



THE UNIVERSITY OF QUEENSLAND
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**Using fine and coarse conservation
targets to maximize cost-effectiveness of
road mitigation and protected areas**

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Abstract

The fundamental role of conservation science is to provide land managers and policy-makers with evidence-based practical guidance. Conservation decisions are usually made with limited information and tight budgets. This dictates the need for efficiency and cost-effective actions. Basically, efficiency is the ratio between benefit and cost. The larger the ratio (compared to other systems) the higher the efficiency of that system. When calculating efficiency, benefits and costs are usually in the same currency. In this thesis, cost-effectiveness is the ratio of a non-economic benefit relative to an economic or semi-economic (e.g. area of land) cost. Using decision science and defining objectives (such as achieving certain conservation targets) of the conservation problem we are addressing, can help us find better actions. Once the objectives of the problem are established, decision makers need to decide what features of biodiversity – genes, species, habitat– we intend to benefit. Different conservation problems involve different kinds of biodiversity features, which can represent different levels of coarseness (e.g. single species versus multiple; species versus ecosystems, etc.); each will have different financial costs and biodiversity benefits. However, the cost-effectiveness of choosing conservation features at different levels of coarseness is not well studied. As such, the overarching questions of my thesis are: How does the cost-effectiveness of the conservation outcomes change with the use of different fine- and coarse-scale biodiversity features as target? What are the trade-offs between biodiversity benefit and conservation cost involved when applying fine- and coarse-scale conservation efforts?

To examine these questions, I investigated the cost-effectiveness of conservation planning for two major conservation problems: 1) mitigating the effects of roads on wildlife (**Chapters 2-3**); and 2) the planning of protected area networks (**Chapters 4-5**). I explored the cost-effectiveness of several aspects of planning at different scales: single species (**Chapter 2**); from single to multiple species (**Chapter 3**) and from multispecies to a set of focal species (**Chapter 3**); and planning at both the multispecies and multi-ecosystem levels (**Chapters 4-5**).

The negative impact of roads on wildlife is a major problem worldwide. The two main direct effects are mortality due to animal-vehicle collision and reduced connectivity due to fragmentation. Mitigation measures such as fences and wildlife passages can be used to

reduce these effects, however they are expensive. The limitation of available conservation funds indicates the need for cost-effective solutions using decision science to decide which mitigation measures to use and where to place them. As such, I first mathematically formulated the problem of which road mitigation measures to place where, for the conservation of the threatened koala (*Phascolarctos cinereus*) population in the Koala Coast of south-east Queensland (**Chapter 2**). Each budget step had an optimal mitigation configuration. However, the linear shape of the trade-off curve between expected population size (the biodiversity benefit) and mitigation cost indicates that there is no clear “win-win” (low cost-high benefit) solution for protecting koala populations through road mitigation management. In **Chapter 3**, I used the problem formulation from **Chapter 2** in combination with a metapopulation mean time-to-extinction model to find optimal mitigation solutions for multiple species. I also compared the cost-effectiveness of using focal species (with selected life history traits) to that of the multispecies analysis. I found that the multispecies analysis was more cost-effective than planning separately for each species. However, using the focal species with the largest home range can provide adequate results and can be used when time or funding are limited and decisions need to be made in a hurry.

The Convention on Biological Diversity (CBD) aims to protect the world’s biodiversity by expanding the current protected area network to comprise 17% of the Earth’s terrestrial area using ecosystem-based targets (Target 11) and preventing the extinction of known threatened species (Target 12). While both targets use protected areas, Target 11 is the main driver for the CBD’s expansion plan. However, the cost-effectiveness of the CBD’s guidelines of using ecosystem-based targets to effectively represent threatened species has not been adequately investigated. In **Chapter 4**, I used Australia as a case study to test how well ecosystem-based targets protect threatened species, and compared the cost-effectiveness of planning for species and ecosystems separately and simultaneously. I used species-specific targets for 1,320 threatened species and a 10% target for each one of Australia’s 85 bioregions. I discovered that, following the CBD’s ecosystem-based approach for protected area expansion, the outcome would be inadequate and inefficient for representation of threatened species. Even filling in the gaps for threatened species protection later (coarse-then fine-scale) proved to be an inefficient strategy, while the reverse (fine- then coarse-scale) was almost as cost-effective as planning for both simultaneously. In **Chapter 5**, I extended this problem to explore the trade-off curves between the target sizes of these two conservation features within several protected area networks of different sizes. These curves

can be used as a planning tool for countries that have either geographical or monetary limitations. Depending on their needs, countries can use the trade-off curves to place more or less emphasis on either ecosystems or species when planning protected areas.

This research is one of the first to address feature-objective coarseness in conservation planning. The methods developed here allow decision makers to understand the cost-effectiveness and trade-offs involved with engaging with different levels of biodiversity features' coarseness. The two problems I address are current and pressing issues in conservation. The conclusions of my research show that: (i) Using all available data on the targeted biodiversity features will generate the most cost-effective solutions. (ii) Large-scale environmental surrogates or focal species might be used when monetary or time limitations prevail but are less cost-effective. (iii) Understanding the necessary trade-offs within the planning process can help decision scientists and planners to make informed choices about how to invest limited conservation resources, taking advantage of near win-win solutions where they exist.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Polak T., Rhodes J.R., Jones D., Possingham H.P. (2014) Optimal planning for mitigating the impacts of roads on wildlife. *Journal of Applied Ecology*, **51**, 726-734.

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Author Jonathan Rhodes	Wrote and edited paper (10%)

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Contributions by others to the thesis

Chapters 2, 4 and 5 of this thesis consist of published papers. Chapter 3 is in the final preparation stages; I aim to submit it in the coming weeks. All chapters retain their published form with the plural first-person pronoun “we” and within these chapters I refer to my work in its published format (e.g. Polak et al. 2015). In Chapters 1 and 6, which are the introduction and discussion of this thesis, I use the singular first-person pronoun “I” and refer to my work by chapter number. This is consistent with the fact that Chapters 2-5 are collaborative papers for which I am the lead author and Chapters 1 and 6 are solely my own work on which my advisors provided editorial comments.

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This chapter was written by the candidate with editorial comments from Hugh Possingham, Joseph Bennett, Josie Carwardine and James Watson

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Chapter 1: Introduction

1.1. Decision making in conservation

The role of conservation biologists is to bridge the gap between science and conservation practice and to provide land managers and policy-makers with practical tools and information to assist with decision-making. These decisions are usually made with limited information and under tight budget constraints. Possingham et al. (2001) devised a seven-point framework for good decision-making in conservation-related problems. In this framework they include the conservation aims, which should come from managers and policy makers (the ‘clients’). The aims are followed by a list of management actions, state variables and their dynamics, constraints and uncertainties, all of which are incorporated into a framework to try to find the best solution or a range of very good solutions to a conservation problem. Decision science incorporates budget constraints (Possingham et al. 2001, Newburn et al. 2005, Strange et al. 2006, McCarthy and Possingham 2007, McDonald-Madden et al. 2008, Tulloch et al. 2011), prioritizes actions (Polak et al. 2014), prepare for climate change (Hodgson et al. 2009), dealing with uncertainties (Regan et al. 2005) and facilitates resource allocation (Wilson et al. 2006, Martin et al. 2007, Game et al. 2008, Wilson et al. 2009).

The two main limitations in conservation practice are funds and information, where funds are usually limited and information is often lacking. When we consider the problem of funds, conservation decision-making deals with their allocation; there is, essentially, an inherent understanding that resources are finite and there is a need to distribute them in a way that will maximize the benefit to biodiversity (Possingham et al. 2001). For example, Joseph et al. (2009) designed a project prioritization protocol to determine how best to distribute funds among New Zealand’s threatened species projects taking costs, benefits and likelihood of success into the decision process.

The data underpinning conservation decision-making is never perfect and we need to be able to make decisions under conditions of uncertainty (Regan et al. 2005, McDonald-Madden et al. 2008). When testing different levels of uncertainty, McDonald-Madden et al. (2008) demonstrated that when uncertainty levels are high, even very large amounts of resources may not achieve good conservation outcomes. Moreover, when we face both limitations (funds and information), the problem can be even greater. For example, Carwardine et al. (2008b) show that choosing the wrong cost surrogate can double the cost of achieving an adequate conservation outcome.

Lastly, while the main goal in conservation biology is to increase the benefit for biodiversity, in conservation decision-making the goal is not singular; the aim is not only to increase the benefit to biodiversity or to reduce cost, but also to try to reach an acceptable compromise between the two. One of the things we can learn from formal decision-making processes is that “you cannot have it all” – there is always a compromise, a trade-off.

1.2. Fine- to coarse-scale conservation

Conservation projects can range in size and complexity, from single species reintroductions to the establishment of vast networks of protected areas. Each project will have different costs and different biodiversity benefits. The first steps of any conservation project are to identify the problem and establish the objective that our choice of actions is trying to achieve. The next step to tackle during the conservation decision-making process is defining the appropriate biodiversity feature(s) (i.e. species, habitats, ecosystems) to use for the outcome that we hope to achieve (Noss 1987, 1990, Lindenmayer et al. 2007). The features used should support the objective of the decision as much as possible and are expected to affect the recommendations and decisions made. In the past, many conservation actions were aimed at preserving species and habitats (Noss 1990, Franklin 1993, Caro and O'Doherty 1999) as these are both easily defined and measurable features (Noss 1987). In the 1990's, conservation practices broadened to include the objectives from the full range of ecological scales, from genetic to landscape (Noss 1990, Poiani et al. 2000).

Different biodiversity features can be collated at differing levels of coarseness. For example, when a new protected area is planned, the area designated for protection can be selected based on a:

- (i) Single species approach – where conservation efforts concentrate on a single species' needs (Caughley 1994), designing the new protected area based on its importance as a habitat for an endangered species (Panwar 1982, Johnsingh and Joshua 1994).
- (ii) Focal species approach – using information from keystone species or taxa that are expected to support other biodiversity features as well (Simberloff 1998), as the focus for protected area planning.
- (iii) Community approach – where conservation efforts consider the needs of a group of species and design the protected area system to reflect their combined needs.
- (iv) Area-based approach – using information from coarse-scale conservation features such as ecosystems that provide habitats and functions and also support the local taxa (Walker 1995). For example, watersheds provide ecosystem functions such as water purification, reduce sedimentation (Brauman et al. 2007) and also provide nursing ground habitat for species (Brummett 2006). In this thesis, I will use the term **coarseness** (i.e. **fine- and coarse-**

scale) to refer to the units of manageable features (e.g. species, community, ecosystems, bioregions, etc.) to which one can apply management or policy actions (Noss 1987, Poiani et al. 2000). For example, a multispecies approach to determine which mitigation measures should be placed on the road represents a coarse-scale feature (community/multispecies) compared to a single species approach. A focal species (e.g. umbrella species) represents a coarser-scale than the two former features and yet it is a single species analysis (see **Chapter 3**).

The debate around whether to use fine or coarse information is not new and both approaches have their merits and shortcomings (Lindenmayer et al. 2007). Coarse scale conservation planning has advantages because it could protect more biodiversity features under one complementary set of actions (Poiani et al. 2000). This can allow for quick and less repetitive conservation outcomes than finer scales. Moreover, as we have information on just a fraction of the species in the world, preserving coarser-scale units such as ecosystems and regions can protect a multitude of species, habitats and processes that are not yet known (Franklin 1993). In addition, information about coarser-scale features is easier and cheaper to find and can reduce the costs of gathering preliminary information (Grantham et al. 2009). However, one of the disadvantages of this approach is that some species are so threatened that only fine-scale species-specific actions will ensure their success, as in the case of the red-cockaded woodpecker (*Picoides borealis*). In this example, the species' dependency on old longleaf pine (*Pinus palustris*) for nesting cavities, which were affected by logging and the intrusion of hardwoods, resulted in a steep decline that required intense measures to ensure its recovery (Simberloff 1998). These measures centred on both the population level by translocation and artificial nesting cavities, and on the habitat level by burning regimes and the protection of old longleaf pine (Simberloff 2004, Lindenmayer et al. 2007). Simberloff (1998) expressed a concern that coarse-scale conservation focuses more on the processes that maintain the health of an ecosystem and not on individual species. This may lead to species loss because their individual needs are not met, as they are not an essential part in preserving the ecosystems' processes. As such, some claim that coarse-scale conservation may be too broad and less effective than single-species conservation and that protection of the "right" species (i.e. keystone, umbrella species) may be a more cost-effective approach to conserving biodiversity (Tracy and Brussard 1994, Simberloff 1998, Walpole and Leader-Williams 2002). Another problem with coarse-scale conservation is that, while a species is a relatively easy feature to define, other features such as ecosystems may be difficult to categorize (Tracy and Brussard 1994). A similar difficulty arises when determining the goal of conservation efforts because species-related goals are often easier to define, explain and quantify (Simberloff 1998).

