, you would only get ~84% of the common species in that case (if the areas are equal and if $z = 0.25$). To guarantee protection to all common species, both frontier and wilderness patches must be protected.

Changes to biodiversity complementarity did not qualitatively affect the impact of frontier and wilderness prioritization, but only reduced the relative difference between strategies (Figure A1.1).

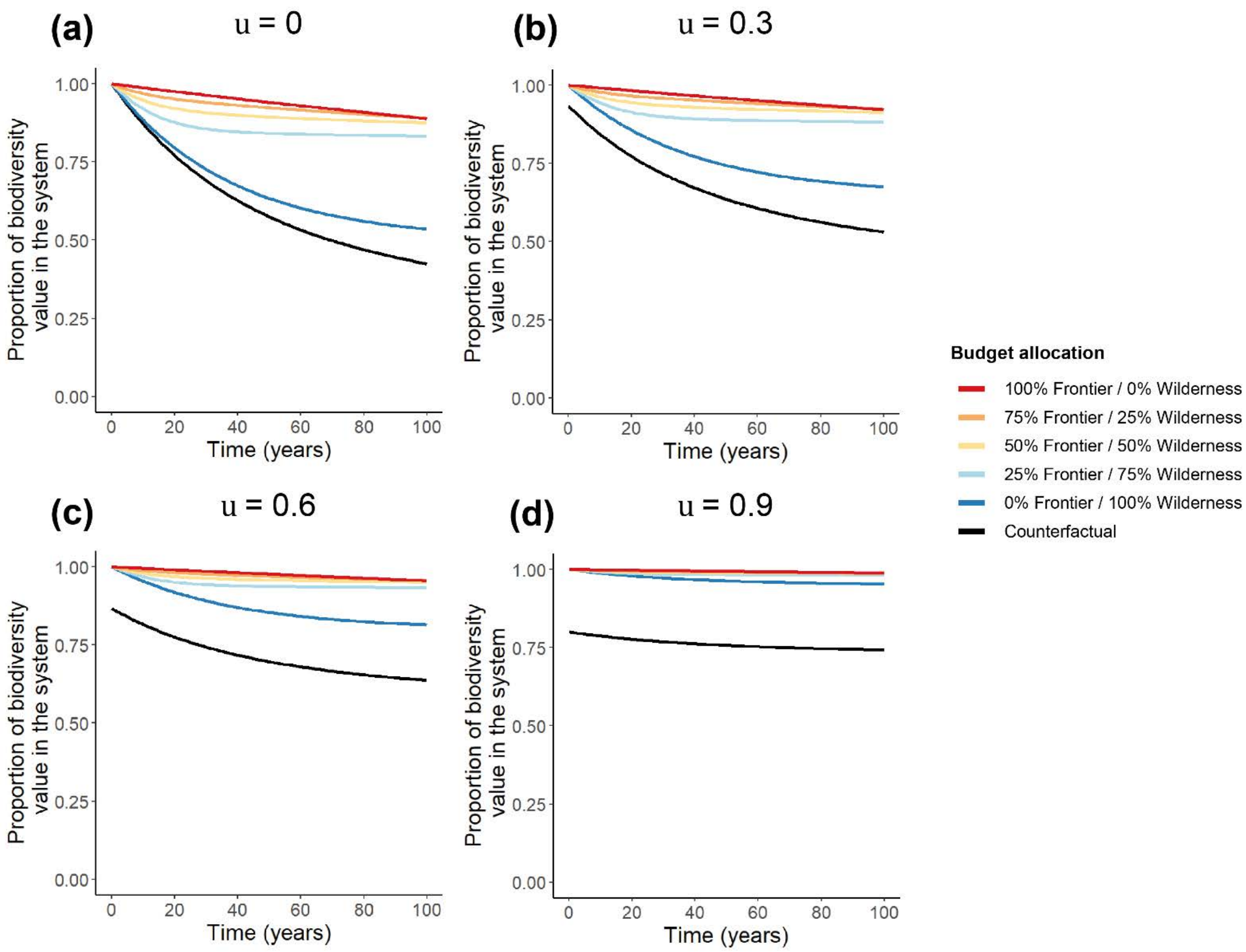

Figure A1.1 The proportion of biodiversity value remaining when different proportions of the budget are allocated to the frontier and wilderness patches. Panel (a) shows the base scenario where all factors are at default values. Panels (b), (c) and (d) show scenarios where 30%, 60% and 90% of the biodiversity value is common to both patches (u = 0.3, 0.6 and 0.9), respectively. The black line represents a counterfactual scenario in which neither patch is protected.

A1.3 Model of recovery of biodiversity value

For this scenario, I tested frontier/wilderness outcomes when the frontier patch was degraded, but had some recovery potential. Liebsch et al. (2008) found that several different measures of biodiversity value recover in logarithmic time. I therefore modelled the recovery of degraded biodiversity value following protection as:

$$R_{x_t} = M_x \frac{\log_{10} t}{\log_{10} N}$$

Equation A1.3

where, R_{x_t} is the amount of recovered biodiversity value added to patch x after t years of protection, M_x is the maximum potential biodiversity value of the patch, and N is the number of years it takes a completely degraded patch (i.e. zero biodiversity value) to recover to the maximum potential biodiversity value (M_x). If a patch initially has some biodiversity value from the beginning of the scenario, recovery starts from that point along the recovery curve (Figure A1.2).

For the default recovery scenario, I tested a scenario where the frontier patch was significantly degraded, having only 25% of its potential biodiversity at the beginning of the simulation. Thus, for this scenario, $s_{F_0} = 25$ and $M_x = 100$. I also tested alternative scenarios, where the frontier patch had 50% and 75% of its potential biodiversity value at the beginning of the simulation (Figure A1.3). Interestingly, the relative efficacy of the frontier strategy increased when the frontier patch was more degraded (lower s_{F_0}). This is because more degraded frontier patches have greater recovery potential, and because the initial biodiversity value of the whole system is lower. Thus, relative to the starting biodiversity value of the system, a frontier strategy can facilitate large amounts of biodiversity gain.

I also tested the sensitivity of my results to alternative recovery functions. Specifically, I tested the following linear recovery function:

$$R_x(t) = \frac{M_x\, t}{N}$$

Equation A1.4

Changes to the recovery function had no qualitative effect on frontier/wilderness impacts. The primary difference was that when recovery was logarithmic, benefits to the frontier strategy were realised earlier on in the time-frame.

Finally, I tested how changes to the time to full recovery (N) might affect frontier/wilderness impacts. This had an intuitive effect, where benefits to the frontier strategy were realised more quickly when recovery times were shorter. The effects of all recovery parameters can be visualised in the online model.

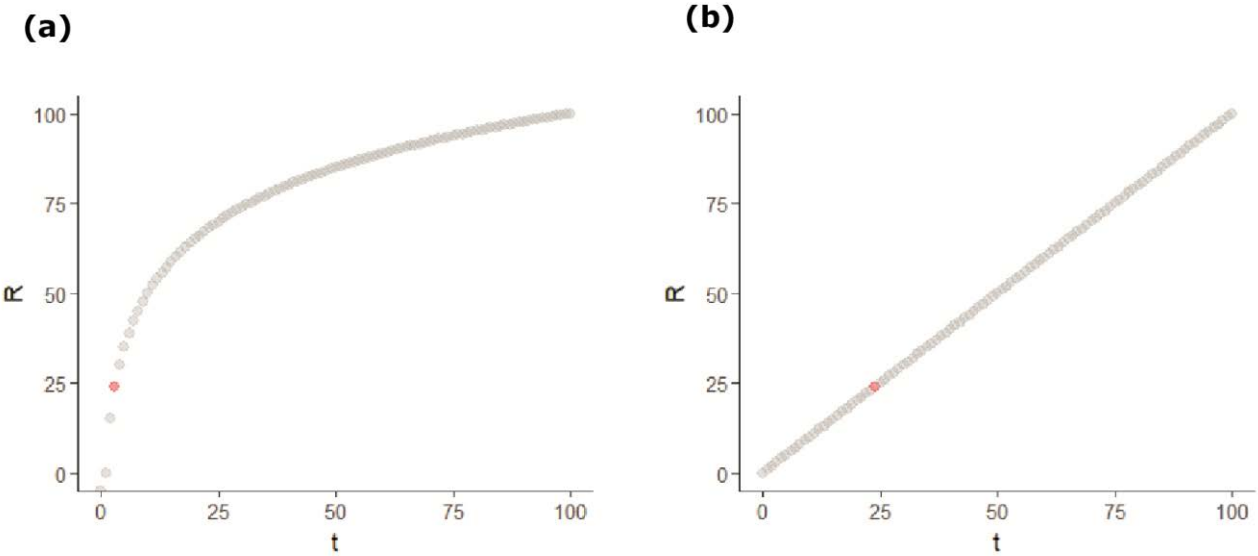

Figure A1.2 Models of the relationship between the amount of recovered biodiversity (R) and the number of years a patch has been protected (t). Panel (a) shows the logarithmic model adapted from Liebsch et al. (2008). Panel (b) shows the linear function also tested. Red points represent the starting point of the frontier patch in the default recovery scenario (starting biodiversity value of 25).

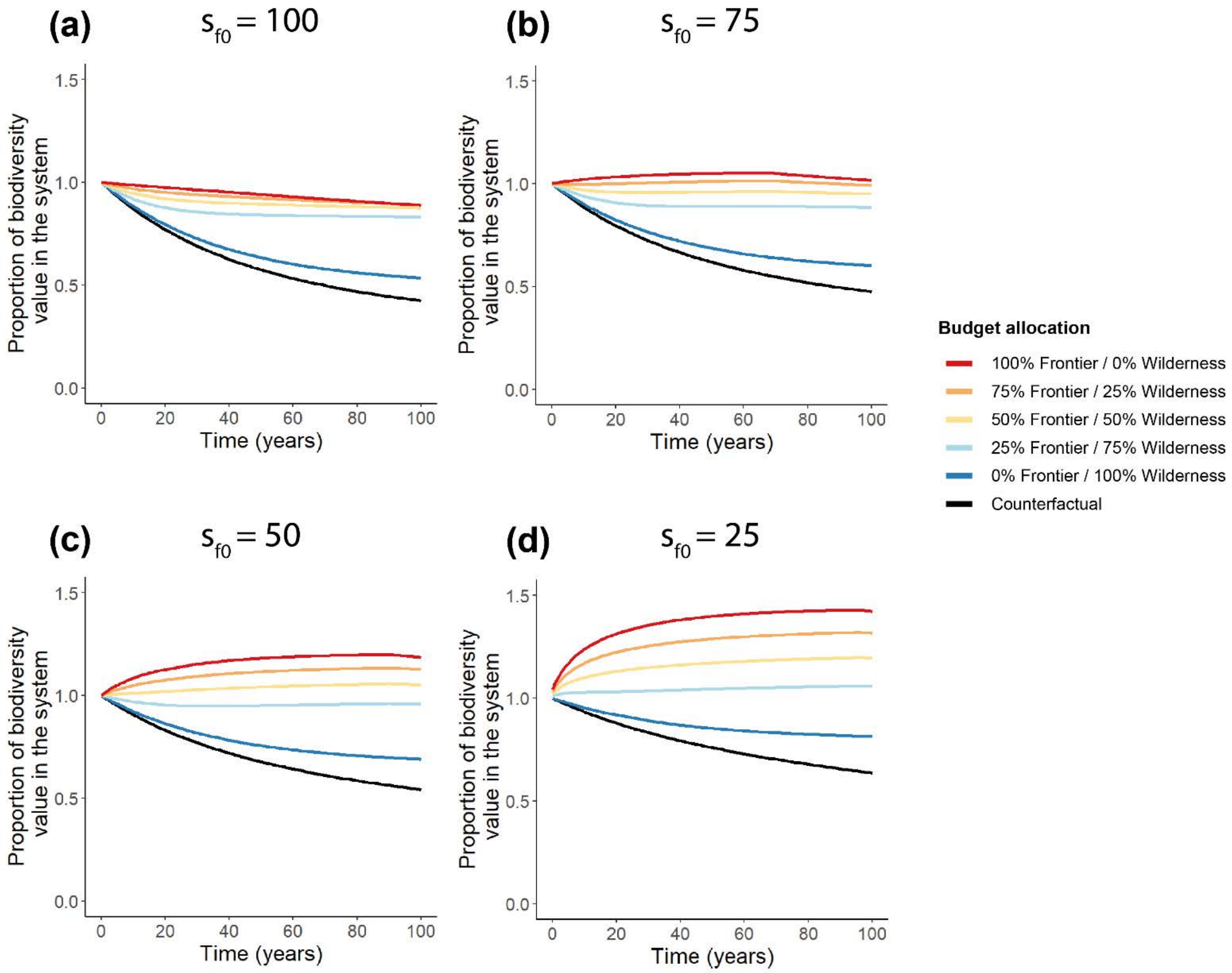

Figure A1.3 The proportion of biodiversity value remaining in the two-patch system under different recovery scenarios. Panel (a) shows the base scenario where the initial biodiversity value of the frontier patch is 100 (default value). Panels (b), (c) and (d) show scenarios where the initial biodiversity value of the frontier patch (s_{F_0}) is 75, 50 and 25, respectively. The black line represents a counterfactual scenario in which neither patch is protected.

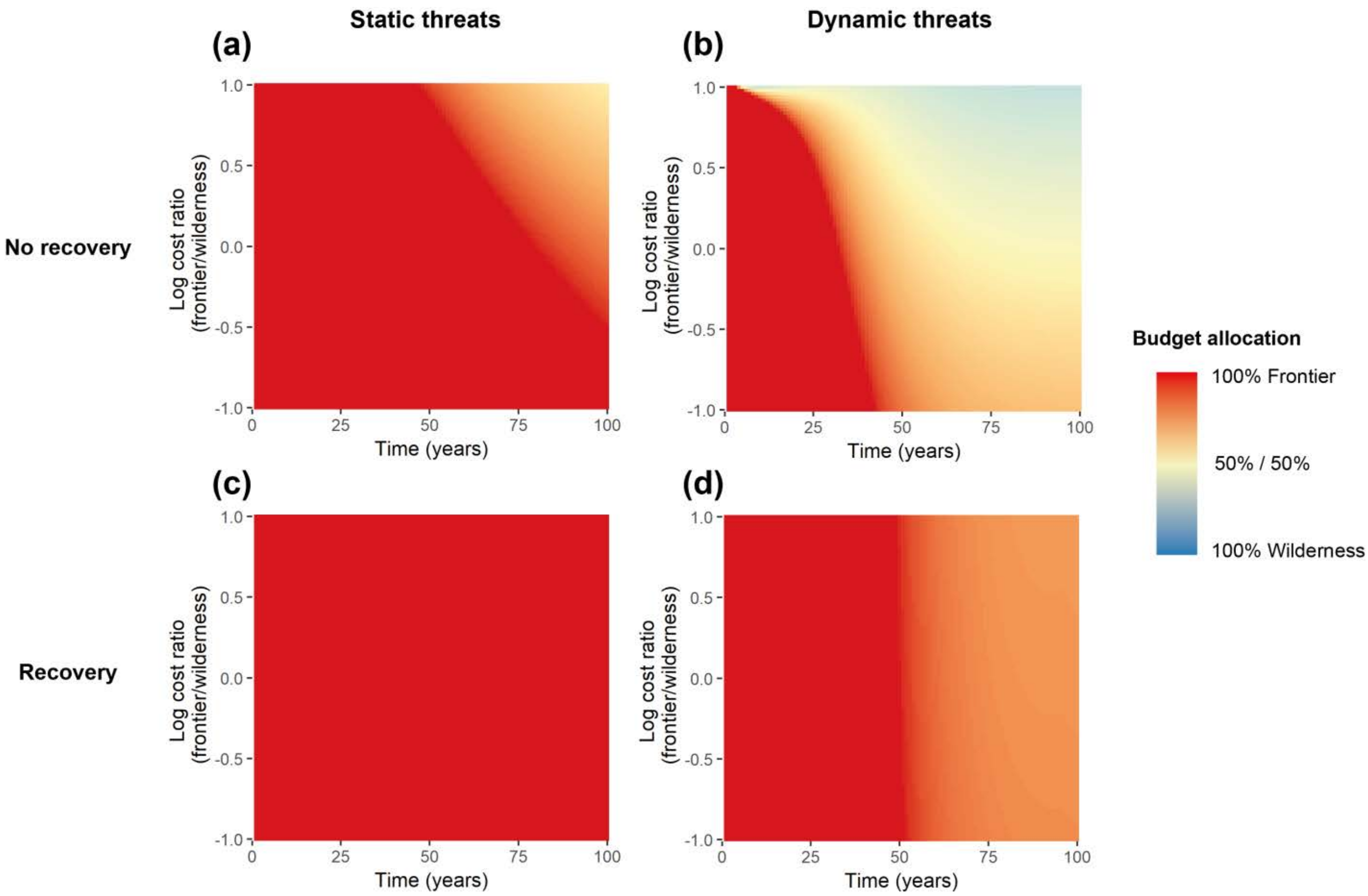

Figure A1.4 Variation in the most effective budget allocation across different time frames. Panels show how the most effective strategy varies according to the ratio of cost between frontier and wilderness patches (c_F / c_W). Panels (a) and (b) show the most effective strategy when all other paramaters are at their default values. Panels (c) and (d) show the most effective strategy when the frontier patch has an initial biodiversity of 25, but can recover to a value of 100 (default value) over 100 years.