In short, a trade-off exists between focusing efforts on different coarse-scale conservation features (community or ecosystem), which may not sufficiently protect all of the target species (Noss 1987), but fine-scale feature conservation may overlook key large-scale factors affecting ecosystems (e.g. a watershed) and probably requires more resources (Noss 1990, Caro and O'Doherty 1999, Poiani et al. 2000). Nonetheless, it appears that more conservation biologists emphasise the benefits of coarse-scale in conservation (Noss 1987, Franklin 1993, Poiani et al. 2000), chiefly because large-scale conservation actions protect a very large percentage of biodiversity that otherwise may go unprotected (Franklin 1993). Indeed, achieving more conservation targets in “one go” should be more cost-effective than fine-scale conservation. However, this premise has not been thoroughly tested. As such, the over-arching question in my thesis is: Will moving to coarse-scale conservation efforts be more cost-effective than fine-scale conservation?

1.3. Trade-off curves

Many applications of decision science in conservation try to find the single best solution. However, in the dynamic world of conservation practice, where there can be several conflicting objectives, one solution might not be practical (Brown and Mumby 2014). As such, giving managers several good solutions from which to pick may be more useful than one best solution. One way to provide decision makers with a range of good solutions is to present trade-off curves (Polasky et al. 2005). Trade-off curves can compare two aspects of any conservation plan or action – for example, its financial cost and its biodiversity benefit. In these curves, an improvement in one objective usually results in a decline in the other objective (Polasky et al. 2008): more biodiversity benefit usually costs more money, and the best solution is dependent on the decision maker's views about the relative importance of each objective (Haight et al. 2005). The aim of this type of research is to help planners and decision makers to make an informed decision taking into consideration the limitation of each objective under a given budget (Haight et al. 2005, Brown and Mumby 2014).

Trade-off curves can be used to plot biodiversity values or other conservation gains against monetary expenses (Faith and Walker 1996), economic return from other land uses (Polasky et al. 2005), the efficiency of a conservation plan (Armsworth et al. 2012), conserving one type of biodiversity features versus another (Di Marco et al. 2015), or any number of other conservation goals (Hamaide et al. 2006). The recurring feature of these curves is the inability to maximise both objectives simultaneously. However, the shape of the curve (Figure 1.1) gives us information about

the potential for near “win-win” solutions and how much an improvement in one outcome diminishes the other outcome. If the trade-off curve is L-shaped (Figure 1.1, green), then we can almost obtain win-win solutions that achieve high conservation values while retaining low costs or losses (Figure 1.1, red dot; Faith and Walker 1996, Polasky et al. 2005). In this situation, we do not need to compromise much on either objective (Polasky et al. 2005). On the other hand, a linear trade-off curve (Figure 1.1, red) means that win-win solutions are not possible, as improving one objective comes at a substantial cost to the other objective (Creel and Christianson 2008).

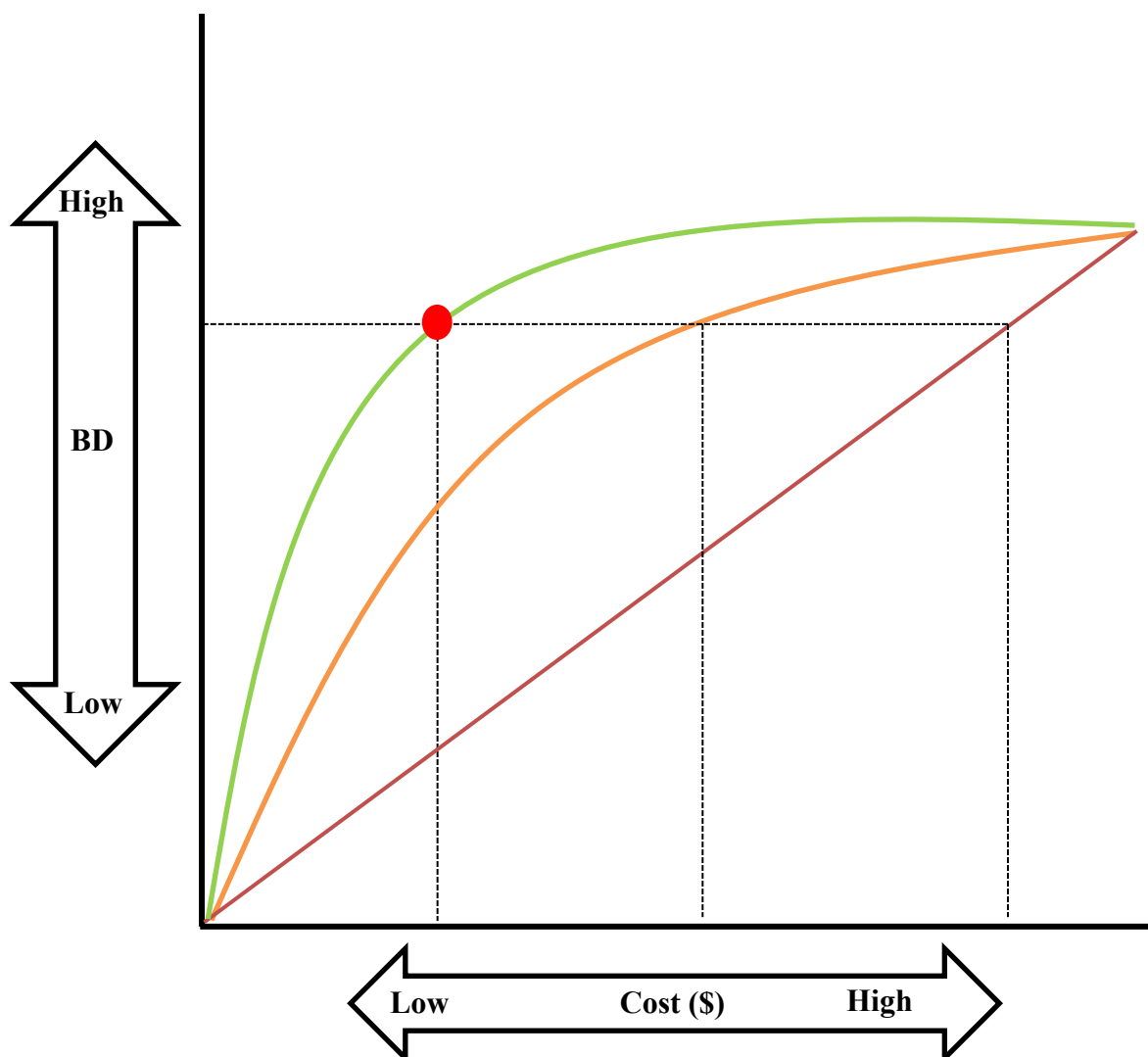


Figure 1.1: Trade-off between biodiversity (BD) and cost. The green curve is an L-shaped curve than can achieve a good biodiversity outcome with low cost. When the curve becomes more linear (orange then red curves), there is a need to invest considerably more money to reach the same biodiversity outcome.

1.4. Efficiency and cost-effectiveness

To compare between fine- and coarse-scale planning approaches, I will use two terms: efficiency and cost-effectiveness. These two terms can be confusing and the distinction between the two is sometimes unclear. Basically, efficiency is the ratio between output and input: when two systems are compared, the system that is more cost-efficient is the system whose ratio between output and input is larger (Rumble 2012). Cost-effectiveness is related to both the benefits the product provides (quality and quantity) and its cost (Rumble 2012). Efficiency is how well an action is done relative to the investment made to it and effectiveness is how useful the action is to the conservation goal. In conservation biology, cost-effectiveness is the term more commonly used than cost-efficiency (ISI web of Knowledge). However, the terms are used interchangeably (Kessler et al. 2011, Lundström et al. 2011).

I believe that this is because, in conservation decision-making, efficiency and cost-effectiveness can be used for different purposes. Efficiency refers to a situation in which two projects have a similar budget but their successes vary, making one project more efficient than the other. Thus, efficiency or cost-efficiency should be when we want to compare apples to apples, meaning outcomes of similar projects (e.g. testing two pesticides used for weed removal or the outcome of the same rabbit eradication program on two different islands). An efficiency frontier (Polasky et al. 2005, Polasky et al. 2008) is a good example of efficiency. The solutions or projects along the efficiency frontier are those defined as the non-dominated solutions (making these points optimal solutions), meaning that all the points on the trade-off curve cannot be out-performed by any other solution at the same budget. Cost-effectiveness is used to compare projects with different budgets because with non-monetary projects, effectiveness should be more important than the bottom line. A program can be very cheap but if it does not deliver substantial outcomes its cost-effectiveness will be very low and essentially a waste of money. Cost-effectiveness analysis can be used to compare between the different solutions along the efficiency frontier, because while each point represents an optimal solution at that cost step, some solutions are more cost-effective than others. Lastly, efficiency, for example, can be used to compare between two culling methods (e.g. traps and shooting) to eradicate invasive rabbits, in which we can quantify how much it costs to kill one rabbit or how many rabbits are culled for a \$1000 spend. Cost-effectiveness can compare the effectiveness (e.g. the reduction in the rabbit population size) of these two culling methods and

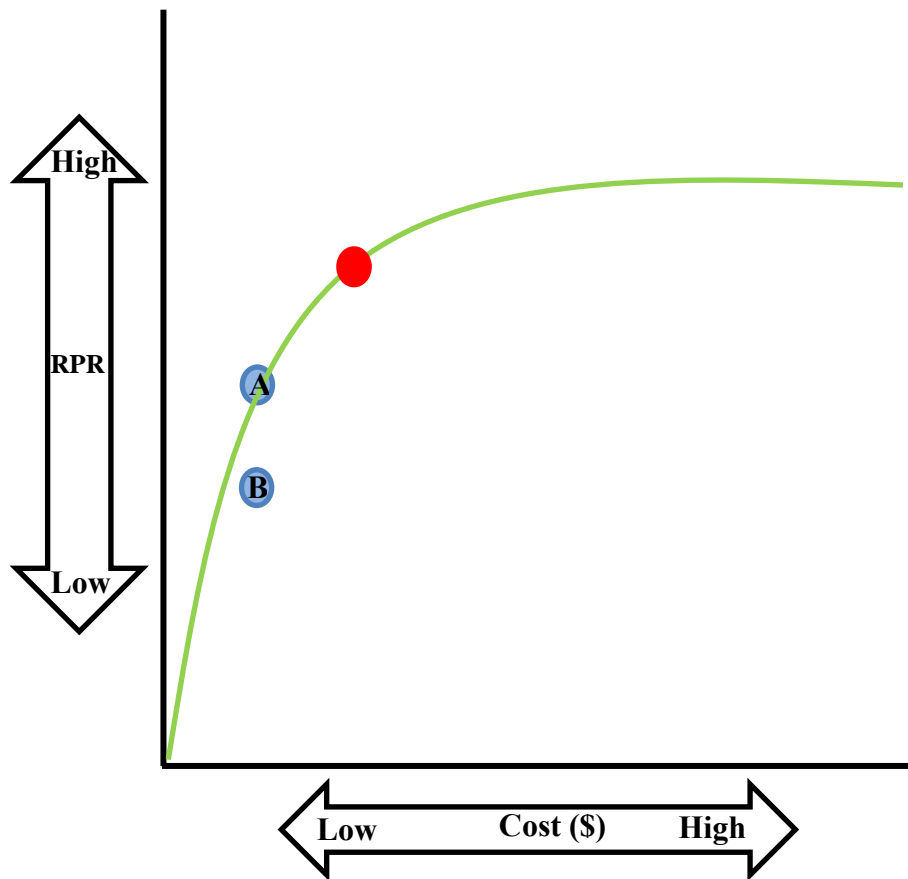


Figure 1.2: Comparing cost-effectiveness between different conservation actions. The y-axis represents the reduction in rabbit population size (RPR) and the x-axis represents cost. Blue dots represent the two culling methods, which cost the same, and method A is more efficient than method B because it provides a higher benefit at the same cost. The red dot represents a different management action at a higher cost. From the location of the red dot on the curve its cost-effectiveness is higher than that of A. other management actions such as exclusion (e.g. fencing), which may vary in cost compared to the culling methods (Figure 1.2).

1.5. Thesis overview

While there have been many conservation plans dedicated to coarse-scale conservation practice (Noss 1987, Franklin 1993, Olson and Dinerstein 1998), none explore the cost-effectiveness of conservation efforts when comparing between fine- and coarse-scale resolution. In other words, while many argue that it will be more cost-effective to plan conservation using ecosystems or communities instead of species as targets for conservation efforts, I was not able to find any study that determined whether this is the case empirically. The novelty of my PhD research

is that this is the first time that decision-science framework has been performed for conservation prioritization based on features of different levels of coarseness comparing the cost-effectiveness of moving from fine- to coarse-scale features. I explore two major conservation problems: 1) mitigating the effects of roads on wildlife (**Chapters 2-3**); and 2) planning of a protected area network (**Chapters 4-5**). To do this, I explored the cost-effectiveness of conservation decision-making at four levels of coarseness: I) single species (**Chapter 2**); II) single species versus community; III) community versus focal species (**Chapter 3**); and IV) species versus ecosystems (**Chapters 4-5**).

1.5.1. Mitigating the effects of roads on wildlife – Chapters 2 and 3

Roads are a common feature worldwide (Forman and Alexander 1998, Fahrig and Rytwinski 2009), encroaching on even some of the most remote places on Earth (Laurance et al. 2014). Trombulak and Frissell (2000) outlined seven different effects roads have on biodiversity and ecosystems. Three of these are population-oriented: increased mortality due to habitat loss and road construction; increased mortality due to wildlife-vehicle collisions; and changes to animal behaviour. Four of these are ecosystem effects: changes to the physical and to the chemical environments, spread of invasive species, and increased accessibility for humans to natural areas. In my research I focused on the impacts of roads on wildlife populations, specifically on the prevention of mortality due to wildlife-vehicle collisions.