A1.4 Model of dynamic threats

To consider the role of change in threats over time, I formulated a model that allowed the wilderness patch to transition into frontier over a set period of time. When threats are static, the proportion of biodiversity p in patch x at time t is given by the equation:

$$p_{x_t} = (1 - q_x)^t$$

Equation A1.5

In the frontier patch, threats were static. Thus, the proportion of biodiversity value remaining in frontier patch p_F at time t is given by the equation:

$$p_{F_t} = (1 - q_F)^t$$

Equation A1.6

For the wilderness patch, I emulated the sigmoidal transition from wilderness to frontier observed in empirical analyses of forest clearing (Etter et al. 2006). Etter et al. (2006) found that as a proportion of the initial biodiversity in a pristine system, losses are initially slow, then speed up, then slow down again. To produce a sigmoidal relationship between the proportion of initial biodiversity in the wilderness patch and time, I incorporated a function that allowed threats to linearly increase until reaching the same level as the frontier patch. Thus, the dynamic rate of biodiversity loss in the wilderness patch $\hat{q}_W$ is given by the equation:

$$\hat{q}_W = q_W + \left(\min\left(1, \frac{t}{a}\right) \cdot (q_F - q_W)\right)$$

Equation A1.7

where q_W and q_F are the proportions of biodiversity lost each year in the static threats scenario in the wilderness and frontier patches, respectively, and a is the number of years required for the wilderness patch to fully transition into frontier. I set a to a default value of 100, which is similar to the transition times observed by Etter et al. (2006).

Thus, the proportion of biodiversity value remaining in the wilderness patch p_W at time t is given by the equation:

$$p_{W_t} = \prod_{t=1}^{n} \left(1 - \hat{q}_{W_t}\right)$$

Equation A1.8

where n is the time-frame to reach conservation objectives. This produced an approximately sigmoidal relationship between the initial biodiversity value in the wilderness patch and time (Figure A1.5).

Finally, dynamic threats were incorporated into the two-patch model, given by the equation:

$$S_t = s_F \left[\frac{b_F}{c_F} + \left(p_{W_t}\left(1 - \frac{b_F}{c_F}\right)\right)\right] + s_W \left[\frac{b_W}{c_W} + \left(p_{F_t}\left(1 - \frac{b_W}{c_W}\right)\right)\right]$$

Equation A1.9

Please note that Equation A1.9 was also used to calculate the counterfactual in the dynamic threats scenario, where $b_F = b_W = 0$ (i.e. threats were also dynamic in the counterfactual scenario).

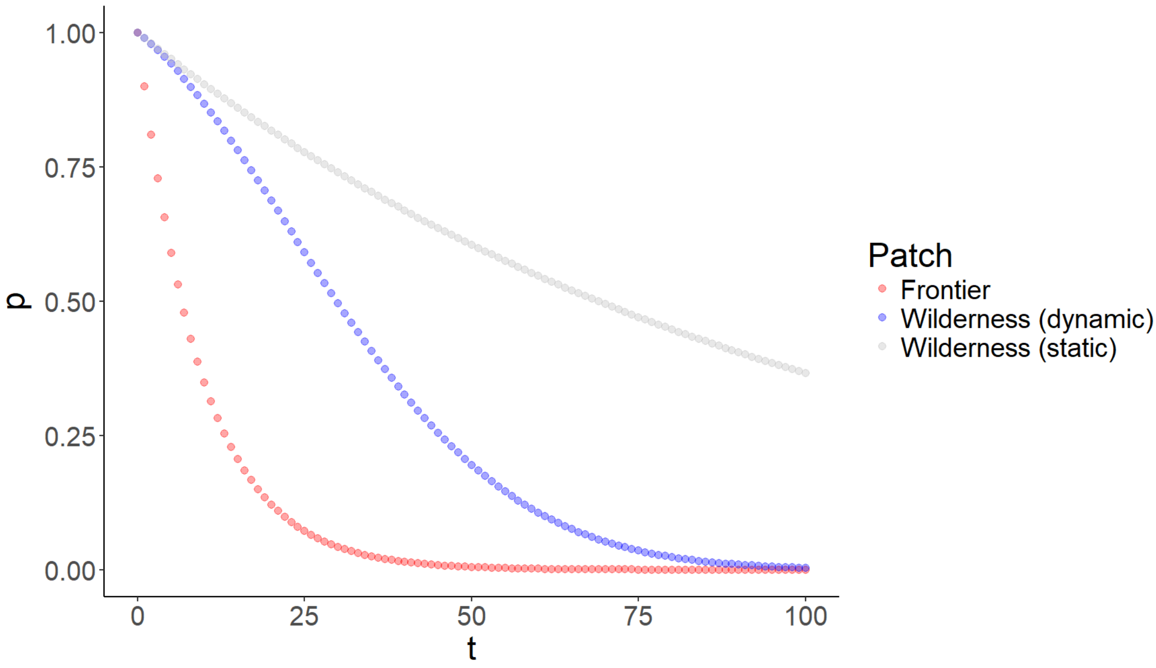

Figure A1.5 The relationship between the proportion of initial biodiversity value remaining in each patch (p) and time (t). Red and grey points represent the proportions remaining when threats are static in the frontier and wilderness patches, respectively (i.e. q_F and q_W constant through time). Blue points represent the proportion of initial biodiversity remaining when threats are dynamic in the wilderness patch. In the dynamic threats scenario, the rate of biodiversity loss in the wilderness patch linearly increases over 100 years, at which point it is equal to that of the frontier patch. In all scenarios, parameters are at the default value defined in Table A1.1.

A1.5 Alternative threat rates

I left threat rates in the frontier and wilderness patch at their default values (q_F = 0.1 and q_W = 0.01) for all analyses. However, outputs from a full range of values for q_x are provided in the online interactive version of the model.

Changes to q_x did not qualitatively change how other factors influenced frontier/wilderness strategies compared to the base scenario. However, differences in the ratio between q_F and q_W did affect the magnitude of differences between strategies, such that the relative difference between strategies was smaller when the ratio was smaller, and vice versa. Additionally, the effects of some factors were amplified when there was a large difference in threats between patches. For example, when there was a large difference between q_F and q_W, the effect of dynamic threats was amplified, because the wilderness patch made a dramatic transition into frontier (Figures A1.6c and A1.6d). Conversely, when there was little difference between q_F and q_W, the transition from wilderness to frontier had a less pronounced effect on outcomes compared to the base scenario (Figure A1.6a).

Changes in the ratio between q_F and q_W also amplified the effect of changes to cost and biodiversity value. When there was little difference in threats between patches, the optimal prioritization became more sensitive to changes in cost and biodiversity value (Figures A1.7 and A1.8).

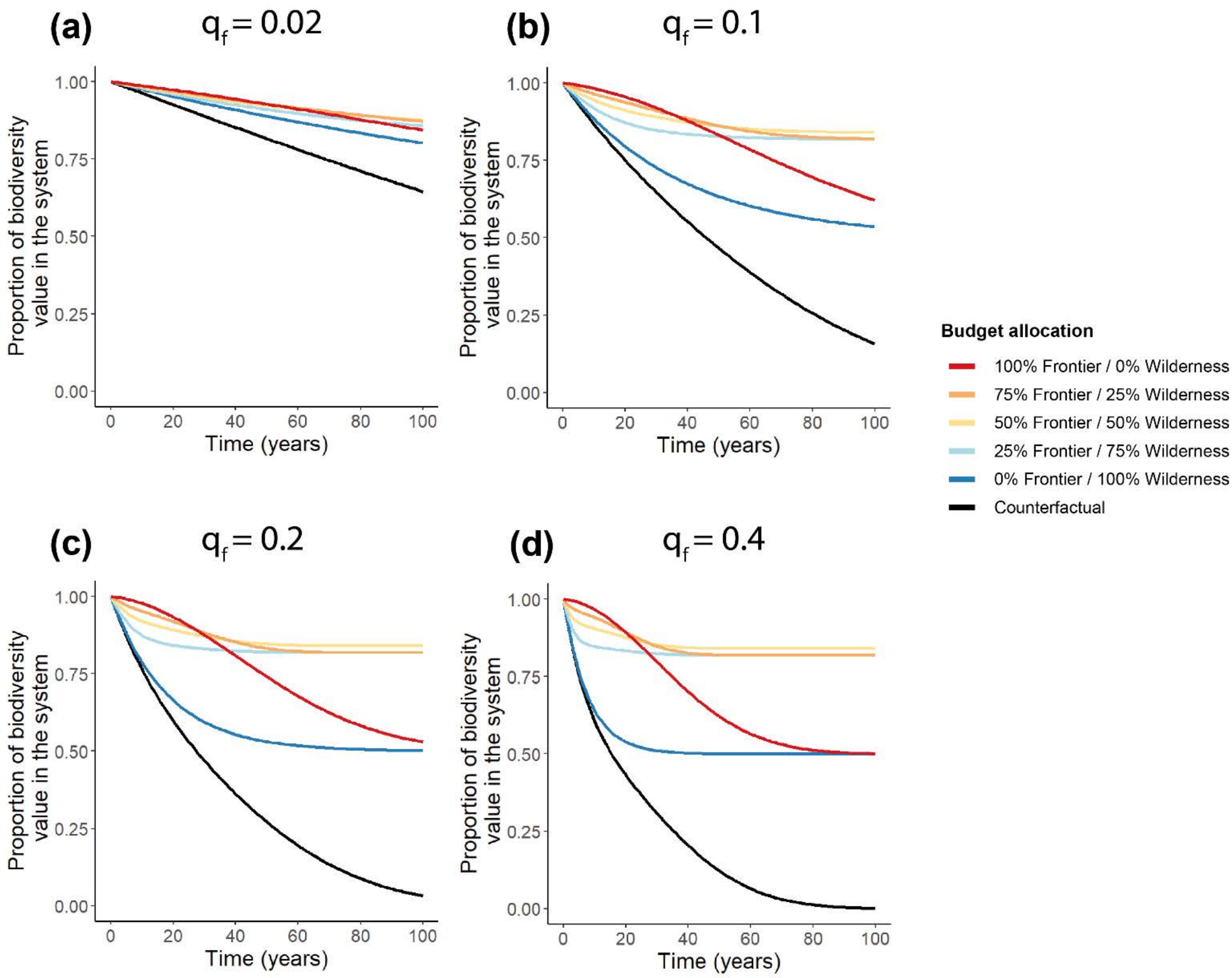

Figure A1.6 The proportion of biodiversity value remaining in the two-patch system when the threats are dynamic in the wilderness patch. Panels (a), (b), (c) and (d) show the biodiversity value remaining when the frontier patch experiences a loss of 2%, 10%, 20% and 40% per year, respectively. In all scenarios, the wilderness patch transitioned into frontier over period of 100 years. The black line represents a counterfactual scenario in which neither patch is protected.

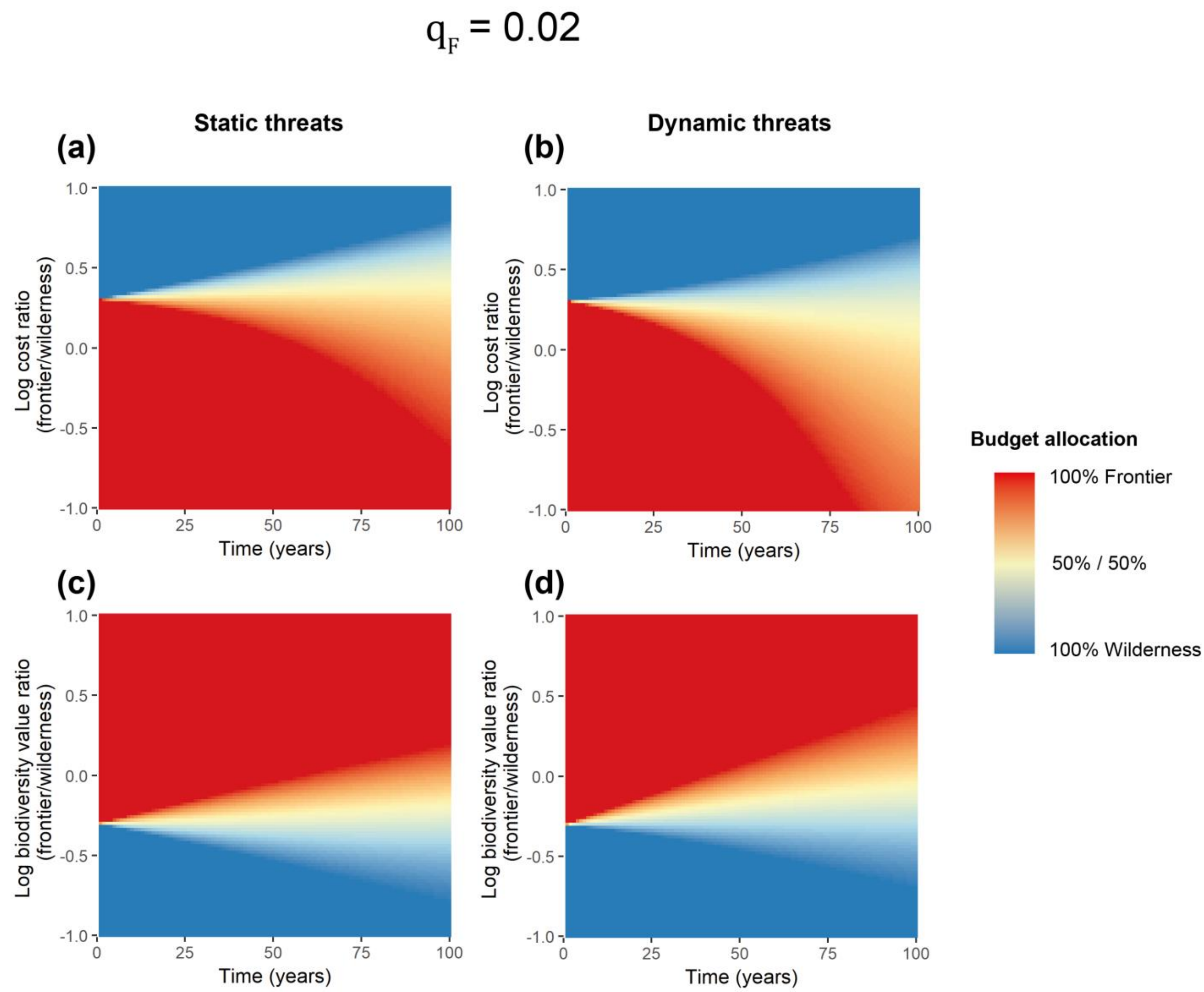

Figure A1.7 Variation in the most effective budget allocation across different time frames when the frontier patch has a loss rate of 2% (q_F = 0.02), and the wilderness patch has an initial loss rate of 1% (q_W = 0.01). Panels (a) and (b) show how the most effective strategy varies according to the ratio of cost between frontier and wilderness patches (c_F/ c_W). Panels (c) and (d) show how the most effective strategy varies according to the ratio of biodiversity value between frontier and wilderness patches (s_F/ s_W). Panels (a) and (c) represent the most effective strategies when threats are static. Panels (b) and (d) represent the most effective strategies when threats are dynamic.

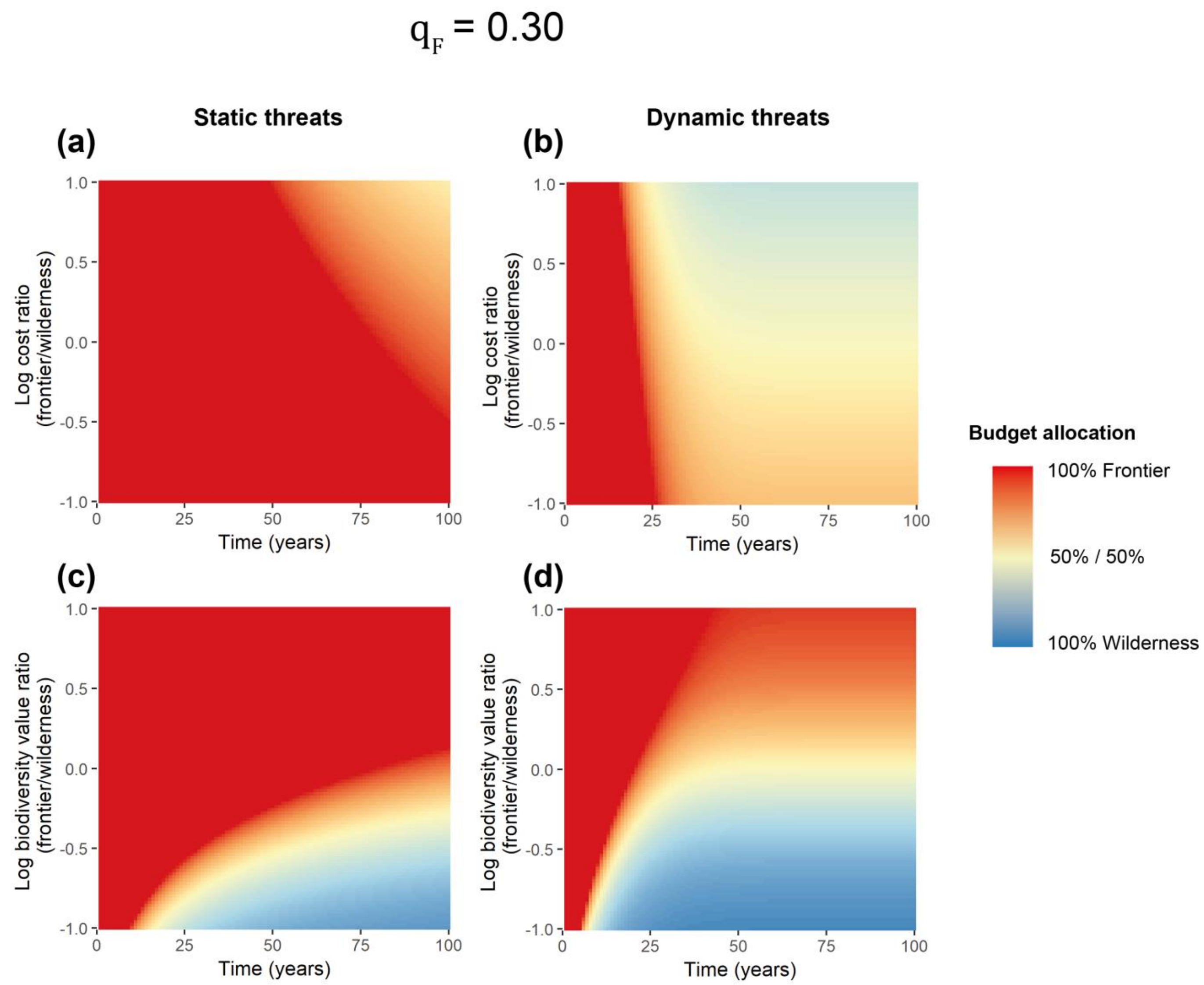

Figure A1.8 Variation in the most effective budget allocation across different time frames when the frontier patch has a loss rate of 30% (q_F = 0.3), and the wilderness patch has an initial loss rate of 1% (q_W = 0.01). Panels (a) and (b) show how the most effective strategy varies according to the ratio of cost between frontier and wilderness patches (c_F/c_W). Panels (c) and (d) show how the most effective strategy varies according to the ratio of biodiversity value between frontier and wilderness patches (s_F/s_W). Panels (a) and (c) represent the most effective strategies when threats are static. Panels (b) and (d) represent the most effective strategies when threats are dynamic.

A1.6 Alternative biodiversity-area relationships

In the primary analysis I assumed a z value of 0.25. When z = 1, there is a linear relationship between the amount of biodiversity value protected and conservation investment. I found that when z = 1, it way always more effect to protect either the entire frontier patch or the entire wilderness patch (Figure A1.9). However, when z is less than 1, there are diminishing returns on conservation investment. Thus, when z is less than 1, cost-effective gains can be made by splitting investment between patches, rather than adding protection to a single patch, for which less additional biodiversity value could be protected. For more in depth analyses of this factor in the context of frontier and wilderness priorities, see Spring et al. (2007).

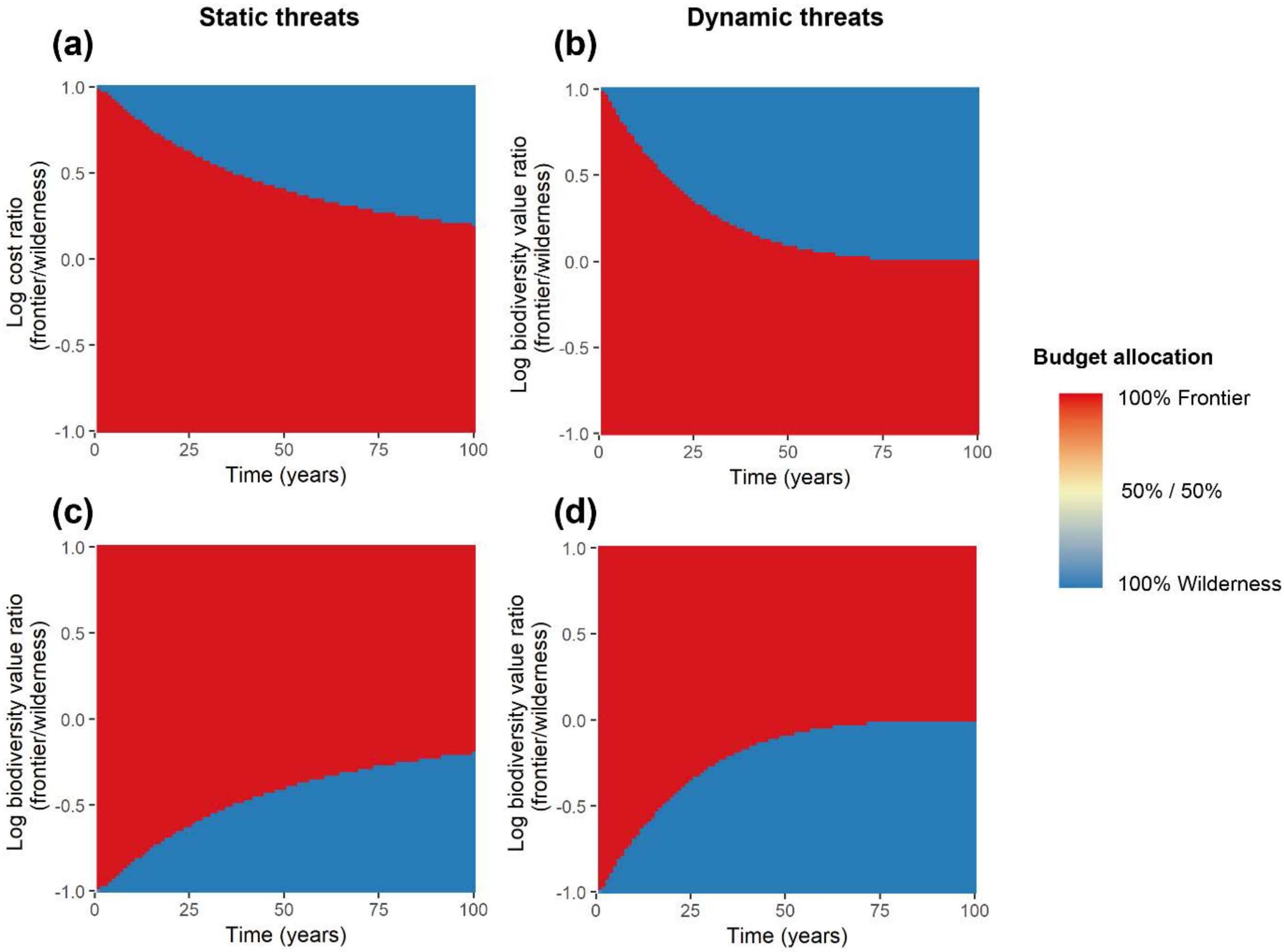

Figure A1.9 Variation in the most effective budget allocation across different time frames when the frontier when there is a linear relationship between the amount of biodiversity value protected and conservation investment (z = 1). Panels (a) and (b) show how the most effective strategy varies according to the ratio of cost between frontier and wilderness patches (c_F/ c_W). Panels (c) and (d) show how the most effective strategy varies according to the ratio of biodiversity value between frontier and wilderness patches (s_F/ s_W). Panels (a) and (c) represent the most effective strategies when threats are static. Panels (b) and (d) represent the most effective strategies when threats are dynamic.

A1.7 Efficacy of protection

There is considerable evidence that biodiversity values can still decline within protected areas (Jones et al. 2018). I have not discussed this factor in the main text because it is poorly understood in the context of the frontier/wilderness debate (but see Pfaff &

Sanchez-Azofeifa 2004). However, it is reasonable to expect differences in how effective protected areas are depending on the level of threats they face, especially if non-compliance is more profitable in frontier areas (e.g. areas with highly sought-after resources). To incorporate this possibility, I allowed the efficacy of protection/management to be adjusted in each patch. When this parameter is incorporated, the effectiveness of investing the budget is given by the equation:

$$S_t = s_F\left[\left((1-(1-e_F)q_F)^t \frac{b_F}{c_F}\right) + \left((1-q_F)^t\left(1-\frac{b_F}{c_F}\right)\right)\right] + s_W\left[\left((1-(1-e_W)q_W)^t \frac{b_W}{c_W}\right) + \left((1-q_W)^t\left(1-\frac{b_W}{c_W}\right)\right)\right]$$

Equation A1.10

where e_F and e_W parameters dictate what proportion of threats (q_x) are mitigated in the frontier and wilderness patches, respectively. When $e_x = 0$, protection is completely ineffective, and both strategies perform as well as the counterfactual. When $e_x = 1$, protection is completely effective. Importantly, I wish to highlight that this way of incorporating protection efficacy might not accurately represent how ineffective protection affects rates of biodiversity loss. The way I have modelled protection efficacy here assumes that some proportion of a protected area is completely effective (e_x), while the other proportion is completely ineffective ($1 - e_x$). Thus, a lack of efficacy is more detrimental in areas facing higher rates of biodiversity loss. In reality, protection efficacy is likely to be much more complicated, depending on a variety of circumstances, such as management tactics, types of threat (e.g. poaching, illegal fishing, illegal timber harvesting), social factors (e.g. shame around poaching), and economic factors.

In my two-patch model, reduced levels of protection had no qualitative effect on the relative efficacy of frontier and wilderness prioritisation, but only reduced the difference between strategies. The full effects of this parameter can be visualised in the online model.

A2 Appendix 2: Supporting information for Chapter 3

A2.1 Additional methods details

Theoretical analysis

Parameter values for the theoretical results shown in Figure 3.2 were generated at random, by selecting each parameter value for each economic activity from a uniform distribution $U[0,1]$. The values were as follows (rounded to the nearest 0.01):

$p_i - c_i = \{0.95, 0.74, 0.46, 0.3\}$.

$\tau_i = \{0.7, 0.35, 0.12, 0.07\}$.

$\lambda_i = \{0.09, 0.51, 0.24, 0.79\}$.

Particular combinations of parameters represent economic activities that are dominated – that is, that are not optimal at any distance from the market. An example would be an activity that produces a low profitability item with very high transport costs. We wanted to illustrate a model with 4 different economic activities (plus wilderness), and so we repeatedly randomly generated values until we found a combination of four activities that were each optimal at some distance. Note that the economic activity shown in Figures 3.2a-b is also present in the other panels, with the corresponding colour.

For the final panels that included economic and ecological heterogeneity, we added random variation to both factors as $\epsilon_x \sim N(0, 0.05)$, and $\delta_x \sim N(0, 0.1)$.

Empirical analysis

All spatial data was processed in ArcGIS 10.4 using a Lambert azimuthal equal-area projection with a central meridian of 145.7167 and a latitude of origin of 19.7833. Remnant vegetation in each parcel was calculated by combining data from National Vegetation Information System (NVIS Technical Working Group 2017), a map of remnant vegetation in 2018 across Queensland, and the SLATS datasets, under the assumption that all land cleared over the study period (according to the SLATS imagery) was remnant vegetation prior to the study period. In some cases, vegetation clearance recorded in a particular year was already recorded in a year preceding that year (i.e., clearing was incorrectly registered twice). When this occurred we assumed that the clearing occurred in the earliest year, and removed said clearing from the subsequent years.

Layers of land use type and bioregion were obtained from the Queensland Spatial Catalogue (Queensland Government 2018). Land use types and bioregions were assigned based on where the centroid of each parcel intersected with these layers.

A2.2 Supporting analyses

Cost layers

In the primary analysis, we estimated conservation acquisition costs using property sales data. However, we also repeated our analysis using two other surrogates for conservation costs. The first was government unimproved land valuations of properties between 2002 and 2006, which we adjusted to 2006 AUD. Like land sales prices, these valuations can be considered a surrogate for conservation acquisition costs. However, they are likely to be a less accurate surrogate than land sale prices, because they do not consider physical improvements to land (e.g. buildings) and do not reflect actual market transactions. For this analysis, land clearing was measured between 2007 and 2018. Our results using land valuation data were consistent with those of the primary analysis (Figure 3.3, Table A2.2).

The third cost layer we used was the agricultural profitability of land as estimated by Marinoni et al. (2012). For this analysis, we took the agricultural profitability (in 2006 AUD per hectare) from the centroid of each parcel. This cost layer can be considered a surrogate for conservation acquisition costs, because the price of agricultural land is likely to reflect its profitability. This cost layer can also be considered a surrogate for opportunity costs, because more profitable land will experience more foregone economic profits that could have been realised if that land was not purchased and protected by a conservation organisation. For this analysis, land clearing was measured between 2007 and 2018. Our results using agricultural profitability data were consistent with those of the primary analysis (Figure A2.1, Table A2.2).

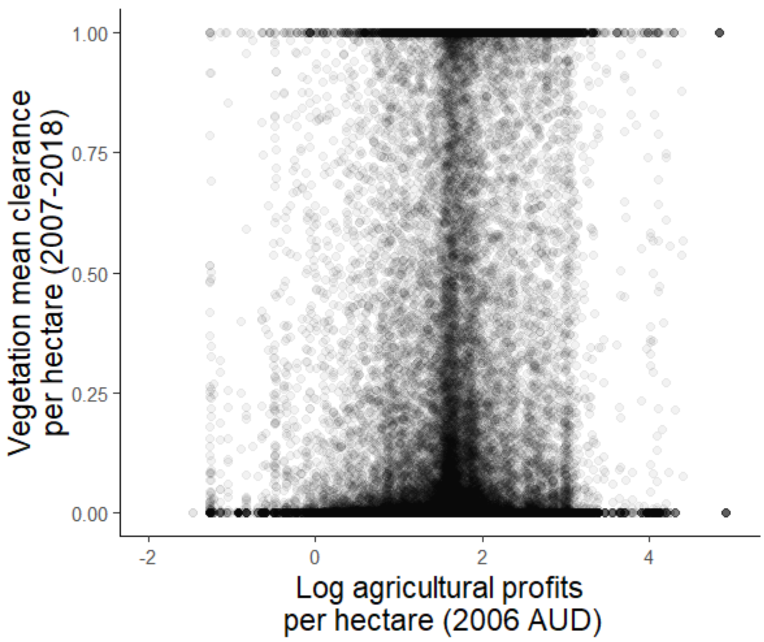

Figure A2.1 Scatter plots of the relationship between the log agricultural profitability of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2007 and mid-2018 on each parcel.

Policy phases

To ensure that our results were not affected by changes in land clearing policy, we repeated our analysis over two different land clearing policy phases. The first phase was a "restrictive" phase, from 2007 to 2012, when broad scale land clearing was banned in the state. The second was a "relaxation" phase, from 2012 to 2018, when the ban was lifted (Simmons et al. 2018). Our results were consistent across both phases (Figure A2.2, Table A2.2).