In most cases, roads have negative effects on wildlife populations. Vehicle-wildlife collisions can increase mortality rates while a reduction in habitat size and quality can affect birth and death rates, especially for density-dependent populations. A decrease in connectivity can affect movement between populations and prevent rescue effects (Fahrig and Rytwinski 2009). In addition, roads can cause disturbance (noise, light, pollution, etc.) and induce behavioural changes (Fahrig and Rytwinski 2009). Roads appear to affect species depending on their life history. Mammals with large bodies, high mobility and low reproductive rates, as well as highly mobile birds and amphibians with low reproductive rates and/or small body size, all exhibit higher road-related mortality (Rytwinski and Fahrig 2012).

In some cases, roads have contributed to species-wide population decline (Aresco and Russell 2005). For example, in the United States, roads contribute to turtle population decline by a combination of fragmentation and movement barriers and increased mortality due to road kills (Gibbs and Shriver 2002). Slow moving amphibian species are more likely to get killed crossing

even low volume roads, with potentially severe effects on population persistence (Hels and Buchwald 2001). In high volume roads, an amphibian's probability of getting killed per road crossing was found to be close to one, especially if the crossing occurred during day or at an angle to the road (Hels and Buchwald 2001). Although birds are perceived to be more capable of avoiding traffic, over 80 million birds are killed annually in the United States. Birds are also highly vulnerable to light and noise related to roads, which can affect their breeding (Kociolek et al. 2015). In south-east Queensland, animal-vehicle collisions are a major cause of the decline in the koala population (Rhodes et al. 2011).

There are several mitigation measures to reduce animal mortality due to vehicle collisions, including wildlife crossing structures (Bissonette and Adair 2008), fencing (Clevenger et al. 2001, Aresco and Russell 2005), traffic signs to alert commuters, roadside vegetation removal, reflectors for the alertness of both wildlife and drivers, and traffic speed and volume control mechanisms (Jones 2000). These mitigation measures have shown different levels of success. In particular, evidence for the efficacy of indirect mitigation like reflectors and road signs is mixed (Bruinderink and Hazebroek 1996, Jones 2000, Dique et al. 2003b). In addition, the effectiveness of fencing was found to depend on a species' road avoidance behavior and the chance of an individual being killed crossing the road (Jaeger and Fahrig 2004b). In cases where behavior avoidance was low and collision mortality was high, fences were found to be most effective. However, if the opposite is true then fences could decrease population persistence (Jaeger and Fahrig 2004b).

Nonetheless, mitigation efforts are generally considered effective and important for reducing the effects of roads on wildlife. For example, in Canada fences were found to reduce wildlife-vehicle collisions by 80%, despite the fact that the locations where fences end result in clusters of higher mortality rates (Clevenger et al. 2001). Road mitigation has also been shown to reduce the risk of population decline in wombats (Roger et al. 2011). In Tasmania, road mitigation managed to save eastern quoll (*Dasyurus viverrinus*) and Tasmanian devil (*Sarcophilus laniarius*) populations from local extinction due to road upgrades (Jones 2000). In Florida, Dodd et al. (2004), found a 65% decline in wildlife mortality and an increase in the use of culverts after the construction of a barrier wall-culvert system.

Several studies have implemented computer modelling with the goal of finding general patterns to assist in the placement of mitigation efforts. High frequencies of animal-vehicle collisions seem to be connected to both landscape and road attributes (Malo et al. 2004, Seiler 2005). These locations with high frequencies of collisions usually occur in diverse habitats with dense vegetation cover (Malo et al. 2004) that hide animals from a driver's line of sight until it is too late to prevent a collision. Traffic volume and speed are also major factors in the probability of

an animal-vehicle collision (Jaeger et al. 2005, Langevelde and Jaarsma 2005, Seiler 2005). Most animals will have low probability of traversing major roads with high traffic volume (Langevelde and Jaarsma 2005) but even minor roads with medium traffic flow can strongly impact population persistence (Seiler 2005, van Langevelde et al. 2009).

Lastly, while multispecies studies appear in the road ecology literature (e.g. Gibbs and Shriver 2002, Dodd et al. 2004, Grilo et al. 2008, Rytwinski and Fahrig 2012), they are not common practice and in many of the cases these studies are confined to closely-related groups of species (Gibbs and Shriver 2002, Grilo et al. 2008). Moreover, the majority of the multispecies studies have tried to find general patterns in the species' responses to mitigation (Dodd et al. 2004, Grilo et al. 2008), including patterns related to life-history traits (Rytwinski and Fahrig 2012) and population dynamics (Gibbs and Shriver 2002). However, none looked at how to plan mitigation in a way that will maximize the benefits to multiple species efficiently.

Decision theory can improve population viability by informing us about which actions are the most effective to use to mitigate the effects of road mortality while minimizing the cost of these mitigation actions. However, to my knowledge, no study into mitigating the effects of roads has directly considered budget limitation in its analytical framework. Thus, no study has looked at the optimal way to use road mitigation strategies to increase population persistence under budget limitations (**Chapter 2**). Moreover, considering the magnitude of disturbances caused by roads and the multitude of species affected by them, it seems intuitive that mitigating the effect of roads to accommodate whole communities should be more cost-effective than efforts aimed at individual species (**Chapter 3**). However, I have found no study that tested this theory and compared the cost-effectiveness of single versus multispecies planning of road mitigation.

Therefore, I first used decision theory and mathematically formulated the problem of mitigating the impact of roads on wildlife to optimize mitigation for a single species population under budget constraints (**Chapter 2**). In this chapter, I explored the optimal mitigation strategy for the endangered Koala (*Phascolarctos cinereus*) population of the Koala Coast in south-east Queensland. The problem formulation tested the cost-effectiveness of all possible mitigation combinations along four roads separating four koala populations and provided the best mitigation strategy to take for any given cost. This is the first ever attempt to mathematically define and solve a decision science problem for mitigating the impact of roads on wildlife. In **Chapter 3**, I extended this problem to a community level with multiple species and different road sensitivities. Moreover, while I tested this as a multispecies problem I also compared the efficiency of mitigation efforts when they focus at the community level versus when they focus on a single flagship species. Lastly, I showed the flexibility of the method and hence the feasibility of the methods to fit other systems,

by testing it on two groups of multiple species from two different continents while also using a different population model than in **Chapter 2**. This chapter will provide an important tool for systematic road mitigation, by using a holistic multispecies model that can be applied to many other systems attempting to reduce the effect of roads on local wildlife.

1.5.2. Ecosystem-based versus species-based protected areas planning – Chapters 4 and 5

Protected areas are important for conservation as they help shield species and ecosystems from many threats (Margules and Pressey 2000). In the past, protected areas were often selected to ensure the persistence of a few endangered species (Lambeck 1997, Caro and O'Doherty 1999). Most often, these were charismatic species attracting the public eye ('flagship' species, Johnsingh and Joshua 1994). However, this criterion may not be the best to represent overall biodiversity (Simberloff 1998, Caro and O'Doherty 1999, Neel and Cummings 2003b, Roberge and Angelstam 2004b, Hoekstra et al. 2005).

Gradually, protected area plans have focused more on preserving community, ecosystem, habitat and ecological processes (Olson and Dinerstein 1998, Margules and Pressey 2000, Hoekstra et al. 2005, Wilson et al. 2007). Nevertheless, species is still the main target for conservation and therefore is expected to be a key consideration in protected areas' network planning. Protecting ecosystems or habitats are often assumed to adequately protect biodiversity (Natural Resource Management Ministerial Council 2004, Stoms et al. 2005, Grantham et al. 2010), including threatened species.

However, this may not really be the case. Gap analyses (Scott et al. 1993) generally checks either species or ecosystem (but usually not both) representation gaps in existing protected area networks. For example in England, Oldfield et al. (2004) found the 79% of the habitat types had less than 10% of their area in protected areas. In a global gap analysis, Rodrigues et al. (2004b) identified over 1,400 "gap" species, which were defined as species for which protected areas cover no part of their distribution. Moreover, among the species that were considered 'covered' (i.e. had some of their range located in protected areas) over 1,400 were not covered by an area larger than 1,000 ha. In addition, only about half of the biomes and two thirds of the habitat types that were examined by Chape et al. (2005) had 10% or more of their area in protected areas.

Currently, the Convention for Biological Diversity (CBD)'s Target 11 promotes the protection of 17% of the Earth's area and each of the 193 member countries is obligated to meet this target (CBD Secretariat 2010), making this the largest protected areas expansion in the world. Moreover, the CBD promotes a systematic planning of the new protected areas, which follows the ecosystem approach whereby area-based targets (ecoregions or bioregions) are used to plan for the placement of the new reserves (Woodley et al. 2012). These protected area systems should be representative, well connected and include areas of particular importance for biodiversity and ecosystem services. . While Target 11 is explicitly about protected areas, Target 12 is about the need to prevent further extinction of threatened species, with protected areas as one of the chief methods to achieve this (CBD Secretariat 2010). While the CBD's targets are admirable they are not clearly defined targets that can be used in systematic planning, leaving member countries to interpret them according to their own individual needs and available information.

The Australian National Reserve System (NRS; Natural Resource Management Ministerial Council 2004) is Australia's interpretation of the CBD's strategic plan. The purpose of the Australian plan is to incentivize the systematic planning and design of a national reserve system, using bioregions as the basis for gap analysis in the current reserve system and future planning. These bioregions are an amalgam of geographic position, climate, land formation, vegetation and fauna, in a way that each is a separate eco-geographical region (Natural Resource Management Ministerial Council 2004). The stated aim of the National Reserve System is "...to contain samples of all regional ecosystems, their constituent biota and associated conservation values" (Natural Resource Management Ministerial Council 2004). As such, targets were set using IBRA – Interim Biogeographic Regionalisation for Australia – a classification of Australia's bioregions (Thackway and Cresswell 1995). The objective is to protect at least 10% of each IBRA bioregion in the National Reserve System, which should include examples of at least 80% of regional ecosystems. The habitats and core areas of threatened, migratory or endemic species should to be included when considering protected areas (Natural Resource Management Ministerial Council 2004, Commonwealth of Australia 2009). Lastly, while Australia has a defined 10% target for bioregions, their species targets are less defined and there is no mention of cost-effectiveness.

Currently, no other study has tested the cost-effectiveness of an ecosystem approach to implementation of Target 11" compared to using a species-based approach (Target 12). Thus, it is unknown whether the up-scaling of targets from species to ecosystems will be more cost-effective while still achieving both goals (protection of species and ecosystems). In **Chapter 4**, I used Australia as a case study to investigate (i) how well threatened species are likely to be captured in the resulting protected area network if Australia aims to meet its 10% targets for all ecosystems

most efficiently (as current policies suggest) by minimizing the area required; (ii) how well ecosystem-based targets are likely to be met if Australia's protected area network is designed to meet targets for threatened species only; and finally (iii) the efficiency and cost-effectiveness of planning for both sets of targets simultaneously versus sequentially (e.g. meeting ecosystem targets first and species targets later, or vice versa). In **Chapter 5**, I explored the trade-off between these two sets of targets, as it is quite probable that reaching full targets for all biodiversity features might be very expensive and/or require more resources than many countries can afford, meaning that countries might need to prioritise how they meet these targets. By trading off between targets' size for species versus ecosystems, I can provide countries with a way to prioritize between Targets 11 and 12 of the CBD while still remaining within the constraint of their pre-set budget.

Chapter 2: Optimal planning for mitigating the impacts of roads on wildlife

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2.1. Abstract

Roads have a significant impact on wildlife world-wide. Two of the ways to mitigate the impact of roads are to improve connectivity and reduce mortality through fences and wildlife crossings. However, these are expensive actions that will have different effects in different places. Thus, deciding where and how to act in order to achieve the greatest return on investment is crucial. Currently, there are no quantitative approaches to prioritize different road mitigation options. Here, we use a decision science framework to determine the most cost-effective combination of actions to mitigate the effects of roads on wildlife under budget constraints. We illustrate our approach using a case study of a threatened koala *Phascolarctos cinereus* population in south-east Queensland. We applied a spatially explicit population model to explore the benefits of three kinds of mitigation actions: no action at all and fences with or without crossings, on different road segments. We explored the trade-off between expected koala population size, relative to the best outcome, and budget. There is a strong demand for mitigation as the already declining population was reduced even further when no mitigation was employed, while applying the most cost-effective combination of mitigation actions minimized that decline. Additionally, uncertainty in species attributes (speed of crossing a road and population growth rate) affected population viability but not the decision about which suite of actions (mitigation measures) to take – so our advice on the best action is robust to uncertainty even if the outcome is not. Most importantly, the trade-off curves between investment and population size are almost linear in this case study. Hence, there is no cheap solution and any reduction in the budget will result in a substantial reduction in expected population size. Synthesis and applications: This is the first time that the problem of mitigating the effects of roads on wildlife was formulated mathematically and systematically using decision science. Our approach is adaptable to a diversity of species and systems affected by road mortality allowing flexibility for a range of mitigation actions and biological outcomes. Our method will allow managers and decision-makers to increase the efficiency of mitigation actions.

2.2. Introduction

Roads are a global threat to biodiversity (Laurance and Balmford 2013). In general, roads have negative effects on species abundance by increasing mortality, reducing connectivity, reducing habitat size and quality, and altering animal behaviour (Fahrig and Rytwinski 2009), all of which usually lower the viability of wildlife populations. Of these effects, direct mortality is the most significant and widespread effect of roads on wildlife (Bissonette 2002). Road mortality is relatively non-selective and can often affect healthy as well as sick or weak individuals (Bujoczek et al. 2011), which means it can affect population viability more than mortality sources that preferentially affect less-fit individuals, such as predation. Previous studies on the effects of roads on wildlife give us information on the impact of roads on populations of different species, or potential management actions that may reduce road related mortality, but none tell us how to choose between different actions. Moreover, none had considered the conservation return on investment from these mitigation actions. Even if we know where to locate mitigation efforts and which species are more vulnerable, there is rarely enough funding to undertake every possible mitigation action.

Road attributes such as traffic intensity negatively impact population densities in many species largely via mortality (Fahrig et al. 1995, Jones 2000, Gibbs and Shriver 2002, Gunson et al. 2003, Summers et al. 2011) but also by changes in behaviour (Jaeger and Fahrig 2004b, Parris and Schneider 2009, Berthinussen and Altringham 2012, Northrup et al. 2012). For example, traffic noise was found to affect the frequency of communication calls in both birds and frogs which can affect their breeding success (Parris and Schneider 2009, Parris et al. 2009). Roads can become dispersal barriers due to road avoidance (Shepard et al. 2008, Jackson and Fahrig 2011) or movement restriction (Pepino et al. 2012). Even minor roads can have significant impacts on mortality rates (van Langevelde et al. 2009) and/or animal behaviour (Moreau et al. 2012). Road-related mortality affects species differentially depending on their life-history traits. For example, mammals that are large, mobile and have a low reproductive rate, highly mobile birds, and amphibians with low reproductive rates and/or small body size will probably exhibit relatively high road-related mortality (Rytwinski and Fahrig 2012). Similarly, butterflies with shorter wingspan (Skórka et al. 2013) or swallows with longer wingspan (Brown and Bomberger Brown 2013) suffer from higher road mortality. For dragonflies, flight height and agility are significant determinants of road related mortality (Soluk et al. 2011).

In response to this threat, there is a growing body of literature on how to mitigate the negative impacts of roads. For example, fencing roads reduces mortality (Clevenger et al. 2001),

increases population persistence (Jaeger and Fahrig 2004b), and can facilitate movement and gene flow when combined with wildlife crossings (Gunson et al. 2003, Roger et al. 2011). Slowing traffic speed and warning signs can also mitigate the effect of roads, although the results of studies are varied, from little evidence of positive effect (Bruinderink and Hazebroek 1996, Dique et al. 2003b) to facilitation in population recovery (Jones 2000). Since road effects are a widespread ecological problem (Bissonette 2002), and the mitigation processes can often be expensive (Forman et al. 2010), there is a need to maximise the cost-effectiveness of road mitigation.

In many studies, researchers have used predictive modelling techniques to try and identify how to increase the efficiency of road mitigation. Most of these studies focused on environmental factors or road attributes to increase animal–vehicle collisions, in order to predict areas prone to high collision rates (Seiler 2004, Seiler 2005, Neumann et al. 2012) and select the best location for mitigation efforts (Malo et al. 2004). Other studies have focused on determining the species most vulnerable to road impacts. For example, Jaeger et al. (2005) compared population persistence depending on different road attributes and species behaviour towards roads. They found that species that avoided roads showed higher vulnerability to the negative effects of roads; further, high traffic volume has the strongest negative influence on population persistence of all road attributes examined. Langevelde and Jaarsma (2005) used traffic flow theory to calculate the probability of successfully crossing a road in a two-patch population model to estimate the impact of road mortality on population dynamics of mammals. This large volume of research on the effects of roads on wildlife has provided valuable ecological information, but in conservation, information needs to be translated into decisions and then actions.

Decision science is a rational and transparent way of determining the best action given multiple objectives. A variety of tools and approaches have been developed to allow managers and policy makers to arrive at ‘optimal’ decisions on how to apply conservation efforts within social and financial constraints (Possingham et al. 2001, Salafsky et al. 2002, Naidoo et al. 2006, McDonald-Madden et al. 2008, Wilson et al. 2009, Shwiff et al. 2012).

Here, we apply decision science to the problem of mitigating the impacts of roads with the aim of finding the best solutions to this problem for a range of possible costs. We mathematically formulate the problem of prioritizing different road mitigation actions to maximise expected population size at different mitigation costs. To illustrate the approach we solve this problem for a vulnerable koala *Phascolarctos cinereus* population living in habitat patches separated by roads on the Koala Coast, southeast Queensland, Australia. We delineate the trade-off between potential biodiversity benefits and economic cost by exhaustively exploring all possible combinations of three mitigation actions (fencing and no wildlife passage, wildlife passage with fencing, and no

action) over a system of patches divided by four road segments. The flexible nature of our method allows it to be adjusted to the needs of other species in different systems, as many of the components of the formulation and the biological model can be changed to fit a new system. As such, our systematic approach can assist decision makers worldwide to make informed decisions on where and how to invest their money, which is a crucial step in increasing the cost-effectiveness of conservation investment in mitigating the effects of roads on wildlife.

2.3. Materials and methods

2.3.1. Study area

The Koala Coast is a 375-km² area located 20 km southeast of Brisbane, Australia (Figure 2.1.). The area is a mosaic of urban, industrial, agricultural and natural habitats, fragmented by a complicated web of roads (Dique et al. 2003a). The Koala Coast contains the largest natural koala population living in an urbanized landscape adjacent to a capital city and is consequently of significant economic and cultural value (Dique et al. 2003b). The Department of Environment and Resource Management (Department of Environment and Resource Management 2012) estimated a decline in population size of 68% between the years 1996 and 2010 in the Koala Coast koala population. Additionally, they found little evidence that the population decline was due to habitat loss. Road mortality is recognized as one of the major causes of mortality in this koala population (Dique et al. 2003b, Rhodes et al. 2011) with an average of nearly 300 deaths a year (Dique et al. 2003b) in southeast Queensland. About half of the deaths of dispersing individuals are due to vehicle collisions (Dique et al. 2003a) with risk of collision increasing with both traffic volume and speed (Dique et al. 2003b). Additionally, roads were found to be a key barrier to genetic flow in the southeast Queensland koala population (Dudaniec et al. 2013). Over recent years, there has been a reduction in the number of koala–vehicle collisions, but this is probably because the population is in decline (Department of Environment and Resource Management 2012).

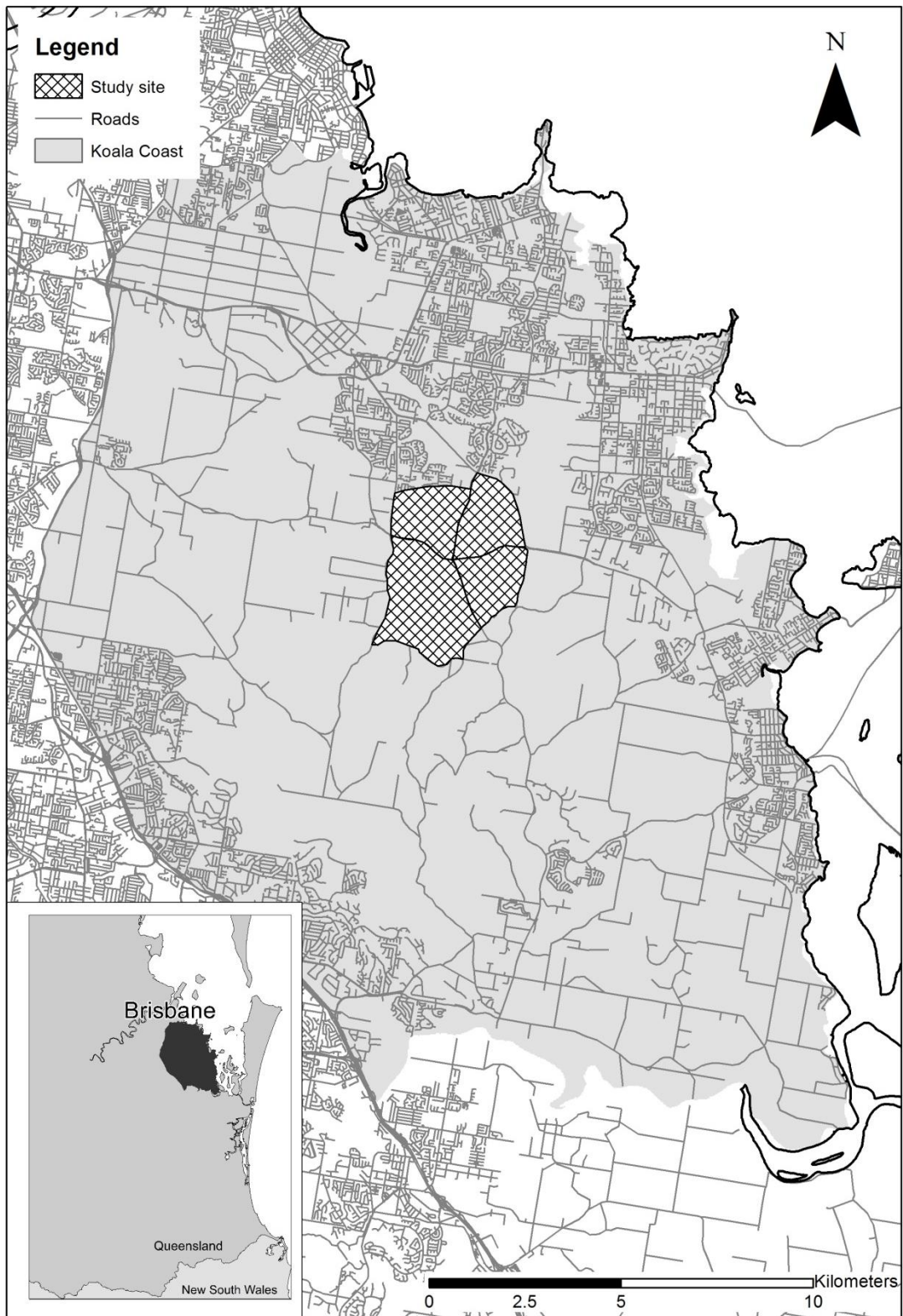


Figure 2.1: Study area – the Koala Coast in southeast Queensland, Australia. Hatched area represents the study site within the Koala Coast.

2.3.2. Road mitigation problem formulation

We created a female-only population model of four populations separated by roads (for details see Table 2.1., Figure 2.2.). For simplicity, we assumed that this is a closed system where movement can only occur among these four populations, and each year individuals have the opportunity to disperse. While decision theory can support more complex model formulations we chose to create a relatively simple population model to serve as a tractable example, as our intent in this study was to explore decision theory application to the problem of road mitigation. We identified three alternative actions for road mitigation: 1. ‘Do nothing’ – animals are free to cross the road and may be hit by a vehicle; 2. ‘Fence only’ – the entire length of the road is fenced so that there is no road mortality at all, but connectivity is eliminated, and 3. ‘Fence and Wildlife crossing’ – the entire length of the road is fenced with a wildlife crossing in the middle, allowing safe passage to the other side to animals that find the crossing. In order to find the optimal solution we explored the consequences of all mitigation combinations ($3^4=81$, each of the four road segments dividing the four populations can have one of three possible actions as mentioned above) on the mean population size with each combination run for 100 years (with 1000 simulation repeats).

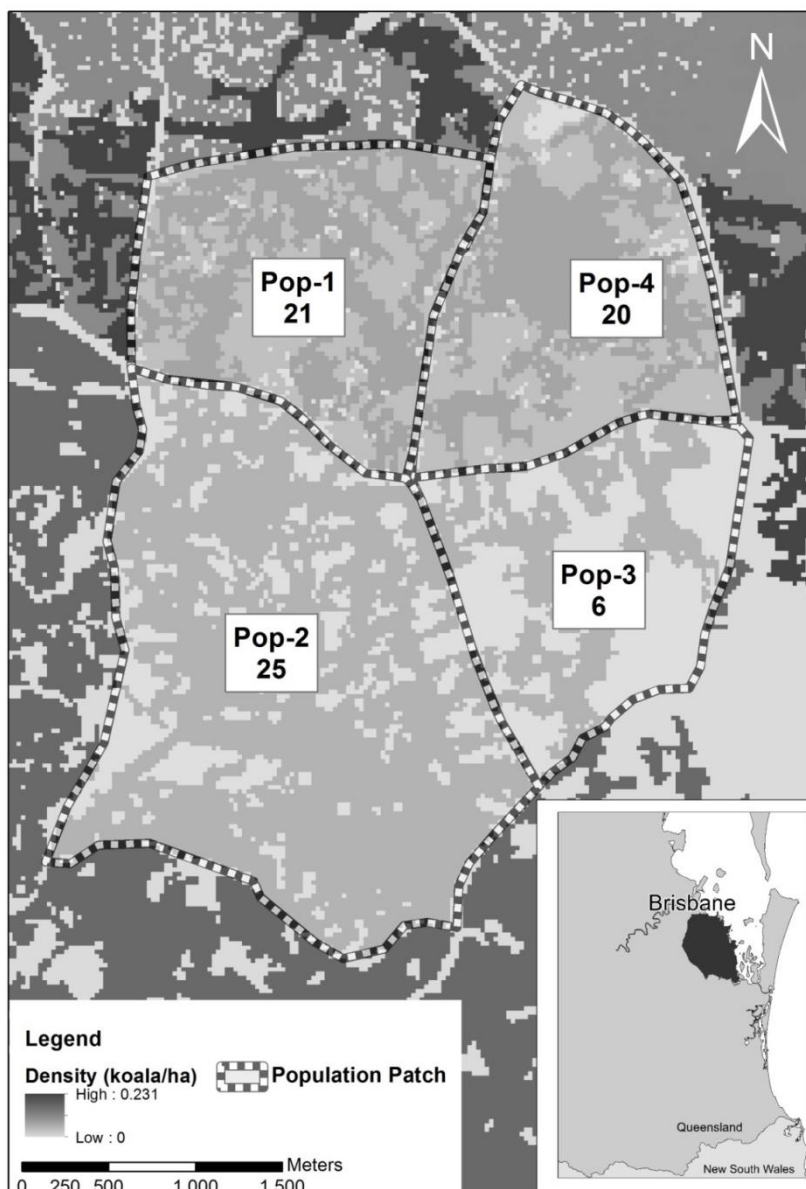


Figure 2.2: Study site within the Koala Coast. Checkered line is the population boundary for the four population incorporated into our analysis. The boundaries between the patches are the roads. The numbers represent the female koala population size.