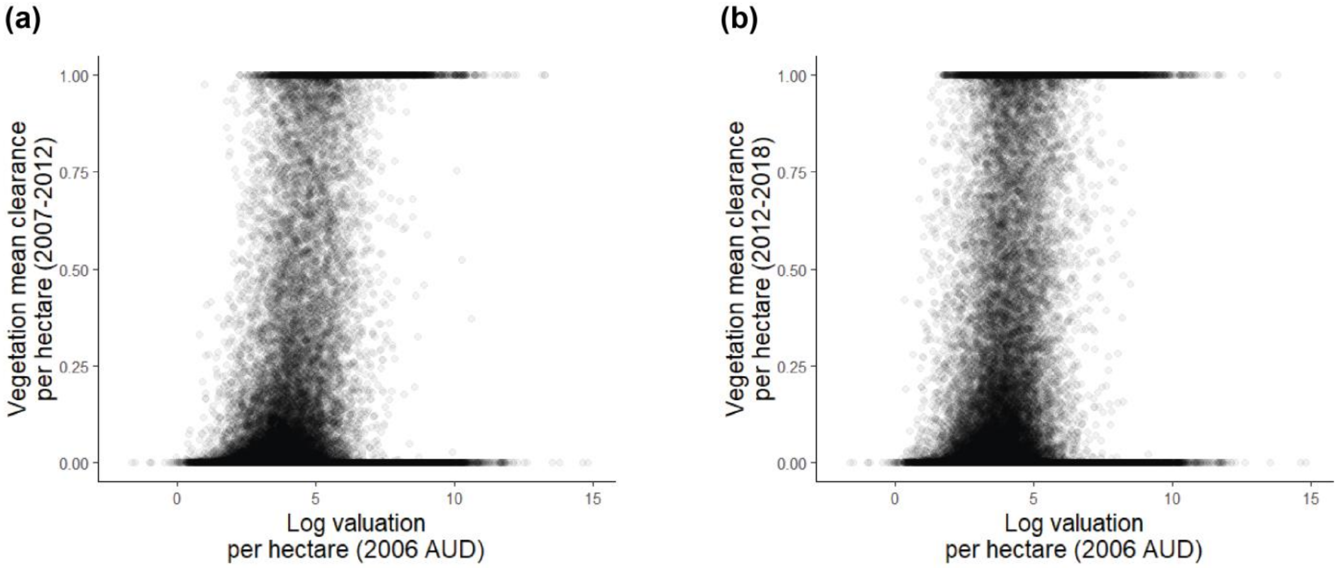

Figure A2.2 Scatter plots of the relationship between land valuation and rates of land clearing in Queensland over different land clearing policy phases. Panel (a) represents the relationship over the "restrictive" phase, from 2007 to 2012, when broad scale land clearing was banned in the state. Panel (b) represents the relationship over the "relaxation" phase, from 2012 to 2018, when the ban was lifted (Simmons et al. 2018).

__Alternative ways of measuring costs__

In the primary analysis, we measured costs assuming that conservation organisations would be required to purchase entire parcels. This was calculated by dividing the total cost of the parcel by the area of vegetation on the parcel. Using this measure increases the per hectare costs of vegetation on parcels with non-vegetation sections. The non-vegetated sections cannot possibly lose vegetation, meaning that there is a reduced efficiency when purchasing vegetation on partially cleared parcels, because it is necessary to purchase "useless" land that cannot contribute toward the preservation of vegetation.

We also provide analyses assuming that it was possible to purchase the vegetated sub-sections of each parcel. For this measure, costs were simply calculated as the total costs of the parcel divided by the size of the parcel. This assumes that the per hectare cost of vegetation on each parcel is unaffected by what proportion of the parcel is vegetated.

When it was possible to purchase vegetated sub-sections, the relationship between sale price and land clearing become more negative (from -0.14 to -0.23). The same occurred for land valuations (from -0.02 to -0.14). These results are still consistent with our primary analysis.

Alternative ways of measuring threats

In the primary analysis, we measured threats as the total amount of vegetation clearing on the parcel divided by the amount of vegetation on the parcel. This measure, therefore, represents the mean rate of clearance per hectare of vegetation. We also present here a supporting analysis where rates of vegetation clearance were standardised by the total are of the parcel, which is calculated as the area of vegetation clearance divided by the total parcel size. This measure reduces the mean rate of vegetation clearance on parcels with un-vegetated land, because it is not possible for un-vegetated land to lose vegetation. Using this measure of threat did not affect our results (Table S2).

This second alternative measure of threats where vegetation clearance is standardised by the total parcel size is likely to be a poor representation of threats for two reasons: (1) conservation organisations would only be interested in the proportion of each hectare of purchased vegetation that was cleared, and, therefore, the amount of non-vegetated land on the parcel would be irrelevant; and (2) because non-vegetated land is unable to be cleared, and therefore threats on non-vegetated land will always equal zero. Thus, measuring vegetation clearing divided by parcel size creates a bias in the dataset where threats become extremely skewed towards zero, because most parcels are only partially vegetated, and therefore can never be completely cleared. However, a conservation organisation is interested not in how much of the parcel they can save, but how much vegetation they can save.

For these reasons, the analyses presented in the main text measure threats standardised by the area of vegetation in each parcel.

Stratified by bioregion

When stratified according to bioregions, our results were consistent with those of the primary analysis (Table S2). However, there were two exceptions. In the Mulga Lands and in South East Queensland bioregions, the relationship became weakly positive (0.21, and 0.04, respectively). The reasons for this change are unclear. However, one possible explanation is that these bioregions have historically been subject to extensive vegetation clearing. As a result, many of the parcels in these regions are likely to be only partially vegetated, and these partially vegetated parcels are likely to be subject to further clearing. Thus, in these regions, requiring the purchase of entire parcels increases vegetation costs on parcels likely to experience vegetation clearing.

Stratified by parcel size

When stratified by parcel size, the relationship between land valuation became weakly positive, ranging from $\tau = 0.05$ among parcels 10-100 ha in size, to $\tau = 0.18$ among parcels 1-10 ha in size (Table S2). One possible explanation for this result is that parcels of similar size might tend to have similar economic and ecological characteristics. For example, very large parcels in Queensland are likely to be used for cattle grazing in semi-arid regions of Queensland, while very small parcels are likely to be used for industrial purposes along the coast, closer to urban centres. However, speculating on the reason for this phenomenon is beyond the scope of this article, and should be addressed in future research. In any case, the relationship is still weak and variable (Figure A2.3). Furthermore, there is no reason to suspect that conservation organisations would be required to purchase parcels within a particular size category.

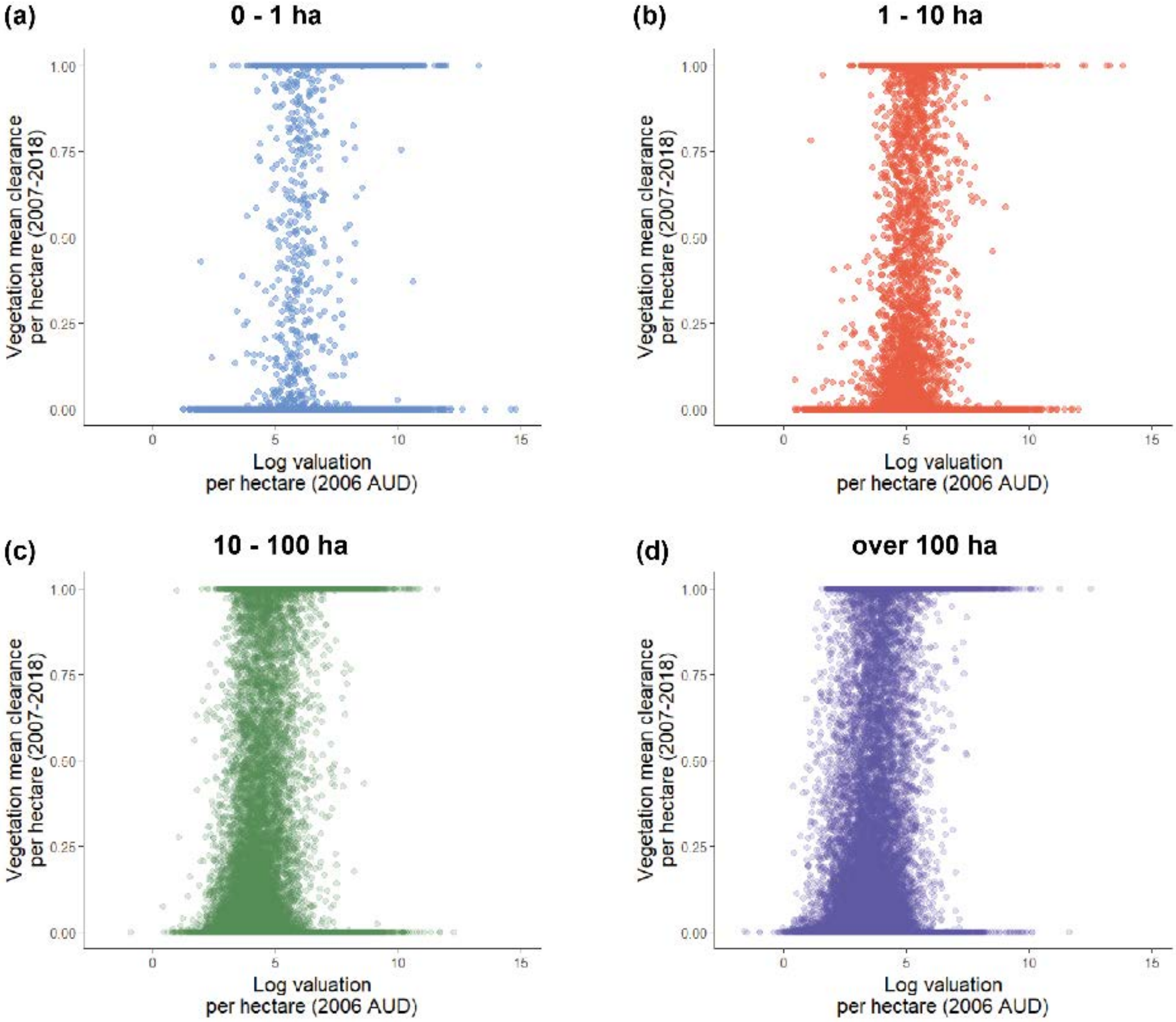

Figure A2.3 Scatter plot of the relationship between land valuations and rates of land clearing in Queensland. This figure shows log unimproved land value of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2007 and mid-2018 in parcels within different size categories: (a) between 0 and 1 ha (blue); (b) between 1 and 10 ha (red); (c) between 10 and 100 (green); and (d) over 100 ha (purple).

A2.3 Other supporting figures

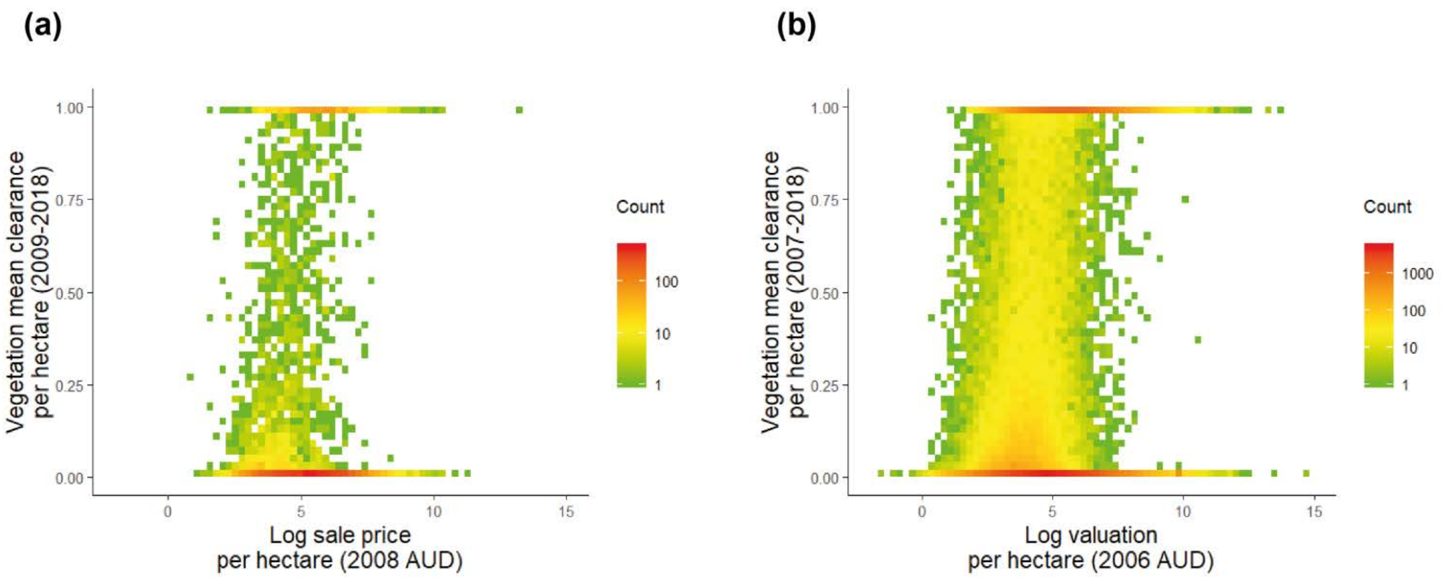

Figure A2.4 Density maps of the relationship between land sales price and valuation, and rates of land clearing in Queensland. Colours indicate the number of parcels with each particular combination of cost and threat. Panel (a) shows a density map of the log sale price of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between 2009 and 2018 on each parcel. Panel (b) shows a density map of the log unimproved land value of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between 2007 and 2018 on each parcel.

Table A2.1 A sample of papers that have either explicitly stated that conservation costs and threats are positively correlated, implicitly made this assumption, or that have tested this assumption. Papers that were found to have tested the relationship involved analyses using similar or identical predictor variables for both threats and costs, and did not therefore test the correlation using independent measures.

Reference	Measure of costs	Measure of threats (in prioritisation)	Statement about relationship	Quote
Boyd et al. 2015, Review of Environmental Economics and Policy	-	-	Assumed	"As a general rule, analyses that seek to protect the greatest amount of existing biodiversity without considering threats to that biodiversity, tend to protect areas that have a low risk of being developed—and thus a generally lower real conservation benefit—because costs and land development probabilities are positively correlated (Merenlender et al. 2009)."
Butsic et al. 2013, Journal of Environmental Management	Hedonic model of land costs – using various predictors (parcel size, distance to shorefront, development density, zoning regulations etc.)	Econometric land use change model – using various predictors (frontage, frontage squared, soil type, distance to towns, zoning regulations etc.)	Assumed, implicit	"Cost and conservation threat are usually correlated (Wilson et al., 2006), and that means that it is not clear a priori whether limited conservation funds should be concentrated on inexpensive land that has a low probability of development, or parcels that are severely threatened but also expensive."
Costello and Polasky 2004, Resource and Energy Economics	-	Probability of development, based on projections of urban expansion	Assumed	"In general, the variables Cjt and Pjt will be correlated; sites that are likely to be developed may cost more to protect because the potential profit from development is capitalized into the land price, a priori leaving ambiguous the optimality of selecting cheap sites (to allow more sites to be purchased) or costly sites (to place threatened sites in reserve)."
Devillers et al. 2015, Aquatic Conservation: Marine and Freshwater Ecosystems	-	-	Assumed	"Therefore, minimizing the costs of MPAs at broad scales has the potential for perverse outcomes: protection avoids the more heavily used and costly areas (in financial and/or political terms) and is not afforded to biodiversity most in need of protection."
Ebeling and Yasué 2008, Philosophical Transactions of the Royal Society B: Biological Sciences	-	-	Assumed	"They will thus favour areas with low land-use opportunity costs which may not coincide with areas of high conservation priorities. For example, global hot spots for biodiversity conservation have high land-use conversion rates (Myers et al. 2000) and are consequently likely to have high opportunity costs for conservation."
Klein et al. 2008, Conservation Biology	Recreational and commercial fishing effort	-	Implicit	-
Leathwick et al., Conservation Letters	Commercial fishing intensity	-	Implicit	"The fishing intensity or "cost" data layer (Figure S1) was created by applying a kernel smoother with a 20 km smoothing neighbourhood to the start locations of a completely independent set of 47,700 commercial trawls conducted during 2005"
Makino et al. 2013, PLoS One	Fishing pressure	-	Implicit	"We estimated the opportunity costs of fishing using the fishing pressure data modeled by Klein et al. [29] for the permanent closure zone."
Merenlender et al. 2009, Conservation Letters	-	-	Assumed	"Because development threat and cost are positively correlated, the "maximize gain" strategy is biased toward inexpensive land where biodiversity is more likely to remain without conservation expenditure."
Moore et al. 2004, Biological Conservation	Management costs from Balmford et al (2003)	-	Assumed	"Analysis of this variation in cost emphasises that high costs are likely to be correlated with high endemism or threat and that focussing exclusively on cheap areas is unlikely to achieve conservation goals"