Table 2.1: Models' input variables – Top half of the table contains attributes of the four Koala populations - patch size (ha), koala density (koala ha⁻¹) and initial population size (overall and females only). Bottom half describes road characteristics - length (m), traffic density (vehicle hr⁻¹) and the probability for a koala to safely transverse the road at three possible koala velocities (5000-15000 mhr⁻¹) for the four roads separating the four koala population.

	Patch Size (ha)	Koala density (koala ha ⁻¹)	Initial pop size			Initial Females
Pop 1	275.65	0.151	42			21
Pop 2	580.82	0.087	51			25
Pop 3	251.93	0.050	13			6
Pop 4	278.04	0.144	40			20
Over all	1386.45	0.1	145			72

	Road length (m)	Traffic density (vehicle hr ⁻¹)	Probability of safely traversing the road			Between
			5000 (mhr ⁻¹)	10000 (mhr ⁻¹)	15000 (mhr ⁻¹)	
Road 1	1940.9	144	0.874	0.935	0.956	Pop 1-3
Road 2	1833.0	311	0.748	0.865	0.908	Pop 1-2
Road 3	1953.2	225	0.811	0.900	0.969	Pop 3-4
Road 4	1924.5	100*	0.911	0.954	0.969	Pop 2-4

[^]The probability of safely traversing the road was calculated using equation 1 $P_s = e^{-\gamma \Delta T}$ (Langevelde and Jaarsma 2005) for each of the 3 koala velocities. All roads had 2 lanes.

* An estimate of traffic density

Our objective is to maximise the expected number of animals across all the patches of habitat separated by roads at the end of the management period which can be written as:

$$Max \sum_{i=1}^n \bar{N}_{i,T} \text{ subject to } \sum_{s \in \{s\}} x_s f_s + y_s d_s \leq B \quad (\text{eqn 1}),$$

where $\bar{N}_{i,T}$ is the average size of population i at the terminal time T , B is our budget, s is a set of all the road segments that separate the different patches, x_s is a control variable ($x_s=1$ if we have a fence at road segment s , 0 otherwise), and y_s is a second control variable ($y_s=1$ if we have a

wildlife crossing at road segment s , 0 otherwise), so $y_s, x_s \in \{0,1\}$. However, in our actions there cannot be a wildlife crossing without a fence and so $y_s \in \{0, x_s\}$, which means that (when $x_s=0$ then $y_s=0$). The parameter f_s is the cost of the fence along road segment s and d_s is the cost of the wildlife crossing on road segment s .

2.3.3. The population model

The population was simulated using a stochastic discrete-time metapopulation model where the numbers of individuals in patch i at time $t+1$, $N_{i,t+1}$, is a function of birth, death, immigration and emigration

$$N_{i,t+1} = R_{i,t} - E_{i,t} + I_{i,t} + G_{i,t} \text{ (eqn 2),}$$

where $R_{i,t} = (1 - \alpha_i)N_{i,t}\lambda_i$, represent both birth and death processes (λ_i is the growth rate of population i); α_i is the proportion of individuals that emigrate from population i , so the number of emigrants, $E_{i,t}$, leaving population i is $E_{i,t} = \alpha_i N_{i,t}$. The number of immigrants $I_{i,t}$, coming into population i from the neighbouring patches is $I_{i,t} = \sum_{j=1}^n p_s \frac{\alpha_j N_{j,t}}{m}$ where n is the number of populations which are adjacent to population i ($j=1 \dots n$), m is the number of populations that population j has a common road with and p_s is the probability of crossing the road between population i and population j and reaching the other side safely. The number of immigrants coming into the population i is divided by m because emigrants from each population were divided equally between the populations to which they could move. There are many different ways to model immigration and emigration, and we have used a fairly basic density-independent approach. When emigrants cannot cross to the other side of the road due to fencing, they will return to their population of origin. The return emigrants are given as $G_{i,t} = \sum_{j=1}^n x_s \frac{E}{n} (1 - p_s)$, were the number of emigrants leaving population (E) i was divided equally between the n neighbouring populations they can move and those that are blocked by fences ($x_s=1$) will return to their original population i depending on the probability p_s .

$p_s(x_s, y_s)$ is the probability of an individual crossing a road and reaching the other side safely, which depends on the action taken for the mitigation for segment s , where x_s and y_s are the control variables. If we ‘Do nothing’, $p_s(0,0) = e^{-\gamma \Delta T}$ (eqn 3) is the probability of successfully crossing the road segment (Langevelde & Jaarsma 2005), where γ is the hourly traffic volume and $\Delta T = \frac{W-l}{v}$ is the time that it takes to cross the road, W is the width of the road, l is the koala length from head to

tail, and v is the velocity of movement of koalas. We assumed that lane width is 2 m and the width of the road (W) is the number of lanes times the width of the lane. We estimated the length (l) of a female koala to be 0.66 m, and its velocity (v) is 5000–15000 m hr⁻¹ (Rhodes et al. 2014). Because of the uncertainty in the koalas' velocity, we performed a sensitivity analysis so that the probability of crossing the road depends on three different koala velocities: 5000, 10000 and 15000 m hr⁻¹ (low, medium, high). If we exclude access to the road with a fence 'Fence only', the probability of an individual reaching the other side is zero, $p_s(1,0)=0$ because we assumed a perfect fence. In this case, the dispersing individuals return to the original population. If we add a wildlife crossing to the fence - 'Fence and Wildlife crossing' then we assume that $p_s(1,1)=0.5$, we assuming that a koala reaching the fenced road will turn either left or right (50% chance for each direction), so it has a 50% chance of finding the crossing. If the koala turns in the direction of the wildlife crossing, we assume that it will find and cross to the other side safely; if it turns away from the wildlife crossing it will remain in the original population.

For simplicity, we allowed only one road crossing movement for dispersing individuals each year. Our decision to allow movement away from the population before letting the population grow is because we assume that only adult koalas move and reproduction occurs after dispersal.

2.3.4. Case study specifics

We used the female-only growth rate (λ) from the age-structured model in Rhodes et al. (2011), but removed the vehicle mortality rates from the analysis as vehicle mortality is explicitly incorporated in our model through failed dispersal. Using the model described by Rhodes et al. (2011) we had 9900 combinations of plausible values of λ , representing birth and death rates of the koala population residing in the Koala Coast area, with an average value of $\lambda = 0.977 \pm 0.014$ (mean \pm SD). At every run of the model, four values of λ were selected randomly from the pool of 9900 λ values and were assigned as that run's growth rates for each of the four populations. As the average growth rate extrapolated from Rhodes et al. (2011), was lower than 1.0, the populations declined in all model runs. Hence, we performed an additional set of runs where we added 0.05 to λ to achieve a positive population growth, our high growth rate scenario. This was done to test if our results will change should additional actions, to increase population growth rate, are employed. Using information on koala densities (Department of Environment and Resource Management 2009), we generated initial population sizes for the four patches for the study site (Figure 2.2., Table 2.1.). We assumed a dispersal probability of 14% for female koalas based on Preece (2007).

2.3.5. Applying cost

Each of the 81 mitigation combinations was given a cost depending on the actions in that combination. Actions were taken at the beginning of each run and were assumed to be constant throughout the runtime of 100 years, where improvements in technology are assumed to balance discount rates. A fence was costed at \$120 m⁻¹, and as fences need to be replaced on average every 20 years (Caneris and Jones 2009), the cost of the fence was multiplied by five to account for the 100 year model run. We assumed there is only one kind of wildlife crossing, and it costs \$200,000 (Veage and Jones 2007). We also added a maintenance cost of 2.5% yr⁻¹ for any infrastructure over the 100 years (Clapperton and Day 2001). If we do nothing along a road segment, it is assumed to cost nothing.

2.3.6. Sensitivity Analysis

We performed six runs of the model using three koala velocity values (low, medium, high) and two koala population growth rates (low and high). The outputs of each run were the average population size at the end of the 100 years (for 1000 repeats). In order to standardise our results, we divided the result of each of the 81 possibilities by the highest population average to achieve a conservation benefit between one and zero. We plotted the standardised results against the cost of the mitigation efforts for each one of the six runs. From these plots, we extracted an efficiency frontier (Polasky et al. 2005, Polasky et al. 2008) of the non-dominated solutions (Moffett et al. 2006). Non-dominated solutions are those that cannot be beaten on both cost and conservation benefit by another solution.

2.4. Results

In all of the model runs, the ‘Do Nothing’ approach of no mitigation on any road segment was the worst for population abundance. Surprisingly, full mitigation (Fence + Wildlife crossing) on all road segments did not maximise mean population abundance – in addition to it being the most costly solution (Table 2.2). When looking only at the non-dominated solutions along the efficiency frontier for each of the two growth rates separately, we found that there are common non-dominated solutions between the different velocities and the two growth rates (Table 2.2). For example, when the budget is large then the non-dominated solution is to fence all road segments and add a wildlife crossing to cross at least one of the road segments. However, when the budget dropped below \$4,000,000 the non-dominated solution becomes to fence road segments one and two (Table 2.2). Below that amount, we needed to spend over \$1,600,000 and employ only one mitigation action – fence road number two. At this point conservation benefit has dropped (7% and 48% for low and high growth rates, respectively) from the outcome with a budget of ~\$4,000,000. A budget of less than \$1.6 million was not sufficient to achieve a significant conservation benefit given the scenarios considered (Table 2.2). Furthermore, the common non-dominated solutions (for costs of between \$0 and ~\$5,100,00) between the two growth rates (Table 2.2), indicating that the efficiency frontier is relatively independent of demographic uncertainty. This means that the actions are less sensitive to parameter uncertainty than the outcome (McCarthy et al. 2003).

Using the non-dominated solutions that were shared between scenarios, we created trade-off curves containing these solutions only (Figure 2.3, A-B). The shape of the plots was barely affected by changes in population growth rate or koala crossing speeds. On the other hand, the koala’s crossing speed was positively correlated with mean population size.

Table 2.2: Efficiency frontier solutions common between the three koala velocities (5000-15000 mhr⁻¹) - The right side of the table presents the non-dominated solutions for the low population growth rate and the left side presents the solutions for the high growth rate. Each solution provides female population size, the cost of the solution (that specific combination of mitigation actions) and the specific action taken at each road (NM- No Mitigation; F- Fence only; F+P- Fence + Passage). Shaded areas are solutions common between both growth rates. All solutions were non-dominated for all of koala road crossing velocities.

Average Growth rate: R=0.977						Average Growth rate: R= 0.977+0.05					
Population size*	Cost (\$)	Road 1	Road 2	Road 3	Road 4	Population size*	Cost (\$)	Road 1	Road 2	Road 3	Road 4
41.83	7,086,386	F	F	F+P	F	690.78	7,286,386	F	F+P	F+P	F
36.61	5,128,524	F	F	NM	F	687.15	7,086,386	F	F+P	F	F
29.51	3,396,483	F	F	NM	NM	564.97	5,128,524	F	F	NM	F
27.38	1,649,709	NM	F	NM	NM	472.9	3,396,483	F	F	NM	NM
15.86	0	NM	NM	NM	NM	245.9	1,649,709	NM	F	NM	NM
						194.51	0	NM	NM	NM	NM

*Population size – is the average female population size between the three velocities for each growth rate

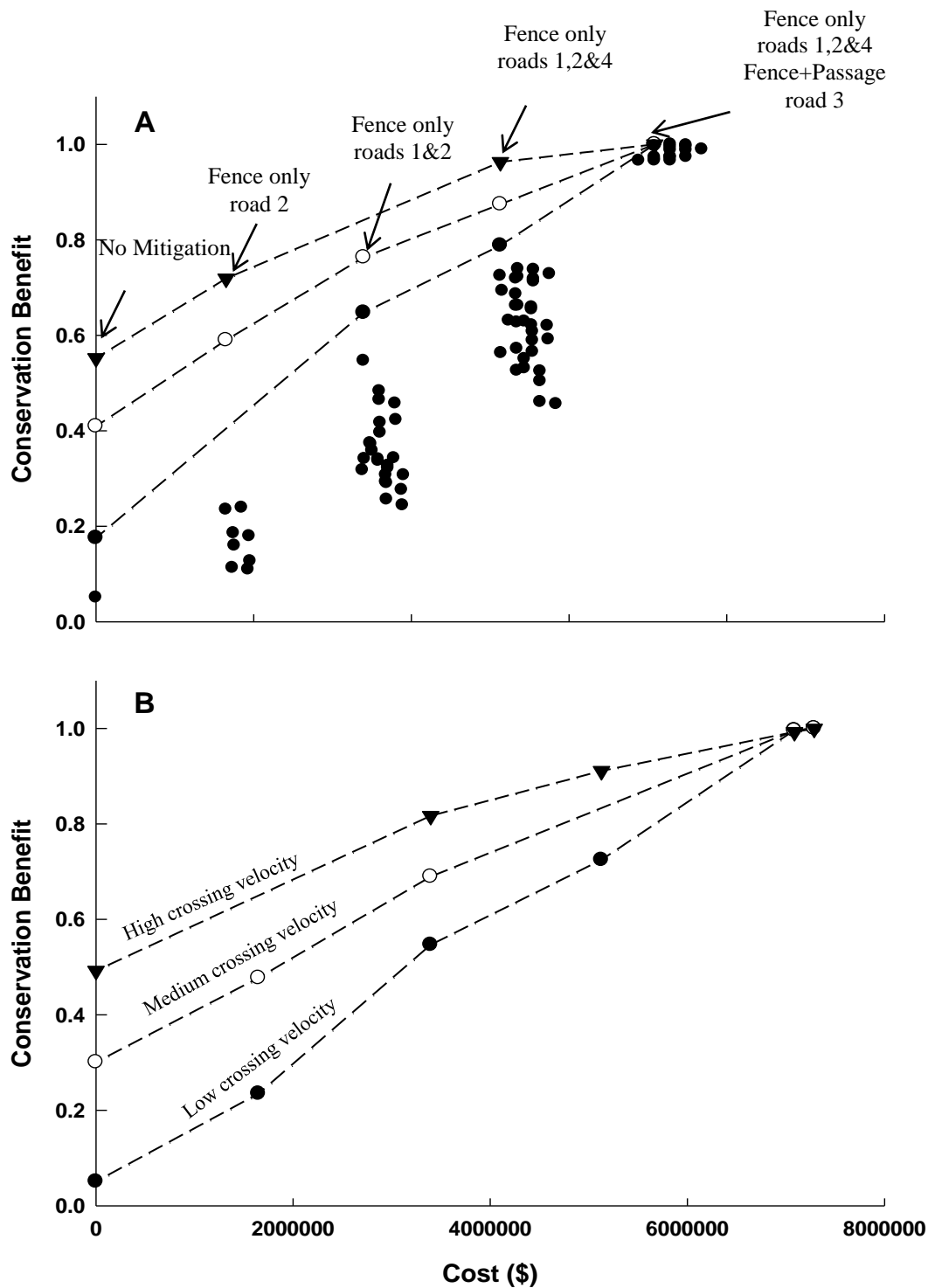


Figure 2.3: Trade-off curves of non-dominated solutions. X-axis is the cost of the mitigation possibilities and Y-axis is the conservation benefit represented as the proximity to the maximum population size (1 is the highest proximity) the population achieved under a given scenario. A and B are the different growth rates ($r=0.977$ and $r=0.977+0.05$, respectively). Curves (dashed lines) represent the three koala' velocities tested, and symbols represent the solutions along the curves, Low (filled circles), Medium (blank circles) and High (filled triangles). The mitigation actions that are needed to be taken at each solution brake are stated on the figure. Scattered dots (filled circle) in graph A is an example of all the different mitigation variations tested in the low velocity at that growth rate.

2.5. Discussion

The impact of roads on wildlife is a worldwide problem which will increase with human population growth and increasing vehicles per capita (Laurance and Balmford 2013), therefore, requiring mitigation to reduce its effects (Forman et al. 2010). These mitigation efforts are costly, but up until now this problem has not been tackled using decision science. In this paper, we formulated and solved a road mitigation problem and tested it using a decision science approach. We illustrated our approach using information about a koala population in southeast Queensland and found the non-dominated solutions for that system over a range of costs.

For the koala population mitigation problem, we discovered that there is no “win-win” solution. In all the model runs the curves (Figure 2.3) are close to linear, lacking the L or J shape that would have indicated good conservation benefits for low economic cost (Halpern et al. 2013). Our analysis shows that achieving very good outcomes for koalas will be expensive and reducing investment will result in a much smaller population. This kind of decrease in population size can be quite significant especially in small populations. Moreover, the population in the Koala Coast is declining, not just because of road mortality but also because of disease and dog predation (Rhodes et al. 2011). Recent work (C. Ng unpublished data) suggests that all these issues must be tackled with cost-effective investments. That said the benefits of koalas to tourism makes koala conservation a profitable investment (Hamilton et al. 2000).

It is important to note that solutions along the efficiency frontier (Table 2.2, Figure 2.3) were not affected by uncertainty in the koala’s biological attributes (speed and population growth rate). This suggests that the solutions presented here are relatively insensitive to these biological uncertainties and given a fixed budget one can identify a robust optimal solution. In our case study, the trade-off curve between cost and conservation benefit was fairly linear suggesting no cheap gains. Other systems, which exhibit more variability, in either population dynamics or road attributes, such as traffic intensity and the cost of mitigation actions, may generate trade-off curves where a relatively large conservation benefit could be generated at low cost.

We recognise that our population model is relatively simple. It does not incorporate age structure, density dependence or daily movements across roads. We also did not account for the effects roads have on inhibiting gene flow (Holderegger and Di Giulio 2010, Dudaniec et al. 2013) which would require a more complex genetic model. That said the main purpose of our analysis was to show how decision science can be applied to the question of road mitigation, using the koala as a case study to demonstrate our method. For this purpose, using a relatively simple model was

necessary in order to focus on the problem formulation and approach. Another caveat in our analysis is that we only considered three mitigation options for each road segment, fences and only one type of wildlife crossing. However, the problem can be adjusted to explore a diversity of crossings structures (i.e. clovers, overpass, bridges; Forman et al. 2010) accounting for their different costs and mitigation successes. Further, we assumed there can be only one crossing per road segment per year, and we did not consider different options for where that crossing is placed. We also assumed that our fences were impermeable to animal crossing, which may not be true in many cases (Ascensão et al. 2013).

There are many possible extensions of the basic problem presented here. Our approach can be expanded to accommodate a much wider variety of mitigation options for each road segment including more populations, additional road segments and multiple possible crossing points. In addition, crossing for one species often assist the viability of others species, so we are formulating a multispecies road mitigation problem. However, because the number of mitigation options grows geometrically with the number of road segments, the exhaustive examination of a large system will be computationally intensive.

The greatest asset of our problem formulation is that it can be easily adjusted to the needs of other species. The literature is replete with recent studies of the effects of roads on wildlife that have the necessary information needed to implement this decision making tool (Dekker and Bekker 2010, Beebee 2013, Nafus et al. 2013, Soanes et al. 2013). Parameters in the problem formulation can change according to the specific mitigation actions needed in that system; the population model can be adjusted or even replaced altogether, as long as the link to the problem formulation, via the probability of crossing the road safely (p_s), is maintained. In particular, the information gathered by Beebee (2013), in a thorough review of the effects of road mortality and mitigation on amphibians can be incorporated along with mitigation costs into our formulation. Furthermore, where a species has a monetary value to a region, our approach could be used to choose mitigation options in a classical cost–benefit analysis approach. While other mitigation prioritization work is becoming available (Ascensão et al. 2013), our work is the first that includes a well-defined mathematical problem that incorporates financial costs, which is essential for application in the real world.

Chapter 3: Optimal planning for mitigating the impacts of roads on wildlife: a multiple species approach

3.1. Abstract

Roads have a major effect on wildlife worldwide through habitat loss, habitat fragmentation and direct road-kill mortality. Two ways to mitigate impacts are to erect wildlife crossings and/or build fences. Both are expensive and have varying levels of success, so deciding where and how to act for the greatest return on investment is crucial. Here, we combined decision theory with a metapopulation model to determine the most cost-effective actions to mitigate the effects of roads on multiple species, illustrated with two sets of species (from Australia and Europe) with a range of life history traits and from a diversity of taxonomic groups. We tested the cost-effectiveness of spatially explicit combinations of three management options for each road section: 1) no mitigation, 2) erect fences without wildlife crossings, and 3) erect fences combined with wildlife crossings. We explored the trade-off between each population's probability of persistence and total mitigation cost, first on a per-species basis and then considering all species. We then tested the cost-effectiveness of different planning strategies: 1) single species, 2) two types of focal species based on different life histories traits, and 3) comprehensive multispecies planning. We found that planning for the needs of all species at the same time (multispecies strategy) will maximize the number of persisting species provided the most robust and cost-effective planning strategy, while single-species strategies were found to be very inefficient. Finally, basing decisions on the focal species with the largest home range can provide reasonably cost-effective results, but should be considered only when there is not enough time or money to collect the necessary information to perform a multispecies analysis. Our method of combining metapopulation models of multiple species with decision theory can be adapted to most road mitigation problems and illustrates the need to consider the entire system when planning cost-effective road mitigation.

3.2. Introduction

Roads are a global threat to biodiversity, causing habitat loss, fragmentation, and degradation as well as direct animal mortality, even in some of the most remote places on Earth (Laurance and Balmford 2013). For many species, roads may reduce abundance and promote population isolation, limiting reproduction or colonization movements and jeopardizing long-term population viability (Epps et al. 2005, McGregor et al. 2008). The widespread effect of roads on biodiversity necessitates mitigation measures to reduce their impact (e.g. Aresco and Russell 2005, Jacobson 2005, Beebee 2013). Since the main impacts of roads are wildlife-vehicle collisions and habitat fragmentation (Bissonette 2002), the most common mitigation measures are fences to reduce mortality and crossing structures to increase connectivity (Clevenger et al. 2001, Taylor and Goldingay 2009). However, such mitigation measures are expensive and the majority are focused on single species mitigation (e.g. Woltz et al. 2008, Klar et al. 2009). There is an emerging need for research on higher order mitigation measures, at the community, ecosystem and landscape level (van der Ree et al. 2011).

Despite the potentially high cost of mitigation measures, relatively few studies have reported on the cost-effectiveness of road mitigation measures (Huijser et al. 2009), and in most cases these studies have focused on a single species (e.g. Putman et al. 2004, Ascensão et al. 2013, Polak et al. 2014). For example, Ascensão et al. (2013) developed a model that tested how different intensities of road mortality and mitigation measures affected the population abundance and genetic differentiation of stone marten (*Martes foina*). Polak et al. (2014) optimized the allocation of conservation funds between different mitigation actions for a koala (*Phascolarctos cinereus*) population in Australia. While these examples are useful for decision makers, there is still an urgent need for tools to assist in making cost-effective decisions on how best to mitigate the effect of roads for many species in the same landscape. Cumulative mitigations of road impacts on multiple species are likely to be cheaper than a measure applied to a single species because it is likely that optimising for single objectives separately and then combining the results will always be suboptimal for multiple-species objectives.

The effect of roads on wildlife are not universal: species' life history traits influence their vulnerability to roads (Kerth and Melber 2009, Rytwinski and Fahrig 2012), making it difficult to find a "one size fits all" solution. For example, large and mobile mammals, highly mobile birds, and amphibians with low reproductive rates and/or small body size, are all particularly associated with vulnerability to traffic volume (Rytwinski and Fahrig 2012). Likewise, the behaviour of each

species on encountering a road affects mortality risk. For example, Soluk et al. (2011) and Grilo et al. (2014) found that the flight height of dragonflies and barn owls (*Tyto alba*), respectively, is a key determinant of the mortality risk when crossing a road.

Effective road mitigation that benefits a greater range of species in the long term requires the inclusion of a wider range of target species' needs, and an understanding of the effectiveness of mitigation measures on population persistence (van der Grift et al. 2003, Jaeger and Fahrig 2004b, Ascensão et al. 2013). One way to analyse the effectiveness of mitigation on the persistence of multiple species is to use a spatially explicit metapopulation model, similar to the approach used by Nicholson et al. (2006) to plan a set of protected sites to maximize the persistence of multiple species. They applied an approximation formula developed by Frank and Wissel (2002) that uses local patch extinction and colonisation rates to estimate the probability of metapopulation persistence.

The aim of this study is to evaluate how road mitigation affects the extinction and connectivity rates and thus the probability of persistence for metapopulations of multiple species. For that we combined the problem formulation presented in Polak et al. (2014) with the Frank and Wissel (2002) formula for metapopulation persistence. Our goal was to find the optimal configuration of road mitigation actions in two model systems (one species set from Australia and one from Europe) that maximises persistence for a group of species with different biological and ecological features. In addition, we aimed to compare the cost-effectiveness of the following planning scenarios at mitigating the entire suite of species: 1) mitigating each species individually; 2) finding a single potential focal species that can be used to plan mitigation for the entire system; and 3) multispecies planning to find a cost-effective mitigation configuration for all species combined.