Murdoch et al. 2010, Proceedings of the National Academy of Sciences	Real estate estimates * population density	Human footprint dataset (population density, land transformation, accessibility and electric power infrastructure)	Assumed, implicit, tested	"The average cost per hectare in an ecosystem is highly correlated with average ecosystem risk (Fig. 3)." (Note: estimate of threat and cost are implicitly linked by using population density as a surrogate for both, hence the observed (but not statistically tested) positive correlation)
Naidoo et al. 2006, Trends in Ecology and Evolution	-	-	Assumed	"For example, the edge of a growing metropolitan area will have high land prices, which are directly tied to the high probability of using the land to build housing or other urban developments. As well as being a proxy for cost, vulnerability or threat measures also have direct relevance for conservation, indicating areas that might be lost if conservation is not undertaken. In a dynamic analysis, such threats should be incorporated along with, rather than as a substitute for, cost."
Newburn et al. 2005, Conservation Biology	-	-	Assumed	"Conservation biologists frequently neglect the implicit positive relationship between expected probability of land-use conversion and land costs for protection. Vulnerable parcels with high land quality for development are typically more expensive than less vulnerable parcels with poor land quality because the relative values in alternative land uses strongly influence landowner conversion decisions. As an intuitive example, consider the probability of urban conversion on a forest or rangeland parcel. When the land value in urban use is high, the probability of urban conversion is expected to be high as well. In contrast, parcels with poor access to urban centers, low land quality, or strict zoning regulations will have much lower land value in urban use. Hence, the expected probability of land-use conversion typically is expressed as an increasing function of the value of developable land."
Newburn et al. 2006, American Journal of Agricultural Economics	Spatial autoregressive model using the following as predictors: slope, growing degree days, elevation, floodplain characteristics, zoning, urban service areas, neighbouring land use	Multinomial logit model using the following as predictors: slope, growing degree days, elevation, floodplain characteristics, zoning, urban service areas, neighbouring land use	Assumed, implicit, tested	"The underlying reason is that land costs and likelihood of future land-use conversion are typically positively correlated. These two targeting approaches, which alternatively omit either vulnerability or land costs, will therefore lead to extreme and opposite solutions."
Sala et al. 2002, Science	Fishing pressure	-	Implicit	"To design a network with the goal of reducing social conflict, we used small boat fishing pressure (mean standardized value per planning unit) (Fig. S2) as a proxy, using it as an additional variable to minimize."
Schmiing et al. 2015, ICES Journal of Marine Science	Fishing effort	-	Implicit	"The fishing effort was used as a surrogate for the spatial distribution of the non-monetary opportunity cost for different fisheries (i.e. the negative impact an MR might have for fishers; Klein et al., 2008b)"
Venegas-Li et al. 2018, Methods in Ecology and Evolution	Threat index using various proxies of threat: including fishing, pollution, shipping, sea surface temperature	-	Assumed	"We used a threat index as a surrogate for conservation cost, assuming that it is a proxy of human use of an area."

	anomalies, and more.			
Visconti et al. 2010, Biological Conservation	Agricultural productivity	Suitability of land for agriculture and distance to urban settlements	Assumed, implicit, tested	"Moreover, land value is a major conservation cost and is often positively correlated with vulnerability to habitat loss because value is related to potential profits from extraction"
Yates and Schoeman 2015, ICES Journal of Marine Science	Commercial fishing preference	-	Implicit	-

Table A2.2 The correlation between different metrics of conservation acquisition cost and rates of land clearing. For the primary analyses, all alternative methods for standardising acquisition costs and rates of land clearing are presented. Supporting analyses were performed using the government valuation data, because not enough samples were present in the sales data to subdivide the dataset further. For all supporting analyses, it was assumed that entire parcels must be purchased, and rates of land clearing were standardised by the amount of vegetation in each parcel for the reasons discussed in Appendix 2. For analyses using sales data, land clearing was measured over the period from 2009 to 2018. For the analyses comparing different land clearing policy phases, clearing was measured from 2007 to 2012 and 2012 to 2018. For all other analyses, land clearing was measured over the period from 2007 to 2018. Kendall's tau coefficients between -0.01 and 0.01 were marked as ~0.00.

Analysis	Number of parcels (n)	**Kendall's** rank correlation τ	p-value
Primary analyses			
Cost assumption 1: Entire parcel must be purchased			
Threat assumption 1: Vegetation clearing standardised by vegetation area			
Sales price	7,377	-0.14	<0.01
Land valuations	104,273	-0.02	<0.01
Agricultural profitability	62,397	~0.00	0.163
Threat assumption 2: Vegetation clearing standardised by parcel area			
Sale price	7,377	-0.19	<0.01
Land valuations	104,273	-0.11	<0.01
Agricultural profitability	62,397	-0.04	<0.01
Cost assumption 2: Allowing purchase of vegetation only within parcels			
Threat assumption 1: Vegetation clearing standardised by vegetation area			
Sale price	7,377	-0.23	<0.01
Land valuations	104,273	-0.14	<0.01
Agricultural profitability	62,397	~0.00	0.163
Threat assumption 2: Vegetation clearing standardised by parcel area			
Sale price	7,377	-0.23	<0.01
Land valuations	104,273	-0.14	<0.01
Agricultural profitability	62,397	-0.04	<0.01
Supporting analyses (all supporting analyses performed under cost assumption 1 and threat assumption 1)			
Excluding grassland dominated bioregions			
Sale price	7,342	-0.16	<0.01
Land valuations	103,060	-0.02	<0.01
Agricultural profitability	61,629	-0.01	<0.01
Alternative land clearing policy phases			
Restriction phase (2007 to 2012)	104,273	-0.07	<0.01
Relaxation phase (2012 to 2018)	104,273	-0.09	<0.01
Within bioregions			
Brigalow Belt	35,781	-0.05	<0.01
Cape York Peninsula	948	-0.16	<0.01
Central Queensland Coast	4,710	-0.15	<0.01

Channel Country	46	-0.08	0.052
Desert Uplands	1,027	-0.09	<0.01
Einasleigh Uplands	4,904	-0.11	<0.01
Gulf Plains	575	-0.14	<0.01
Mitchell Grass Downs	1,167	-0.14	<0.01
Mulga Lands	2,142	0.20	<0.01
New England Tableland	1,485	NA*	NA*
Northwest Highlands	971	-0.12	<0.01
Southeast Queensland	46,181	0.04	<0.01
Wet Tropics	4,287	-0.09	<0.01
By parcel size			
0 – 1 ha	17,426	0.15	<0.01
1 – 10 ha	20,604	0.18	<0.01
10 – 100 ha	39,391	0.05	<0.01
> 100 ha	26,852	0.12	<0.01

*No statistical analysis could be performed within the New England Tableland because all vegetation on parcels included in this analysis within this bioregion were completely cleared by the year 2018. There was, therefore, no variation between parcels to compare.

A3 Appendix 3: Supporting information for Chapter 4

Below I provide supplementary details of the methodology used in my analyses. Specifically I provide details for the procedures of the analysis measuring impact according to differences in the budget allowance, and formulae for each impact metric. I also provide several supporting analyses below, including strategies using alternative representation targets, and impacts when displacement of land clearing occurs from protected to unprotected parcels.

A3.1 Budget allowance analysis

I tested how the budget allocated for protection of parcels affected the impact of each strategy. I test a budget allocation ranging from 200 million AUD to 10 billion AUD, over the entire period from 2006 to 2016. For this analysis, I specified the cost threshold in Marxan for each strategy, increasing the budget in increments of 200 million AUD (200, 400, 600, etc.). In some cases, even if Marxan has a strict cost threshold, it might exceed the threshold in order to better achieve the set targets. To avoid this situation, when a strategy exceeded the allocated budget, I increased 'Penalty Factor A', which determines the level of precedence the cost threshold has over conservation targets. For each strategy, I increased Penalty Factor A in increments of 10 until each strategy was below the cost threshold.

A3.2 Impact metric details and alternative parameters

Impact metric 1: Area of vegetation saved

The first impact metric I used was simply the total amount of vegetation in each broad vegetation group (BVG) that was saved with the implementation of each prioritisation strategy, relative to the counterfactual scenario. For each broad vegetation group, the impact of each strategy is given by the equation:

$$I_S = A_C - A_S$$

Equation A3.1

where I_S is the impact of strategy S, A_C is the area of vegetation lost in the counterfactual scenario between 2006 and 2016 in the vegetation group, and A_S is the area of vegetation lost in vegetation group between 2006 and 2016 when strategy S was implemented. The total impact of each strategy was then calculated as the sum of impact across all vegetation groups.

Impact metric 2: Proportion of vegetation group saved

The second impact metric I used was the proportion of each BVG that was saved with each prioritisation strategy. This impact metric more account for the natural difference in the extent of each BVG in Queensland. For each broad vegetation group, the proportional impact was calculated as:

$$I_S = \frac{A_C - A_S}{V}$$

Equation A3.2

where V is the total area of the vegetation group in the year 2006.

Impact metric 3: Weighted impact according to the rarity and vulnerability of broad vegetation groups

My third metric was a relative impact score that more heavily weighted the preservation of BVGs according to their rarity (i.e. higher weighting on BVGs with smaller extents) and their historical rate of clearing (henceforth 'vulnerability', i.e. higher weighting on BVGs that have a lower proportion of their pre-European extent remaining in 2006).

This metric of impact was implemented according to the following axioms, which I assumed would be desirable objectives for conservation practitioners:

> *Axiom 1 (rarity): If, ceteris paribus, the extent of remnant vegetation of vegetation group A is less than vegetation group B, then saving 1 ha of vegetation group A will have a higher impact than saving 1 ha of vegetation group B.*
>
> *Axiom 2 (vulnerability): If, ceteris paribus, vegetation group A has a lower proportion of its original pre-European vegetation remaining than vegetation group B, then saving 1 ha in vegetation group A will have a higher impact than saving 1 ha in vegetation group B*

I implemented these axioms by weighting the impact of saving vegetation in each BVG according to its rarity and vulnerability. The rarity, k_R, of each BVG was calculated as:

$$k_R = \frac{2006\ extent}{extent\ of\ all\ vegetation\ types}$$

Equation A3.3

such that BVGs with low values of $k_R$were deemed more rare. The vulnerability of each BVG, k_U, was calculated as:

$$k_U = \frac{2006\ extent}{pre-European\ extent}$$

Equation A3.4

such that BVGs with low values of k_U were deemed more vulnerable. I then applied a weighting to each BVG where the weighting score increased according to a power function as rarity and vulnerability increased. This weighting method was used in the primary analysis. For this metric, the weighting for rarity, w_R , was calculated as:

$$w_R = 0.01^{k_R}$$

Equation A3.5

and the weighting for vulnerability, w_U, was calculated as:

$$w_U = 0.01^{k_U}$$

Equation A3.6

However, I also tested a linear weighting (Figure A3.1), where the weighting for rarity, w_R, was calculated as:

$$w_R = 1 - k_R$$

Equation A3.7

and the weighting for vulnerability, w_U, was calculated as:

$$w_U = 1 - k_U$$

Equation A3.8

Finally, the impact of each strategy for each BVG was calculated as:

$$I_S = \left(\frac{w_R}{2} * \frac{A_C - A_S}{V}\right) + \left(\frac{w_U}{2} * \frac{A_C - A_S}{V}\right)$$

Equation A3.9

such that both rarity and vulnerability were considered equally important.

My results were consistent regardless of whether rarity and vulnerability were weighted according to the power function or the linear function (Figure A3.2).

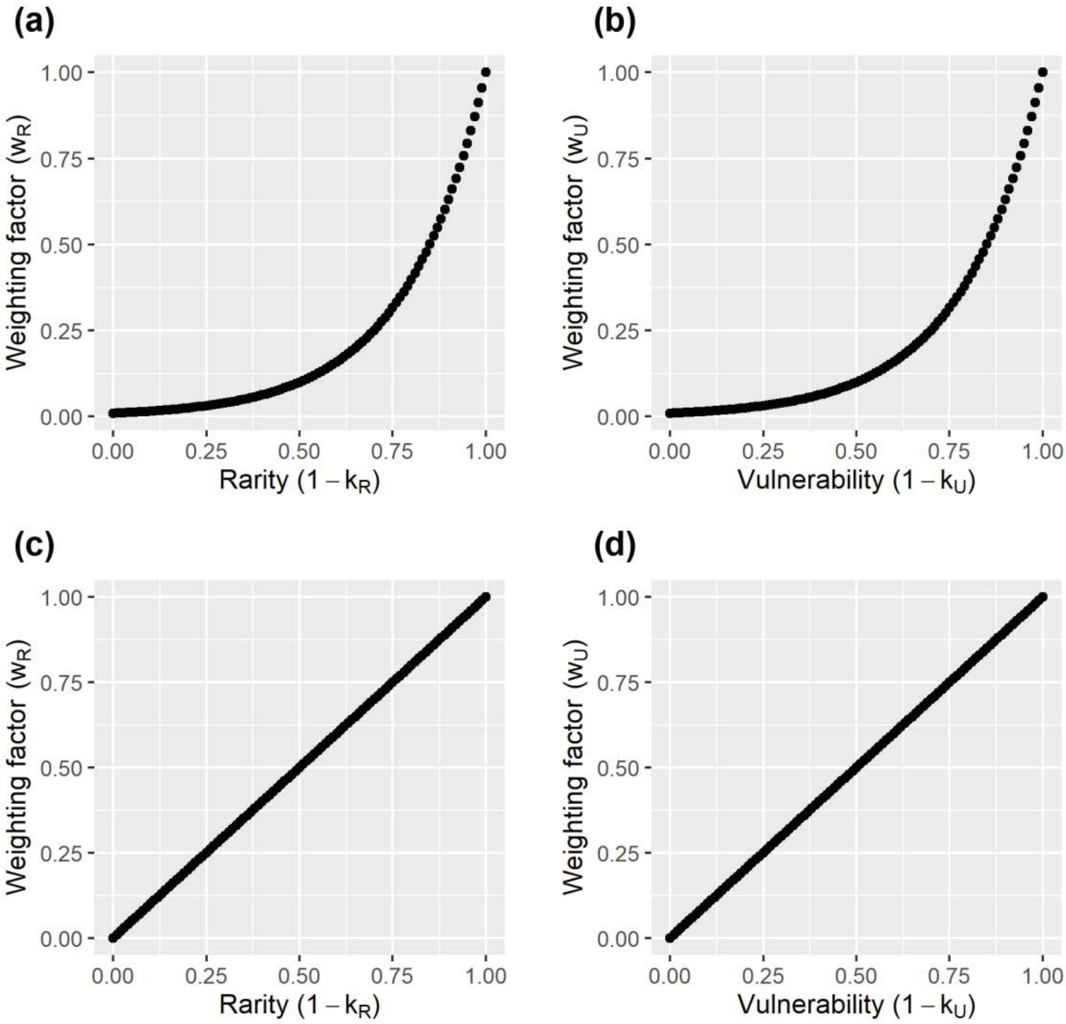

Figure A3.1 The relationship between the rarity and vulnerability of each broad vegetation group (BVG) in my analysis, and the weighting factor placed on BVGs for my third metric of impact. Panels (a) and (b) show the power relationship between rarity and vulnerability, respectively, and the weighting factor ($\boldsymbol{w}$). This was the weighting method used in the primary analysis presented in the main text. Panels (c) and (d) show the linear relationship between rarity and vulnerability, respectively, and the weighting factor ($\boldsymbol{w}$).

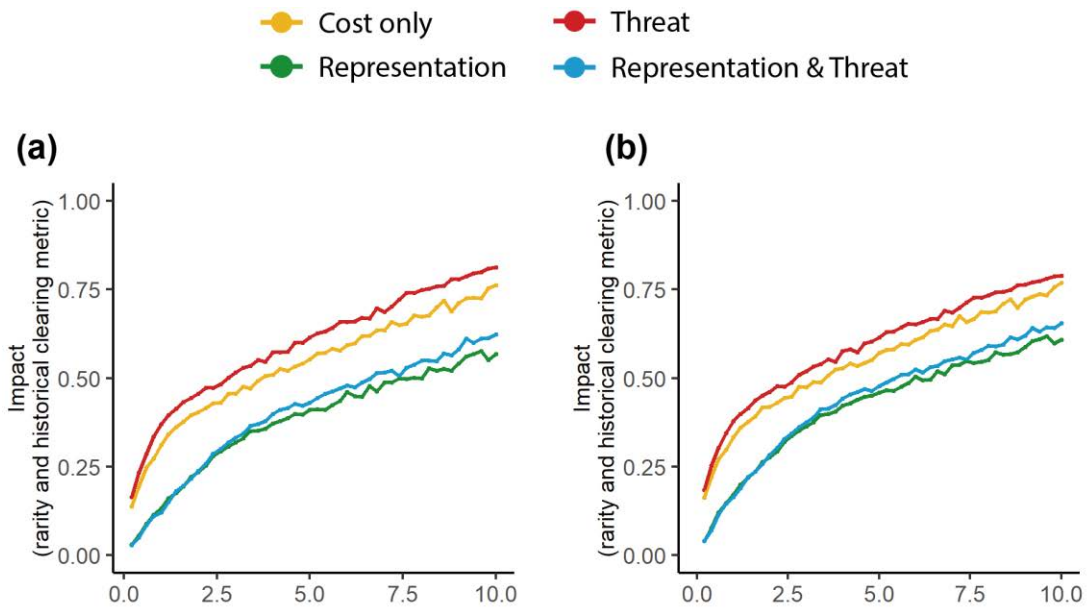

Figure A3.2 The effect of budget on the impact of alternative prioritisation strategies according to different weightings of rarity and proportion of remnant vegetation. Impact is measured as the proportion of each BVG saved relative to the area of each BVG lost in the counterfactual scenario. Proportions are then weighted according to the rarity of each BVG and how extensively it has been cleared in the past. Panel (a) shows impacts when the relationship between rarity and historical clearing exhibit a power relationship (as shown in Figure A3.1a and b), such that impacts are increasingly more heavily weighted as BVGs increase in rarity and the degree of historical clearing. Panel (b) shows impacts when the relationship between rarity and historical clearing exhibit a linear relationship (as shown in Figure A3.1c and d).