3.3. Methods

3.3.1. Study area and species

Consider a stylised landscape divided into eight patches separated by ten roads. We assume each patch is rectangular shaped, with its size determined by the length of the roads surrounding it. The length of the roads increases as a geometric progression ($scale\ factor=1$ and $common\ ratio=2$) from the north-west corner, two units to the south and four units east (Figure 3.1). This design was chosen to represent an urban-rural gradient from smaller patches and shorter roads that increase in size as the distance from the city increases. Similarly, the road traffic volume and number of lanes increases to reflect a transition from urban roads to highways and country roads (Figure 3.1, Table S3.1). We chose to use a stylised landscape because we wanted to be able to control the landscape variables in the model and remove unnecessary noise from the analysis. Also, a stylised landscaped allowed us to test roads with different traffic volumes and to have the same landscape for both species sets, which occur on different continents.

We tested for optimal mitigation options using this road configuration and two sets of species from Australia and Europe (Table S3.2). The Australian species were taken from Nicholson et al. (2013): greater glider (*Petaurus Volans*), mountain brushtail possum (*Trichosurus cunninghami*), common ringtail possum (*Pseudocheirus peregrinus*), common brushtail possum (*Trichosurus vulpecula*), red-browed treecreeper (*Climacteris erythrops*), white throated treecreeper (*Cormobates leucophaea*), laughing kookaburra (*Dacelo novaeguineae*), sacred kingfisher (*Todiramphus sanctus*), bush rat (*Rattus fuscipes*), and agile antechinus (*Antechinus agilis*). The European species were compiled from the peer-reviewed literature (Table S3.2): European rabbit (*Oryctolagus cuniculus*), European hedgehog (*Erinaceus europaeus*), red squirrel (*Sciurus vulgaris*), European pond turtle (*Emys orbicularis*), and Lataste's viper (*Vipera latastei*). We chose to use the Australian species used by Nicholson et al. (2013). The European species set was constrained by species that had a home range within the scale of the smallest patch in the system (see detailed explanation in the Discussion of this chapter) and to species for which we were able to find species specific model parameters. We tried to find the most diverse and road sensitive species set within these constraints.

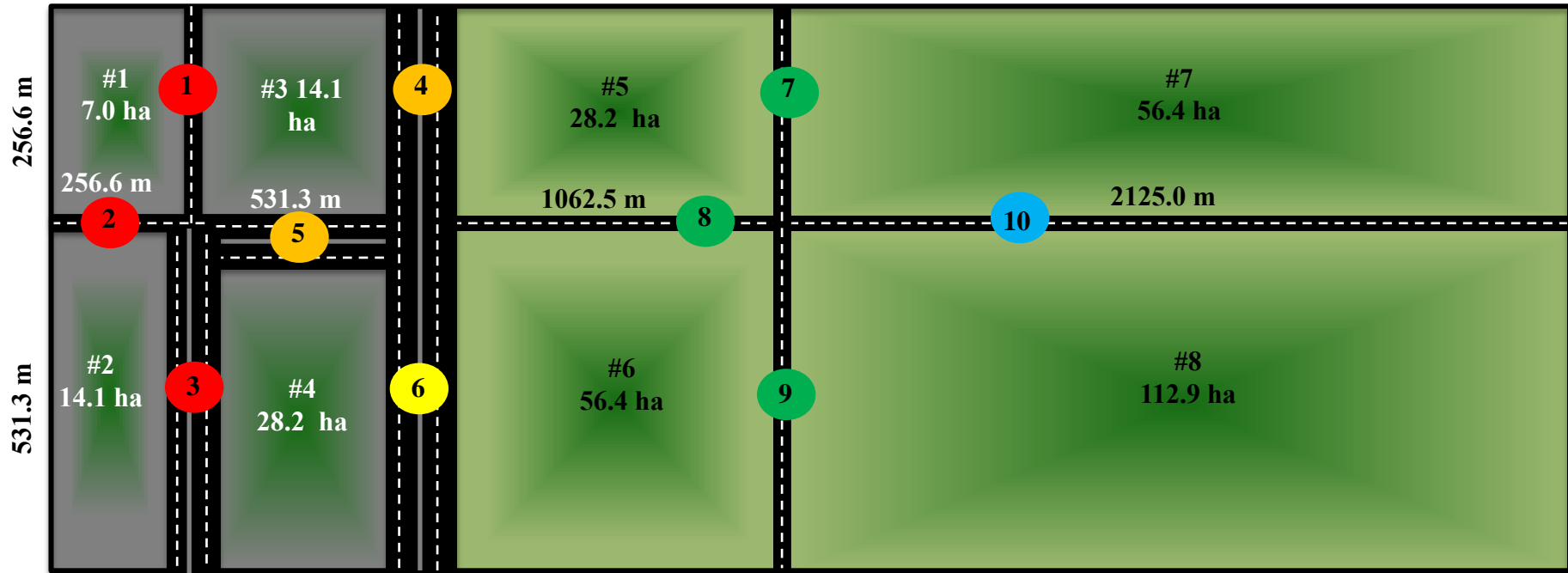


Figure 3.1: Abstracted landscape used for the metapopulation model. The size of the patches increases from the north-west to the south-east (grey to green gradient), separated by roads (black lines dashed with white). Patch size is marked within the patch in ha with patch identity number. Road length (in m) for the west-east roads are marked above the roads and on the left of the diagram for the north-south roads. Circles on top of the roads represent each road number (marked within) and traffic density in cars per hour: red – 2000; orange – 1500; yellow – 1000; green – 500; and blue – 200 cars/hr. We considered roads one and two as city roads; roads three to six as highways; roads seven and eight as suburban roads; and roads nine and ten as country roads.

3.3.2. Problem formulation

Our objective is to maximize the number of species persisting in the landscape with habitat patches separated by roads subject to wildlife mitigation measures, which can be written as:

$$\text{Maximize } \sum_{k=1}^n q_k(\mathbf{S}, t, \mathbf{r}) \text{ subject to } \sum_{s \in \{S\}} x_s f_s + y_s d_s \leq B \quad , \quad \text{eqn 3.1}$$

where $q_k(\mathbf{S}, T, \mathbf{r})$ is the probability of persistence of species k for a given management combination of road mitigation options \mathbf{r} , at a terminal time t [$T = 100$ years], subject to the mitigation actions on the roads for a given budget B for the set S of all the road segments that separate the different patches. There are two mitigation control variables: 1) x_s determines the location of fences ($x_s=1$ if we have a fence at road segment s , 0 otherwise); and 2) y_s represents wildlife passages ($y_s=1$ if we have a wildlife crossing at road segment s , 0 otherwise), so $y_s, x_s \in \{0,1\}$. However, in our actions there cannot be a wildlife crossing without a fence and so $y_s \in \{0, x_s\}$, which means that (when $x_s=0$ then $y_s=0$). Thus, there are three possible mitigation actions represented by (x_s, y_s) : 1) Do nothing (0,0) – placing no mitigation measures along the road; 2) Fence only (1,0) – erecting a fence along the road; and 3) Fence and Passage (1,1) – erecting a fence but connecting the patches with a wildlife passage. The parameter f_s is the cost of the fence along road segment s and d_s is the cost of the wildlife crossing on road segment s , as described in Polak et al. (2014).

3.3.3. Calculating the probability of persistence

The probability of persistence of a species in the landscape is:

$$q_k(\mathbf{S}, t, \mathbf{r}) = e^{\frac{-t}{T_k(\mathbf{r})}} \quad , \quad \text{eqn 3.2}$$

where, $T_k(\mathbf{r})$ is the mean time to extinction of the metapopulation for species k under mitigation configuration \mathbf{r} (McCarthy et al. 2005) and T_k was approximated with the formula developed by Frank and Wissel (2002):

$$T_k(\mathbf{r}) \approx T_k^a = \frac{1}{v_{agg}} \frac{(M-1)!}{M(M-1)^{M-1}} e^{\frac{M}{z}} z^{M-1} \quad , \quad \text{eqn 3.3}$$

where z is an aggregation of the effective colonization abilities of the subpopulations

$$Z = \prod_{i=1}^M \max \left(\sqrt{2}, \sqrt{\left\{ \frac{1}{2} \left[\left(\frac{\sum_{j(\neq i)} c_{ij}}{v_i} \right)^{-2} + \left(\frac{\sum_{j(\neq i)} c_{ji}}{v_i} \right)^{-2} \right] \right\}^{-1}} \right)^{1/M} \quad \text{eqn 3.4}$$

which is the geometric mean of the In and Out colonization rate (sum for each of the patches) for all patches (M). The parameter v_{agg} is the effective local extinction rate, which is the geometric mean calculation of the system's local patches' extinction rate:

$$v_{agg} = \left(\prod_{i=1}^M v_i \right)^{1/M} \quad , \quad \text{eqn 3.5}$$

3.3.4. Modelling the metapopulation

Local extinction rate v_i was modelled by:

$$v_i = \left(\frac{A_i - h_{ik}}{H_k} \right)^{-\varepsilon_k} \quad , \quad \text{eqn 3.6}$$

where A_i is the area of patch i (in ha), H_k is the home range size of a breeding female of species k in an optimal habitat; ε_k is the extinction-area exponent, a species-specific parameter representing the effects of environmental stochasticity on species k (Hanski 1994, Moilanen and Hanski 1998, Frank 2005); h_{ik} is the species-specific area (in ha) along the edges of patch i which is affected by the proximity to roads, specifically by their effects on daily mortality events (not included in the Frank and Wissel (2002) metapopulation model), a function of the diameter of the home ranges size H_k of species k ($2\sqrt{\frac{H_k}{\pi}}$) and the mitigation impacts:

$$h_{ik} = \sum_{s \in \{s\}} 2\sqrt{\frac{H_k}{\pi}} \beta_s(x_s, y_s) l_s \quad , \quad \text{eqn 3.7}$$

where $\beta_s(x_s, y_s)$ is the magnitude of the effect in relation to the mitigation actions implemented (x_s, y_s) along the specific road segments s around patch i with l_s as the length of each specific road. When mitigation measures are in place (i.e. fence only – $\beta_s(1,0)$, or a fence and a wildlife passage – $\beta_s(1,1)$), $\beta_s(x_s, y_s) = 0.01$ since we consider the risk of accidental daily mortality only, and we assume that mitigation measures will almost completely eliminate this risk. When there is no mitigation (i.e. do nothing – $\beta_s(0,0)$), $\beta_s(x_s, y_s) = 1$. We tested the sensitivity of the outcomes to the assumed impacts of unmitigated roads on daily survival of the species, reducing $\beta_s(0,0)$ by 0.25 intervals (0.75, 0.5 and 0.25).

Local colonization rate between patches i and j (c_{ij}) was modelled as follows:

$$c_{ij} = p_{ij} \left(\gamma_k \frac{A_i - h_{ik}}{H_k} e^{-\frac{d_{ij}}{d_k}} \right) \quad \text{eqn 3.8}$$

where d_{ij} is the distance between the centres of patches i and j , d_k is the dispersal distance of species k , and γ_k is the fecundity, defined as the species-specific (k) output of female dispersers per home range. The parameter p_{ij} is the probability of crossing successfully all the roads between patches i and j :

$$p_{ij} = \prod_{s \in \{s_{ij}\}}^{s_{ij}} p_s(x_s, y_s) \quad \text{eqn 3.9}$$

$p_s(x_s, y_s)$ is the probability of an individual crossing a road and reaching the other side safely, which depends on the action taken for the mitigation of segment s , where x_s and y_s are the control variables.

If we ‘Do nothing’:
$$p_s(0,0) = e^{-\mu \frac{W - l_k}{\delta_k}} \quad , \quad \text{eqn 3.10}$$

which is the probability of successfully crossing the road segment (Langevelde and Jaarsma 2005), where μ is the hourly traffic volume, which is multiplied by the time that it takes to cross the road. The time that it takes to cross the road is the ratio of the difference between W (the width of the road; assuming 3.75 m width per lane) and l_k (the length of species k), and δ_k (the velocity of species k). Species velocity is defined as 25% of the species’ maximum velocity (Langevelde and Jaarsma 2005).

If a fence is built: $p_s(1,0) = 0.1 * p_s(0,0)$, because, in this model, we assumed an imperfect fence, with a 10% probability of finding a hole in the fence (Frank and Wissel 2002). Therefore, we assume that animals that find the holes in the fence will have the same probability of successfully crossing the road as with no mitigation.

If a fence and a wildlife passage are built: $p_s(1,1) = 0.5 + 0.1 * p_s(0,0)$. Here, we assumed a 50% chance of finding and using the wildlife passage and crossing safely (Polak et al. 2014), which is added to the probability of finding a hole in the fence as in $p_s(1,0)$. For a full list of all parameters, see Table S3.