Impact metric 4: Impact equality

The fourth metric I used to measure impact was the 'impact equality' of each strategy, which measures how evenly distributed impacts were across BVGs. The metric was adapted from Chauvenet et al. (2017)'s 'protection equality' metric, which measures how evenly distributed protection is across different biodiversity features. However, this protection equality only considers the amount of area protected across biodiversity features, and not impacts within biodiversity features. The focus of this article is not on the area protected by prioritisation strategies, but rather the impact (i.e. vegetation saved) by each strategy. Therefore, I adapted this metric to measure the equality of impact across broad vegetation groups. I adapted Chauvenet et al. (2017)'s proportional protection equality metric (area protected as a proportion of the total area of the biodiversity feature), PE, which is given by the equation:

$$PE = \frac{\frac{1}{N} \times \left(\frac{1}{2} \sum_{i=1}^{N} p_i + \sum_{i=1}^{N-1} p_i \times (N - i) \right)}{\frac{1}{2} \sum_{i=1}^{N} p_i}$$

Equation A3.10

where N is the number of biodiversity features (in our case BVGs), i is the biodiversity feature, and p_i is the proportion of biodiversity feature i protected relative to its total area. To measure impact equality for each strategy, I simply substituted p_i with the proportional impact of each strategy, I_S, from Equation A3.2.

A3.3 Alternative representation targets

For the strategies that incorporated representation, I measured impact when different representation targets were set. In the primary analysis, presented in the main text, representation targets were set to 30%, such that Marxan attempted to protect 30% of each of 29 woody broad vegetation groups present in Queensland (Neldner et al. 2014). To ensure that my results were robust to variation in these targets, I also measured impacts when representation targets were set to 50% and 90%. The same procedures and budget limitations were used for these analyses as in the primary analysis.

My results were unchanged by variation in representation targets (Figure A3.3). Specifically, I found that a strategy that attempted to prioritise threats still outperformed representation-based strategies, regardless of representation targets.

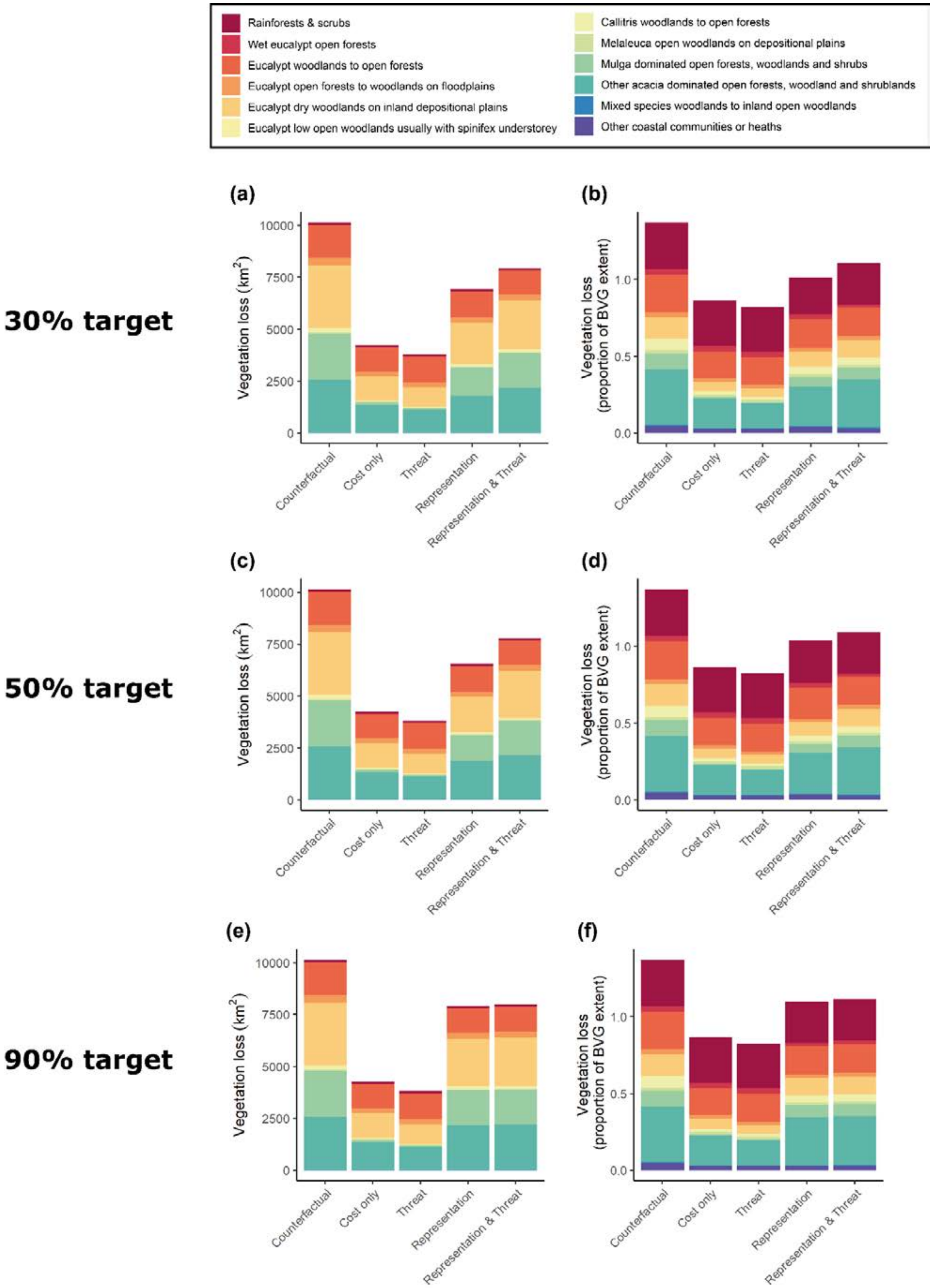
Rainforests & scrubs
Wet eucalypt open forests
Eucalypt woodlands to open forests
Eucalypt open forests to woodlands on floodplains
Eucalypt dry woodlands on inland depositional plains
Eucalypt low open woodlands usually with spinifex understorey
Callitris woodlands to open forests
Melaleuca open woodlands on depositional plains
Mulga dominated open forests, woodlands and shrubs
Other acacia dominated open forests, woodland and shrublands
Mixed species woodlands to inland open woodlands
Other coastal communities or heaths
30% target
50% target
90% target
(a)
(b)
(c)
(d)
(e)
(f)
Vegetation loss (km^2)
Vegetation loss (proportion of BVG extent)
0
2500
5000
7500
10000
0.0
0.5
1.0
Counterfactual
Cost only
Threat
Representation
Representation & Threat

Figure A3.3 Vegetation loss across broad vegetation groups (BVGs) when no protection is implemented (counterfactual) and when alternative prioritisation strategies are implemented, and when alternative representation targets were set for representation-based strategies. Panels (a), (c) and (e) show total vegetation loss within BVGs when representation targets were set to 30%, 50% and 90%, respectively. Panels (b), (d), and (f) show vegetation loss as a proportion of the total extent of each BVG in 2006 when representation targets were set to 30%, 50% and 90%, respectively. Please note that BVGs have been simplified into the above 12 categories (according to citation) for ease of interpretation.

A3.4 Alternative displacement scenarios

In my primary analyses, presented in the main text, I assumed that no displacement occurred. Displacement (also known as 'leakage') is a phenomenon where threats are displaced from protected land to nearby unprotected lands. To account for the possibility that land clearing in Queensland could shift from protected parcels to nearby unprotected parcels after protection, I developed a model that distributed all land clearing that occurred between 2006 and 2016 to all unprotected parcels within a given radius. I measured the impact of each strategy when displacement occurred within a 1 km, 5 km, 10 km, 20 km radius.

The model was implemented using custom Python code for ArcGIS. This code is available upon request, and can be used for any spatial planning analysis utilising planning units. Once each parcel was selected for protection by each prioritisation strategy, the amount of displaced land clearing in each parcel was calculated by dividing the land clearing within each given protected parcel equally among all unprotected parcels within the specified radius. For example, if a parcel selected for protection experienced 10 square kilometres of land clearing between 2006 and 2016, and contained 10 unprotected parcels within the displacement radius, each of the unprotected parcels would receive an additional 1 square kilometre of land clearing between 2006 and 2016. The total amount of displaced land clearing in each unprotected parcel was not allowed to exceed to amount of vegetation in the parcel in 2006.

Incorporating the displacement model had no qualitative effect on my results (Figure A3.4). It did, however, reduce the effect of all strategies substantially, particularly when the displacement radius was large. When the displacement radius was approximately 20 km or higher, all strategies had no impact.

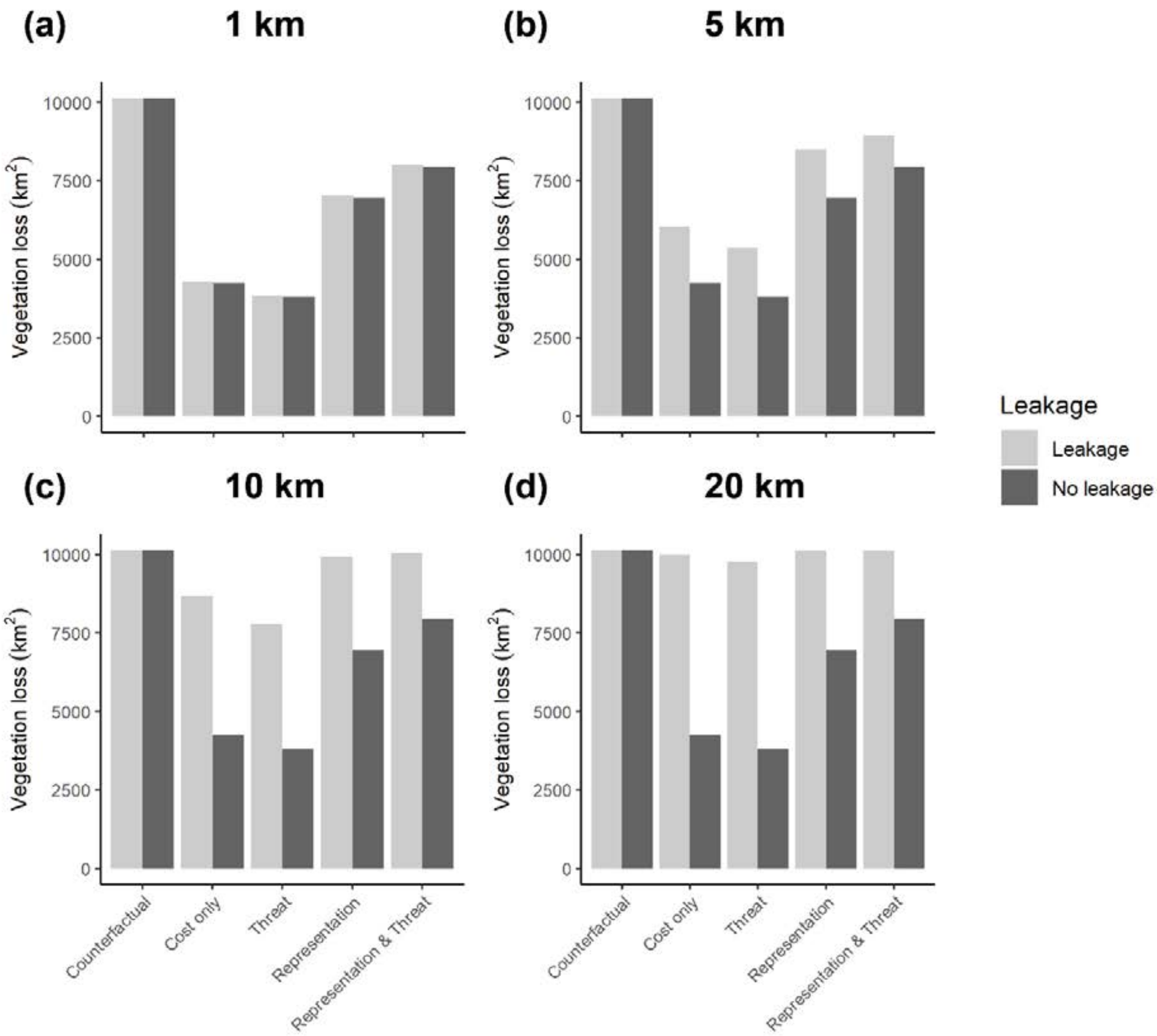

Figure A3.4 Vegetation loss between 2006 and 2016 in Queensland when no protection was implemented (counterfactual) and when alternative prioritisation strategies were implemented under different displacement scenarios. Light grey bars represent impact when displacement occurred, and dark grey bars represent impacts when no displacement occurred. Panels (a), (b), (c), and (d) show impacts when displacement of land clearing occurred from protected parcels to all unprotected parcels within a 1 km, 5 km, 10 km, and 20 km radius, respectively.

A3.5 Additional figures and tables

Table A3.1 Descriptions of broad vegetation groups (BVGs) as classified by Neldner et al. (2014). BVGs are classified into broader groups ("BVG group") which are used in Figure 4.1. The extent of vegetation clearing that occurred in the counterfactual scenario is also provided. Amounts of vegetation clearing are only provided for each BVG within the parcels included in the analysis.

BVG	Description	BVG group	Vegetation loss between 2006 and 2016 (ha)	Extent in 2006 (ha)	Vegetation loss as a proportion of extent	Proportion of pre-Eurpoean extent intact in 2006	Proportion of region covered by BVG in 2006
1	Complex mesophyll to notophyll vine forests of the Wet Tropics bioregion	Rainforests, scrubs	73	3434	0.02	0.15	0.00
2	Complex to simple, semi-deciduous mesophyll to mesophyll-notophyll vine forest, sometimes with *Araucaria cunninghamii* (hoop pine)	Rainforests, scrubs	591	16192	0.04	0.32	0.00
3	Notophyll vine forest/ thicket (sometimes with sclerophyll and/or Araucarian emergents) on coastal dunes and sandmasses	Rainforests, scrubs	10	169	0.06	0.53	0.00
4	Notophyll and mesophyll vine forest with feather or fan palms on alluvia, along streamlines and in swamps on ranges or within coastal sandmasses	Rainforests, scrubs	164	17307	0.01	0.50	0.00
5	Notophyll to microphyll vine forests, frequently with *Araucaria* spp. or *Agathis* spp. (kauri pines)	Rainforests, scrubs	1438	27904	0.05	0.41	0.00
6	Notophyll vine forest and microphyll fern forest to thicket on high peaks and plateaus	Rainforests, scrubs	78	2654	0.03	0.36	0.00
7	Semi-evergreen to deciduous microphyll vine thicket	Rainforests, scrubs	9,379	97334	0.10	0.29	0.01
8	Wet eucalypt tall open forest on uplands and alluvia	Wet eucalypt open forest	936	25054	0.04	0.51	0.00
9	Moist to dry eucalypt open forests to woodlands usually on coastal lowlands and ranges	Eucalypt woodlands to open forests	25,354	585208	0.04	0.54	0.03
10	*Corymbia citriodora* (spotted gum) dominated open forests to woodlands on undulating to hilly terrain	Eucalypt woodlands to open forests	34,360	587013	0.06	0.56	0.03
11	Moist to dry eucalypt open forests to woodlands mainly on basalt areas	Eucalypt woodlands to open forests	3526	214838	0.02	0.47	0.01
12	Dry eucalypt woodlands to open woodlands, mostly on shallow soils in hilly terrain (mainly on sandstone and weathered rocks)	Eucalypt woodlands to open forests	26,931	576479	0.05	0.77	0.03
13	Dry to moist eucalypt woodlands and open forests, mainly on undulating to hilly terrain of mainly metamorphic and acid igneous rocks	Eucalypt woodlands to open forests	58,932	4481035	0.01	0.77	0.23
14	Woodlands and tall woodlands dominated by *Eucalyptus tetrodonta* (Darwin stringybark) (or *E. megasepala*), and/or *Corymbia nesophila* (Melville Island bloodwood) and/or *E. phoenicea* (scarlet gum)	Eucalypt woodlands to open forests	2325	854138	0.00	0.99	0.04

15	Temperate eucalypt woodlands	Eucalypt woodlands to open forests	5800	92651	0.06	0.46	0.00
16	*Eucalyptus* spp. dominated open forest and woodlands drainage lines and alluvial plains	Eucalypt open forests to woodlands on floodplains	36,292	1096092	0.03	0.47	0.06
17	*Eucalyptus populnea* (poplar box) or *E. melanophloia* (silver-leaved ironbark) (or *E. whitei* (White's ironbark)) dry woodlands to open woodlands on sandplains or depositional plains	Eucalypt dry woodlands on inland depositional plains	267,895	2831732	0.09	0.42	0.15
18	Dry eucalypt woodlands to open woodlands primarily on sandplains or depositional plains	Eucalypt dry woodlands on inland depositional plains	36,551	765079	0.05	0.71	0.04
19	*Eucalyptus* spp. (*E. leucophloia* (snappy gum), *E. leucophylla* (Cloncurry box)*, E. persistens, E. normantonensis* (Normanton box)) low open woodlands often with *Triodia* spp. dominated ground layer	Eucalypt low open woodlands usually with spinifex understorey	1495	1978312	0.00	0.99	0.10
20	Woodlands to open forests dominated by *Callitris glaucophylla* (white cypress pine) or *C. intratropica* (coast cypress pine)	Callitris woodland - open forests	18,385	255324	0.07	0.54	0.01
21	*Melaleuca* spp. dry woodlands to open woodlands on sandplains *or* depositional plains.	Melaleuca open woodlands on depositional plains	2926	230044	0.01	0.87	0.01
22	*Melaleuca* spp. on seasonally inundated open forests and woodlands of lowland coastal swamps and fringing lines. (palustrine wetlands)	Melaleuca open woodlands on depositional plains	839	112315	0.01	0.86	0.01
23	*Acacia aneura* (mulga) dominated associations on red earth plains, sandplains or residuals.	Mulga dominated open forests, woodlands and shrubs	222,832	2133951	0.10	0.64	0.11
24	*Acacia* spp. on residuals. Species include *A. clivicola, A. sibirica, A. shirleyi* (lancewood), *A. microsperma* (bowyakka), *A. catenulata* (bendee), *Acacia rhodoxylon* (ringy rosewood)	Other acacia dominated open forests, woodland and shrublands	42,469	1132658	0.04	0.84	0.06
25	*Acacia harpophylla* (brigalow) sometimes with *Casuarina cristata* (belah) open forests to woodlands on heavy clay soils	Other acacia dominated open forests, woodland and shrublands	191,841	707106	0.27	0.13	0.04
26	*Acacia cambagei* (gidgee) */ A. georginae* (Georgina gidgee) */ A. argyrodendron* (blackwood) dominated associations	Other acacia dominated open forests, woodland and shrublands	20,597	391026	0.05	0.50	0.02
27	Mixed species woodlands - open woodlands (*Atalaya hemiglauca* (whitewood), *Lysiphyllum* spp., *Acacia tephrina* (boree), wooded downs	Mixed species woodlands - open woodlands (inland)	1341	191960	0.01	0.89	0.01
28	Open forests to open woodlands in coastal locations. Dominant species such as *Casuarina* spp., *Corymbia* spp., *Allocasuarina* spp. (she-oak), *Acacia* spp., *Lophostemon suaveolens* (swamp box), *Asteromyrtus* spp., *Neofabricia myrtifolia*	Other coastal communities or heaths	196	19365	0.01	0.88	0.00
29	Heathlands and associated scrubs and shrublands on coastal dunefields and inland rocky substrates	Other coastal communities or heaths	564	15773	0.04	0.77	0.00

Table A3.2 Vegetation loss prevented with each prioritisation strategy within each broad vegetation group (BVG).

		Counterfactual losses		Prioritisation strategy: Cost		Representation		Threat		Representation & Threat	
Broad vegetation group	*Extent in 2006 (ha)*	*Vegetation loss between 2006 and 2016 (ha)*	*Vegetation loss as a proportion of extent*	*Vegetation saved (ha)*	*Proportion of counterfactual loss prevented*	*Vegetation saved (ha)*	*Proportion of counterfactual loss prevented*	*Vegetation saved (ha)*	*Proportion of counterfactual loss prevented*	*Vegetation saved (ha)*	*Proportion of counterfactual loss prevented*
1	3,434	73	0.02	0	0.00	2	0.02	0	0.00	2	0.02
2	16,192	591	0.04	2	<0.01	21	0.04	0	0.00	22	0.04
3	169	10	0.06	0	0.00	3	0.29	0	0.00	3	0.29
4	17,307	164	0.01	8	0.05	37	0.22	15	0.09	36	0.22
5	27,904	1,438	0.05	9	<0.01	76	0.05	22	0.02	80	0.06
6	2,654	78	0.03	0	0.00	<1	<0.01	0	0.00	<1	<0.01
7	97,334	9,379	0.10	970	0.10	1,071	0.11	978	0.10	796	0.08
8	25,054	936	0.04	1	<0.01	448	0.48	<1	<0.01	447	0.48
9	585,208	25,354	0.04	1,742	0.07	5,472	0.22	916	0.04	4,805	0.19
10	587,013	34,360	0.06	6,438	0.19	18,397	0.54	4,395	0.13	17,692	0.51
11	214,838	3,526	0.02	246	0.07	207	0.06	134	0.04	205	0.06
12	576,479	26,931	0.05	14,810	0.55	5,231	0.19	15,140	0.56	6,789	0.25
13	4,481,035	58,932	0.01	14,919	0.25	9,932	0.17	9,023	0.15	10,211	0.17
14	854,138	2,325	0.00	1,254	0.54	928	0.40	12	0.01	894	0.38
15	92,651	5,800	0.06	2,051	0.35	648	0.11	2,286	0.39	346	0.06
16	1,096,092	36,292	0.03	11,327	0.31	7,037	0.19	12,489	0.34	6,237	0.17
17	2,831,732	267,895	0.09	173,740	0.65	68,719	0.26	198,065	0.74	67,741	0.25
18	765,079	36,551	0.05	12,050	0.33	4,871	0.13	12,842	0.35	4,364	0.12
19	1,978,312	1,495	0.00	985	0.66	466	0.31	211	0.14	415	0.28
20	255,324	18,385	0.07	13,572	0.74	6,644	0.36	13,582	0.74	6,816	0.37
21	230,044	2,926	0.01	404	0.14	608	0.21	260	0.09	598	0.20
22	112,315	839	0.01	88	0.11	92	0.11	17	0.02	84	0.10
23	2,133,951	222,832	0.10	210,334	0.94	51,112	0.23	217,447	0.98	51,847	0.23
24	1,132,658	42,469	0.04	34,227	0.81	18,933	0.45	37,094	0.87	17,295	0.41
25	707,106	191,841	0.27	76,770	0.40	20,742	0.11	95,748	0.50	18,812	0.10

26	391,026	20,597	0.05	9,756	0.47	1,561	0.08	12,276	0.60	1,480	0.07
27	191,960	1,341	0.01	650	0.48	37	0.03	461	0.34	31	0.02
28	19,365	196	0.01	22	0.11	43	0.22	7	0.04	40	0.20
29	15,773	564	0.04	294	0.52	279	0.49	291	0.52	284	0.50
Total	19,442,148	1,014,118	0.05	586,670	0.58	223,620	0.22	633,712	0.62	218,371	0.22

A4 Appendix 4: Supporting information for Chapter 5

A4.1 Representation targets

For the primary analysis, presented in the main text, representation targets were set to 30% in Marxan. However, I also measured impacts when representation targets were set to 50% and 100%. The same procedures for determining the Boundary Length Modifier (BLM), and the same budget limitations were used for these analyses as in the primary analysis.

My results were consistent with those from the primary analysis, regardless of the representation targets set (Figure A4.1).

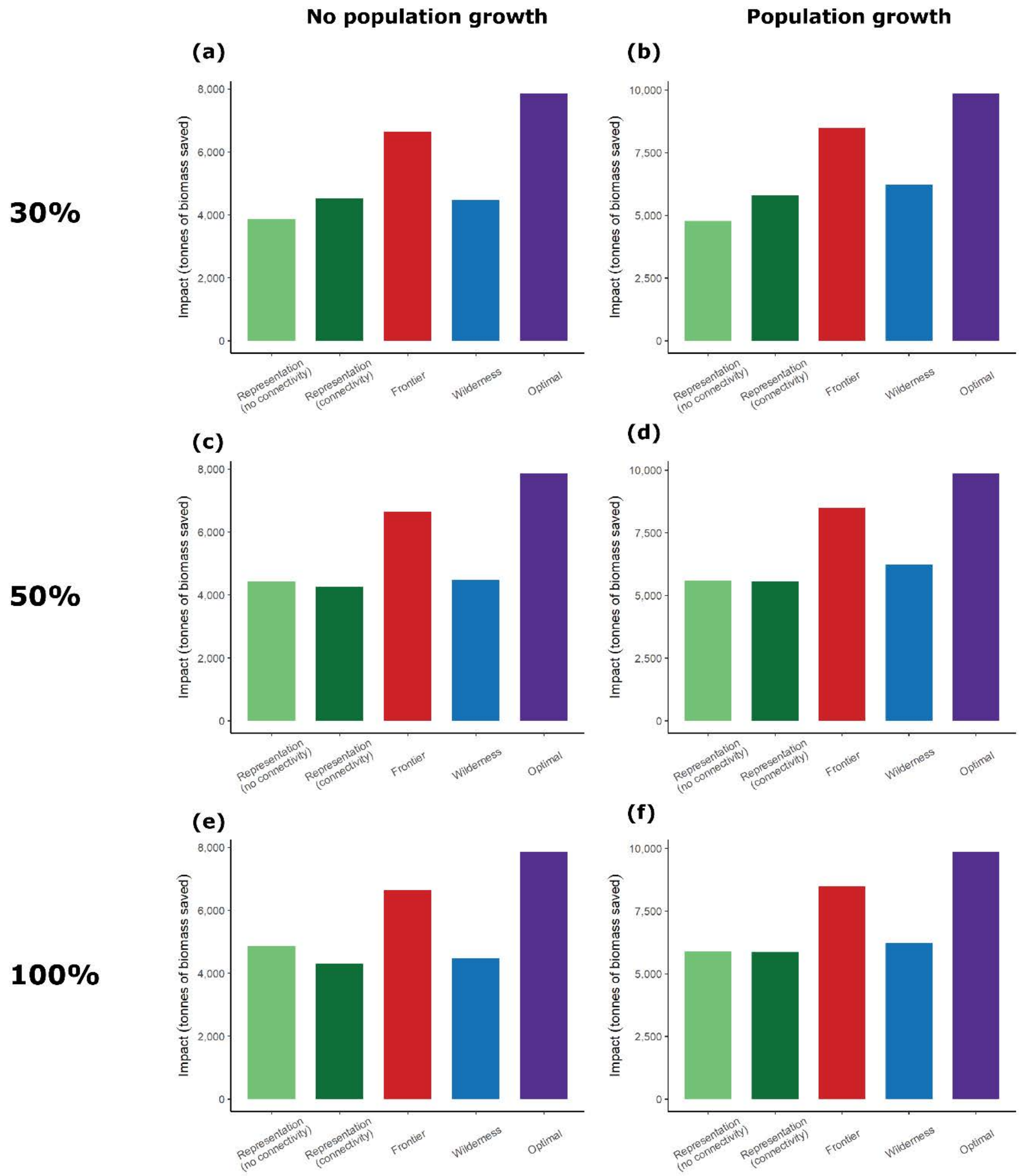

Figure A4.1 The impact of alternative conservation prioritisation strategies in Micronesia compared to counterfactual and optimal scenarios. Bars represent the total coral reef fish biomass (tonnes) saved relative to the counterfactual over 50 years when each strategy is implemented. Panels (a) and (b) represent impacts when representation targets were set to 30%. Panels (c) and (d) represent impacts when representation targets were set to 50%. Panels (e) and (f) represent impacts when representation targets were set to 100%. Panels (a), (c) and (e) represent scenarios where there was no population growth. Panels (b), (d) and (f) represent scenarios where there was population growth of 2% per year. Bars are colour coded for ease of interpretation. Light green, dark green, red, blue, and purple bars represent impacts when representation (no connectivity), representation (connectivity), frontier, wilderness, and optimal prioritisation strategies were implemented, respectively.

A4.2 Displacement distances

For the primary analysis, presented in the main text, I tested how the displacement of fishing threat affected the impact of each prioritisation strategy. For the primary analysis, I set the displacement radius to 20 km, such that fishing threat from planning units selected for protection was evenly distributed to all unprotected cells within a 20 km radius. Here I also provide supporting analyses where displacement radii were set to 1 km and 5 km.

Changing the displacement radius did not affect my results (Figure A4.2). However, when the displacement radius was larger, the impact of each strategy was reduced slightly.

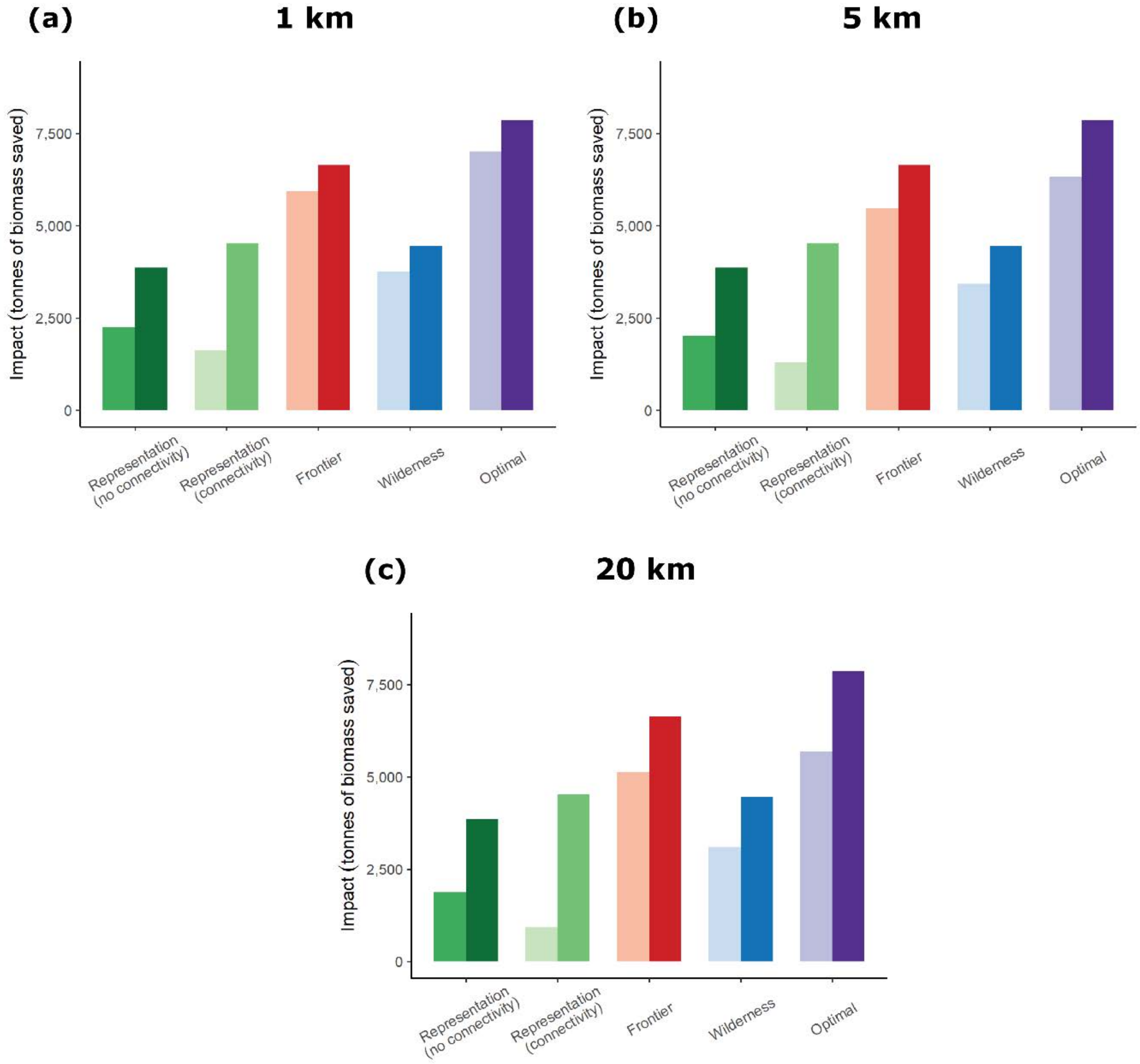

Figure A4.2 The impact of alternative conservation prioritisation strategies in Micronesia compared to counterfactual and optimal scenarios. Bars represent the total coral reef fish biomass (tonnes) saved relative to the counterfactual over 50 years when each strategy is implemented. Panels (a), (b) and (c) represent impacts when the displacement of fishing threat from protected to unprotected planning units occurred over a 1 km, 5 km, and 20 km radius, respectively. Bars are colour coded for ease of interpretation. Light green, dark green, red, blue, and purple bars represent impacts when representation (no connectivity), representation (connectivity), frontier, wilderness, and optimal prioritisation strategies were implemented, respectively.

A4.3 Functions for rate of biomass decline

For my primary analysis I assumed a power relationship between fishing threat and the percentage of biomass that is lost in each planning unit each year, according to Equation 5.1 of the main text. Here I present my results using alternative assumptions. Specifically, I estimate the impact of each strategy when the relationship between fishing threat and annual biomass loss is linear ($a = 1$), and when the power relationship is less pronounced ($a = 2$ and $a = 3$). I compare these to results from the primary analysis, where $a = 4$. These alternative relationship are depicted in Figure A4.3.

Variation in the relationship between fishing threat and annual biomass loss in unprotected planning units did not have any qualitative effect on my results (Figure A4.4). However, the overall impact of each strategy was affected by variation in this relationship. When the relationship was more linear, biomass losses were higher across the planning region. As such, higher amounts of biomass were lost in the counterfactual scenario, and the total amount of biomass saved by each strategy was higher (Figure A4.4).

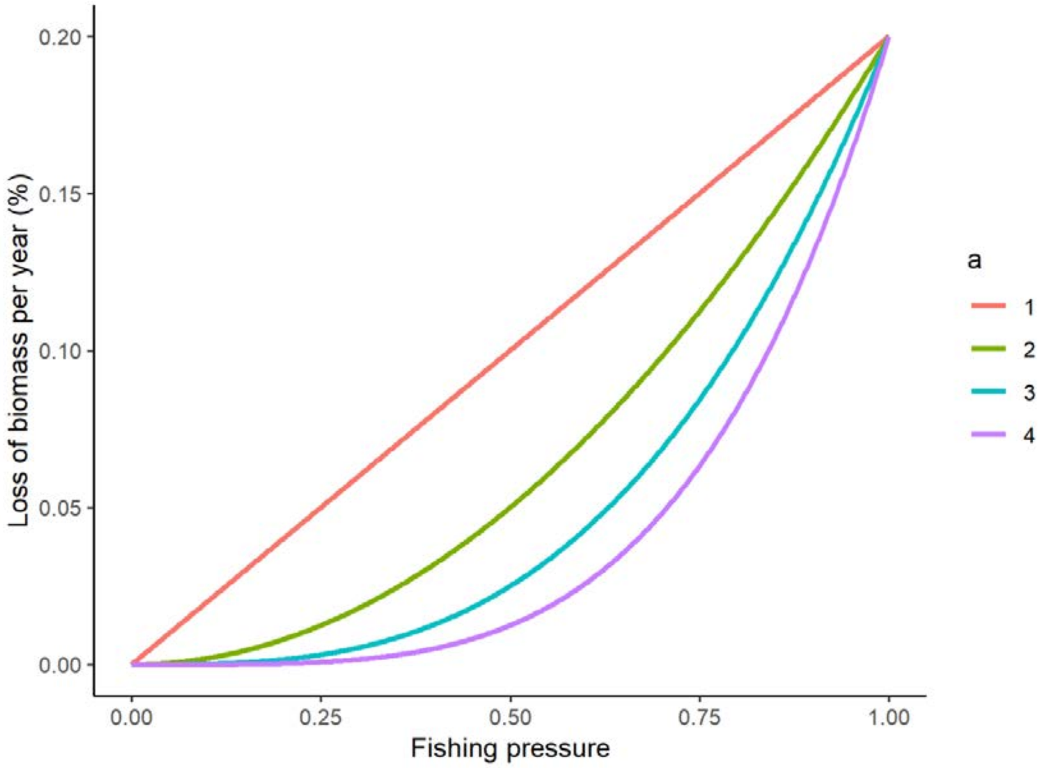

Figure A4.3 Alternative functions explored for the relationship between fishing threat and the annual loss of fish biomass in each planning unit. In the primary analysis, an $\boldsymbol{a}$ value of 4 was used. I also explored scenarios (see Figure A4.4) where $\boldsymbol{a}$ was set 1, 2 and 3.

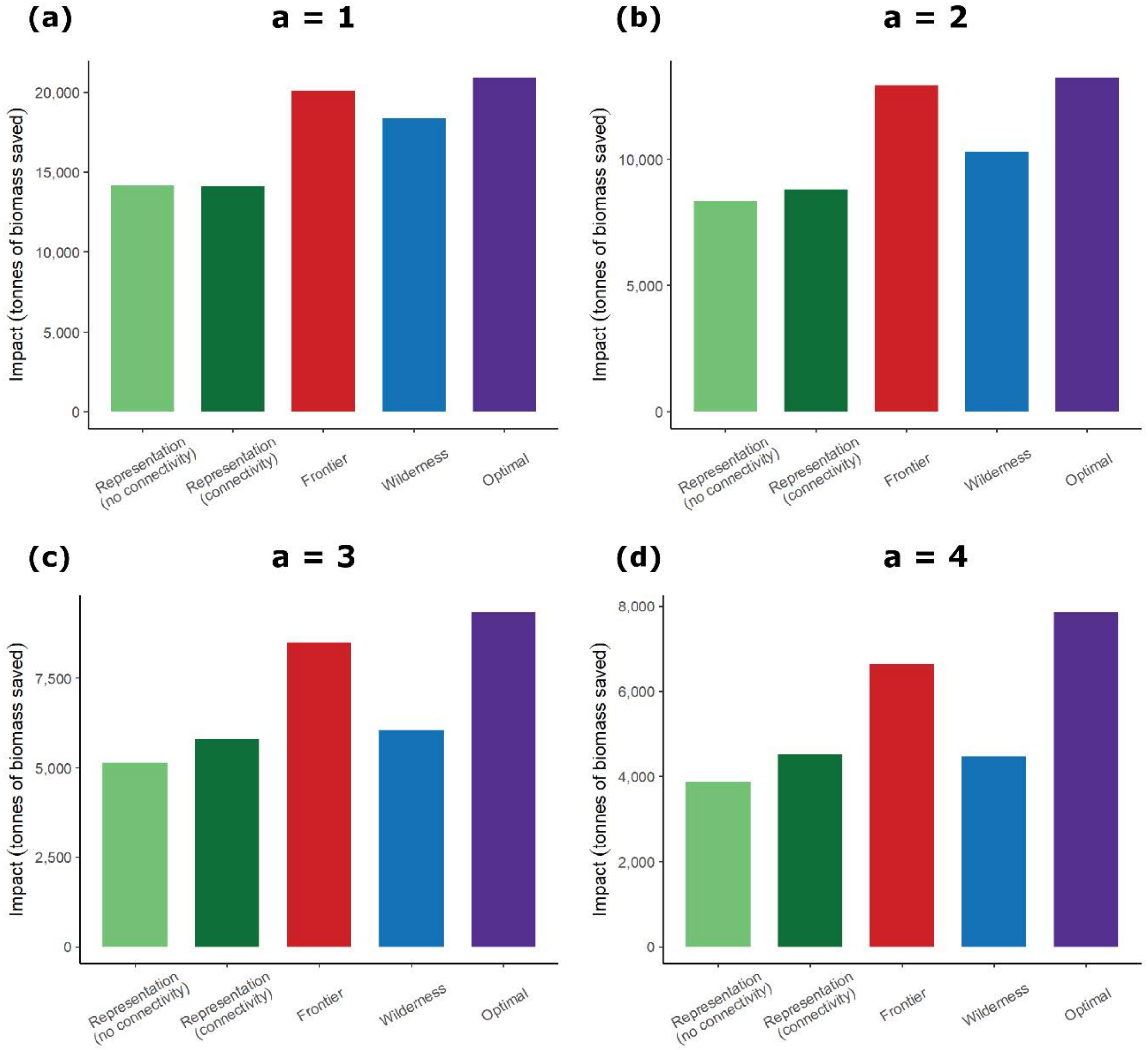

Figure A4.4 The impact of alternative conservation prioritisation strategies when alternative relationships between fishing threat and annual biomass loss are used. Panels (a), (b), (c) and (d) represent biomass saved when *a* values of 1, 2, 3, and 4 were used, respectively. These values correspond to the functions depicted in Figure A4.3. Bars are colour coded for ease of interpretation. Light green, dark green, red, blue, and purple bars represent impacts when representation (no connectivity), representation (connectivity), frontier, wilderness, and optimal prioritisation strategies were implemented, respectively.

A4.4 Functions for rate of biomass recovery

Here I provide supporting analyses using alternative rates for the recovery of fish biomass in planning units selected for protection. In the primary analysis, $B1$ controls the rate of recovery. In the primary analysis I assumed a value of $B1 = 0.2$, which allowed biomass to recover to potential unfished levels within approximately 50 years. Here I also provide analyses using values of $B1 = 0.8$, $B1 = 0.15$, and $B1 = 0.1$, which allows biomass to recover within approximately 10, 60, and 100 years, respectively (Figure A4.5). Changes to $B1$ had no effect on my results (Figure A4.6).

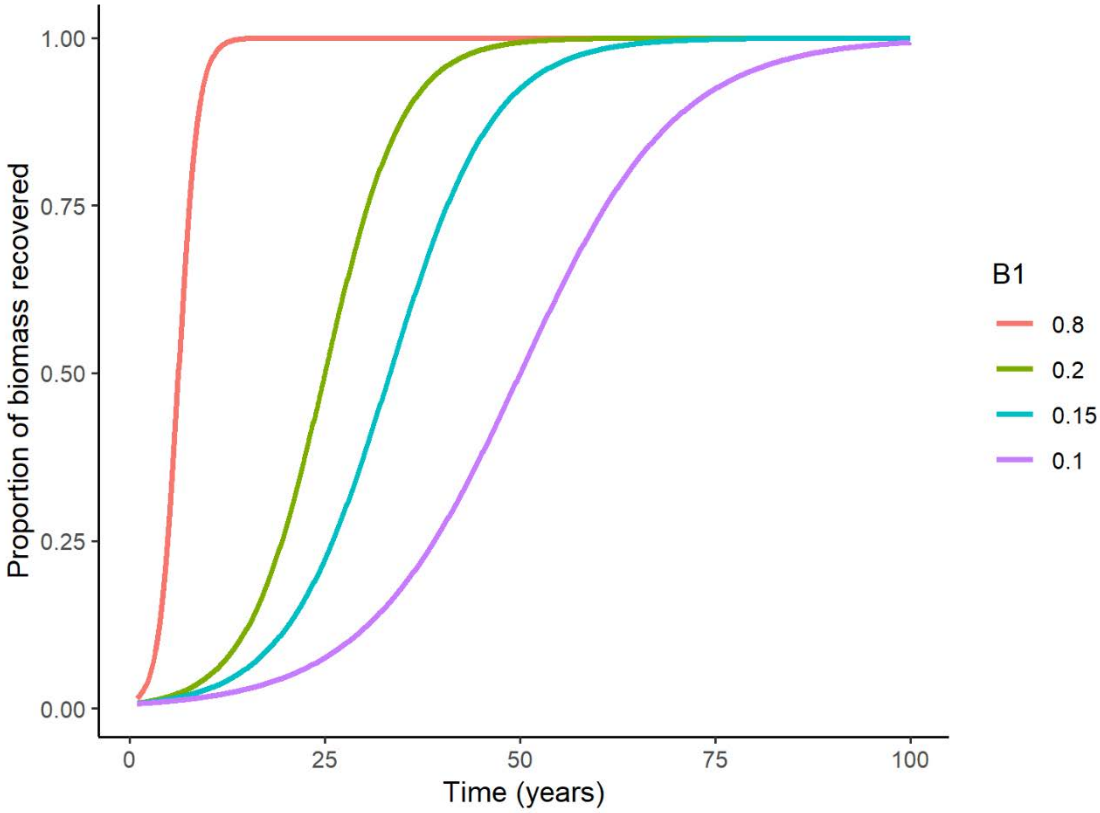

Figure A4.5 Alternative functions explored for the relationship between time (years) and the amount of biomass recovered in each planning unit. In the primary analysis, a $\boldsymbol{B1}$ value of 0.2 was used, which allows biomass to recover to potential unfished levels within approximately 50 years. I also explored scenarios (see Figure A4.6) where $\boldsymbol{B1}$ was set 0.8, 0.15 and 0.1, which allows biomass to recover within approximately, 10, 70, and 100 years, respectively.

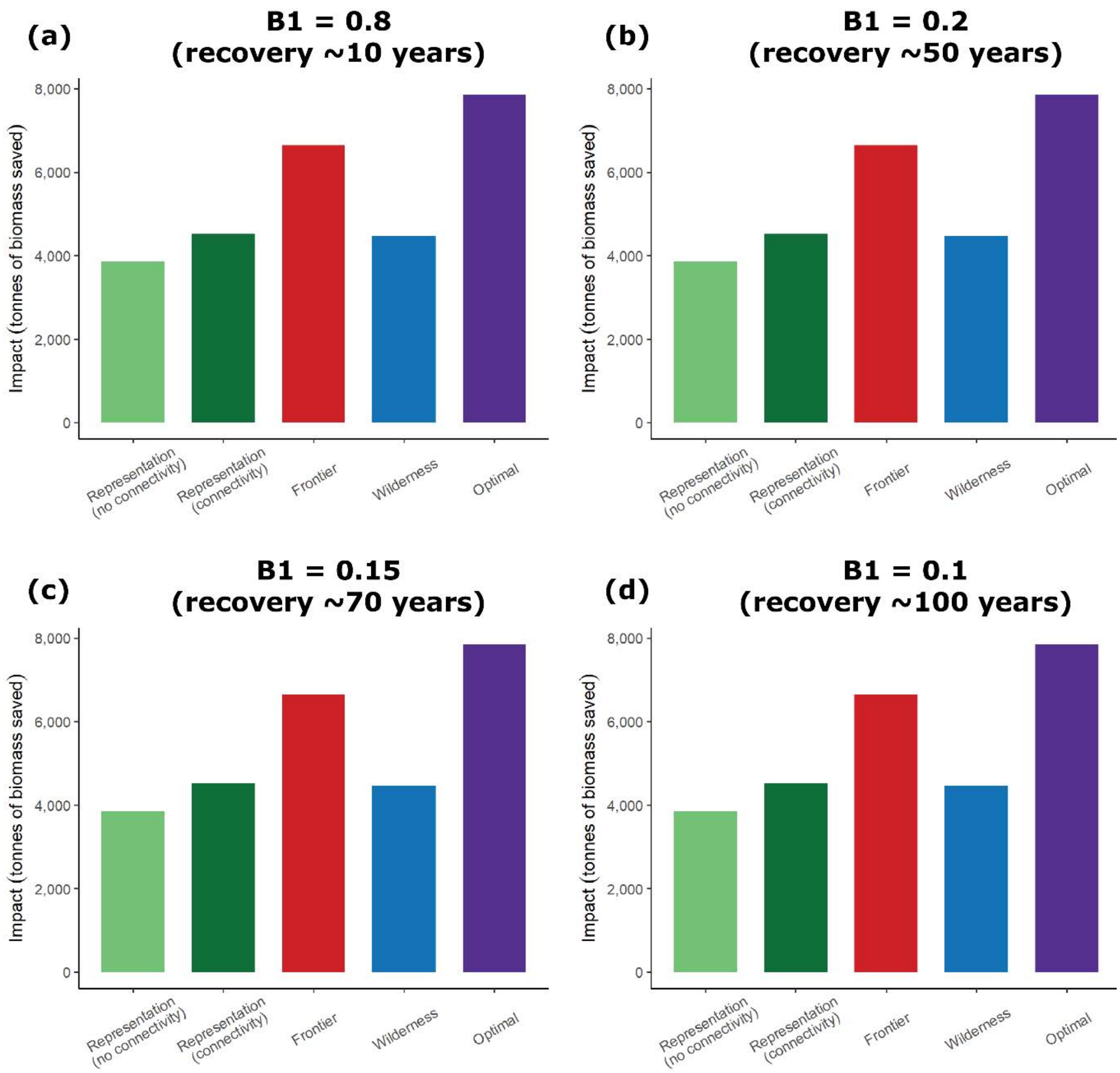

Figure A4.6 The impact of alternative conservation prioritisation strategies when alternative functions are used for the recovery rate of fish biomass after protection. Panels (a), (b), (c) and (d) represent impacts when *B1* values of 0.8, 0.2, 0.15, and 0.1 were used, respectively. These values correspond to the functions depicted in Figure A4.5. Bars are colour coded for ease of interpretation. Light green, dark green, red, blue, and purple bars represent impacts when representation (no connectivity), representation (connectivity), frontier, wilderness, and optimal prioritisation strategies were implemented, respectively.