3.3.5. Cost-effectiveness analysis

To perform the cost-effectiveness analysis we calculated all the unique combinations of the spatial configuration of the three measures along the ten roads of the system – do nothing, fence,

and fence with crossing – raised to the power of the number for roads in the system; for our system, this was $3^{10} = 59,049$ combinations. The cost for each combination was calculated following Polak et al. (2014): a fence was $\$120 \text{ m}^{-1}$, and as fences need to be replaced on average every 20 years (Caneris and Jones 2009), the cost was multiplied by $\frac{t}{20}$. We also added a maintenance cost of $2.5\% \text{ yr}^{-1}$ multiplied by t (Clapperton and Day 2001). We assumed there is only one kind of wildlife crossing, costing $\$200,000$ (Veage and Jones 2007). We assumed no cost for doing nothing along a road segment. Actions were taken at the beginning of each assessment and were assumed to be constant throughout the runtime- t , where improvements in technology are assumed to balance discount rates.

We determined the extinction probability for each species and unique mitigation combination, and for each of our sensitivity analyses increments. For each assessment, the probability of persistence for all combinations was plotted against the cost of those mitigation combinations. From these plots, we determined the efficiency frontier (Polasky et al. 2005) of the non-dominated solutions, which are the solutions that are the best in both cost and conservation benefit compared to the other solutions (Moffett et al. 2006). The efficiency frontiers can assist decision makers to make informed decisions on which actions should be taken at any given budget.

3.3.6. Multispecies analysis

For each species set, we calculated the expected number of persisting species (Nicholson and Possingham 2006) as $\sum_{k=1}^n q_k(\mathbf{S}, t, \mathbf{r})$ (see problem formulation above – eqn. 3.1), which is the sum of the probability of persistence over all species. For each species set we determined the non-dominated solutions based on the expected number of persisting species to create multispecies efficiency frontiers for each of our two-species sets. From these efficiency frontiers we calculated the frequency of fences and of wildlife passages for each road, per species set. We documented how many times a fence or a passage appeared in the solutions along the efficiency frontier per road divided by the number of solutions along the frontier.

3.3.7. Single species, stepwise and focal species cost-effectiveness analyses

For each species we used their efficiency frontier to locate which of the solutions provides a probability of persistence of at least 0.9 at the lowest cost. We chose this probability of persistence because it indicates a high likelihood that the species will survive. If a probability 0.9 could not be achieved the highest probability was selected. We use these 0.9 probability points to perform several cost-effectiveness analyses – 1) expected number of persisting species (on the y-axis) and mitigation cost (on the x-axis), and 2) benefit/cost analyses (best value for money) – where the benefit (the expected number of persisting species) is divided by the cost of its mitigation configuration (in millions of dollars); the larger this value the better value for money the scenario provide. In addition, we also compared the cost of the solution along the multispecies efficiency frontier, which has a similar benefit to that of each of the scenarios below.

We compared the multispecies analysis (above) to the following scenarios:

1) Single species – each species is treated independently and the cost of each 0.9 probability scenario is added to the others, assuming the mitigation structures provide benefits to only a single species. The probabilities of persistence for all species are added to receive a single value of the expected number of persisting species. This represents the worst-case scenario where none of the mitigation measures for a species assist any of the other species and the mitigation cost for each species is added up for a final sum.

2) Single species accumulative – each species is considered individually but the existing mitigation infrastructure is assumed to work for all species and only the cost of the additional mitigation infrastructure is added. In this scenario the expected number of persisting species is the same as scenario 1.

3) Home range focal species – for each species set we selected the species with the largest home range ($\max H_k$) as the focal species (Lambeck 1997, Rytwinski and Fahrig 2012, Nicholson et al. 2013), using its selected scenario with its single cost. We added each species' probabilities of persistence at this scenario to calculate the value of the expected number of persisting species.

4) Fecundity focal species – for each species set we selected the species with the lowest fecundity ($\min \gamma_k$) as the focal species, using its selected scenario with its single cost. The expected number of persisting species was calculated the same as scenario 3.

Lastly, we performed two additional analyses to test the effectiveness of the ad-hoc selected focal species: 1) Cluster analysis – we calculated the frequencies of fences and wildlife passages (as

in the multispecies analysis) and produced a similarity matrix among the mitigation frequencies for each species compared to all other species and those of the multispecies analysis. Then we used the function `hclust()` using the average and the single-linkage clustering methods (as both presented similar results, we only present the ones from the average method) from the `fastcluster` package in R (Müllner 2013) to create a similarity dendrogram between all the different species and the multispecies analysis, to determine which species provided the most similar solutions to the multispecies analysis for either fences or passages. 2) Cost-effectiveness and benefit/cost analyses – comparing the multispecies analysis to both single species scenarios (scenarios 1 and 2) and all individual species (not just the two focal species), to determine if there are other species with common traits, which can be used as the focal species.

3.4. Results

3.4.1. Individual species analyses

The change in probability of persistence for species in the Australian dataset in response to roads and mitigation measures varied among species (Figure 3.2). Some species exhibited little response to the different mitigation combinations (i.e. white throated treecreeper, laughing kookaburra, bush rat and agile antechinus; Figure 3.2). These species will likely fare reasonably well with little or no mitigation. One species (the common brushtail possum; Figure 3.2) exhibited very low persistence with a positive but slight response to the increase in mitigation measures, implicating a biological response to the landscape, which is only weakly related to the roads. Species with intermediate sensitivity presented a more classical L- or J-shaped efficiency frontier curve, which can indicate a “win-win” solution between maximizing the ratio between probability of persistence and the cost of mitigation (i.e. mountain brushtail possum, common ringtail possum, red-browed treecreeper, sacred kingfisher and greater glider; Figure 3.2). The intermediate sensitivity to mitigation of the two bird species here (red-browed treecreeper, sacred kingfisher) might come as a surprise. However, Kociolek et al. (2015) noted that many bird species are positively affected by mitigation measures (fences and wildlife passages) that were designed for mammals.

The species from the European database presented a similar pattern of responses, including species with little response to mitigation efforts (i.e. the European pond turtle and hedgehog; Figure 3.2) and species with an intermediate response (i.e. the European rabbit, red squirrel and the Lataste’s viper; Figure 3.2). The hedgehog is known to be found killed on many European roads which makes its’ minimal response to mitigation surprising. This result might be related to the fact the hedgehogs are found to avoid large roads almost completely and cross small roads only (Rondinini and Doncaster 2002), making mitigation on only the few small roads sufficient to reduce mortality.

The magnitude of the effect of the road, $\beta_s(x_s, y_s)$, was also a factor that affected the shape of the curve and thus the optimal mitigation combination for each species (Figure 3.2). The lower the assumed road effect (the magnitude of $\beta(x_s, y_s)$; lighter grey, Figure 3.2), the less effect mitigation had on the persistence of the species.

The cost of the mitigation that achieved probability of persistence of 0.9 (or the maximum probability of persistence if 0.9 could not be reached), ranged between \$0 to \$13,387,819 and \$757,825 to \$10,725,212 for the Australian and the European species, respectively (Figure 3.2; Table S3.4).

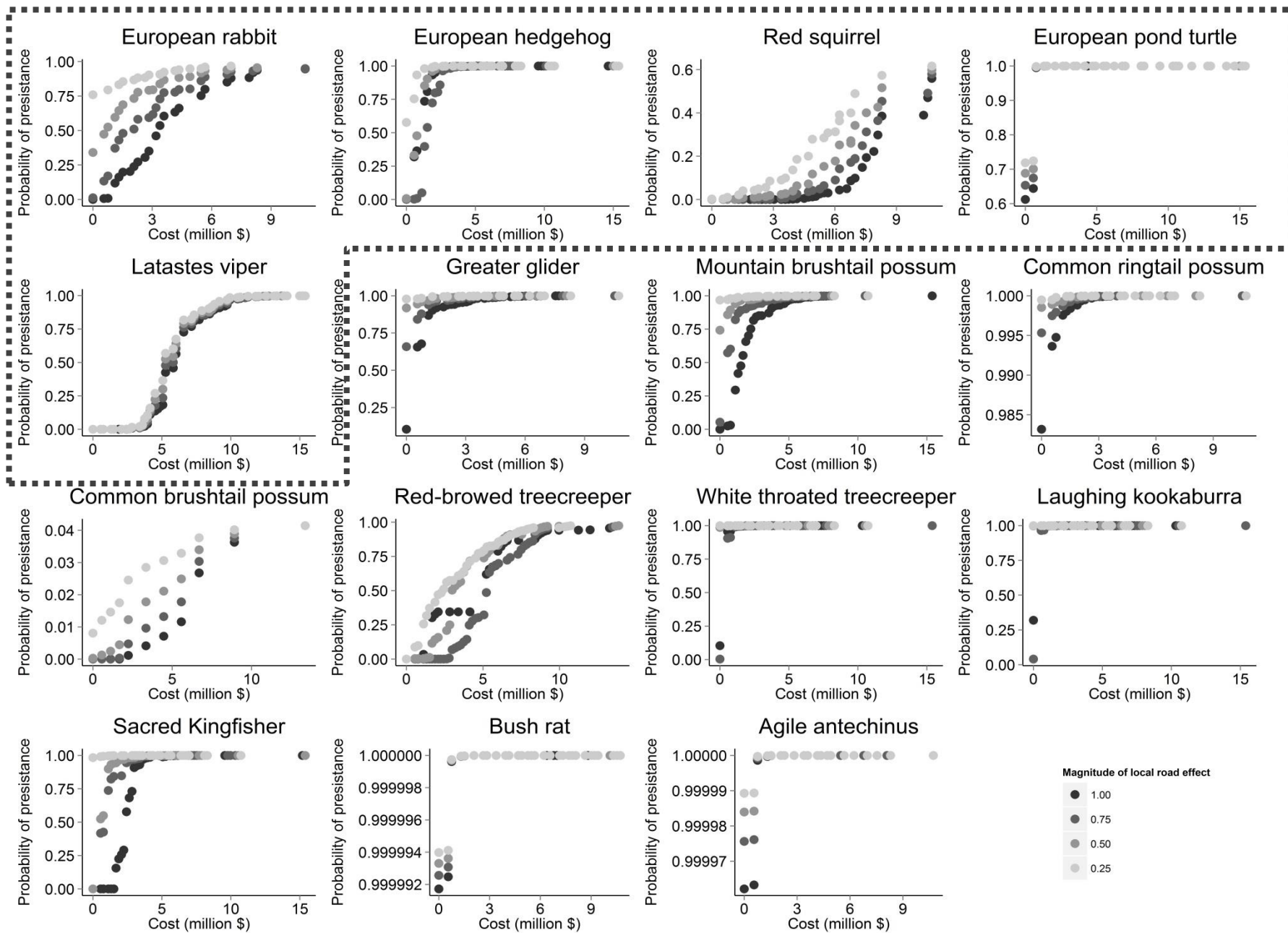


Figure 3.2: Per species response to the increase in road mitigation. Efficiency frontiers of non-dominated solutions for each species in the Australian database and the European database (within the dashed outline). Each species' efficiency frontier changes when the magnitude of the local effect of the roads is reduced in descending grey darkness from $\beta(x_s, y_s) = 1$ (dark grey), $\beta(x_s, y_s) = 0.75$ and 0.5 to 0.25 (lightest grey). X-axes are the cost of the different mitigation combinations along the frontier and y-axes are the probability of persistence of each species as a result of these mitigations being implemented.

3.4.2. Multispecies analyses

We created an efficiency frontier that represented the non-dominated solutions that provided the highest number of persisting species along the cost axis (Figure 3.3). We found that without mitigation on any of the roads we would expect to have 3.51 and 0.61 persisting species for the Australian and European species sets, respectively. The curve for the Australian species set exhibited the desired J-shape (Figure 3.3A) while the curve for the European species set was linear in shape (Figure 3.3B). Thus, there is a higher likelihood of locating a better “win-win” solution for the Australian species set than the European species set (Figure 3.3). However, we should consider that this result might be related to the number of species in the set. If we would have had more species in the European species set, we might have achieved a J-shaped curve as well. This suggests the possibility of a minimum number of species required to achieve cost-effectiveness. This possibility should be explored when applying this problem formulation to a real-life mitigation problem.

3.4.3. Frequency of mitigation measures on modelled road configurations

For the Australian species, the two most important roads to fence (the roads with the highest frequency of fencing at the solutions along the efficiency frontier; Figure 3.3A) are road seven followed by road four, which separates between patches five and seven, and patches three and five, respectively. These are the two shorter north-south roads that separate the suburbs from the city (road four) and the suburbs from the country (road seven) in our schematic landscape (Figure 3.4A, Table S3.5 – top half). The most important wildlife passages are on road nine followed by road seven, between patches six and eight and patches five and seven, respectively. This is the north-south traffic artery, which separates the suburbs and country (Figure 3.4A, Table S3.5 – top half). For the European species, roads seven and four also emerge as the two most important roads to fence (Figure 3.4B, Table S3.5 – bottom half). However, there were no roads that presented a high (≥ 0.8) frequency of wildlife passages – the highest frequencies for passages for the European species are ~ 0.7 for roads one and five (Table S3.5 – bottom half).

The main differences between the two species sets was in roads two and nine (Figure 3.4), where road nine is a country road and had higher fencing and passage frequencies in the Australian landscape than in the European one (0.8 versus 0.29, for both mitigation; Table S3.5). Conversely, road two, which is a city road, had higher fencing and passage frequencies in the European

landscape than the Australian one (0.77 versus 0.36 and 0.71 versus 0.14, for fences and passages respectively, Table S3.5).

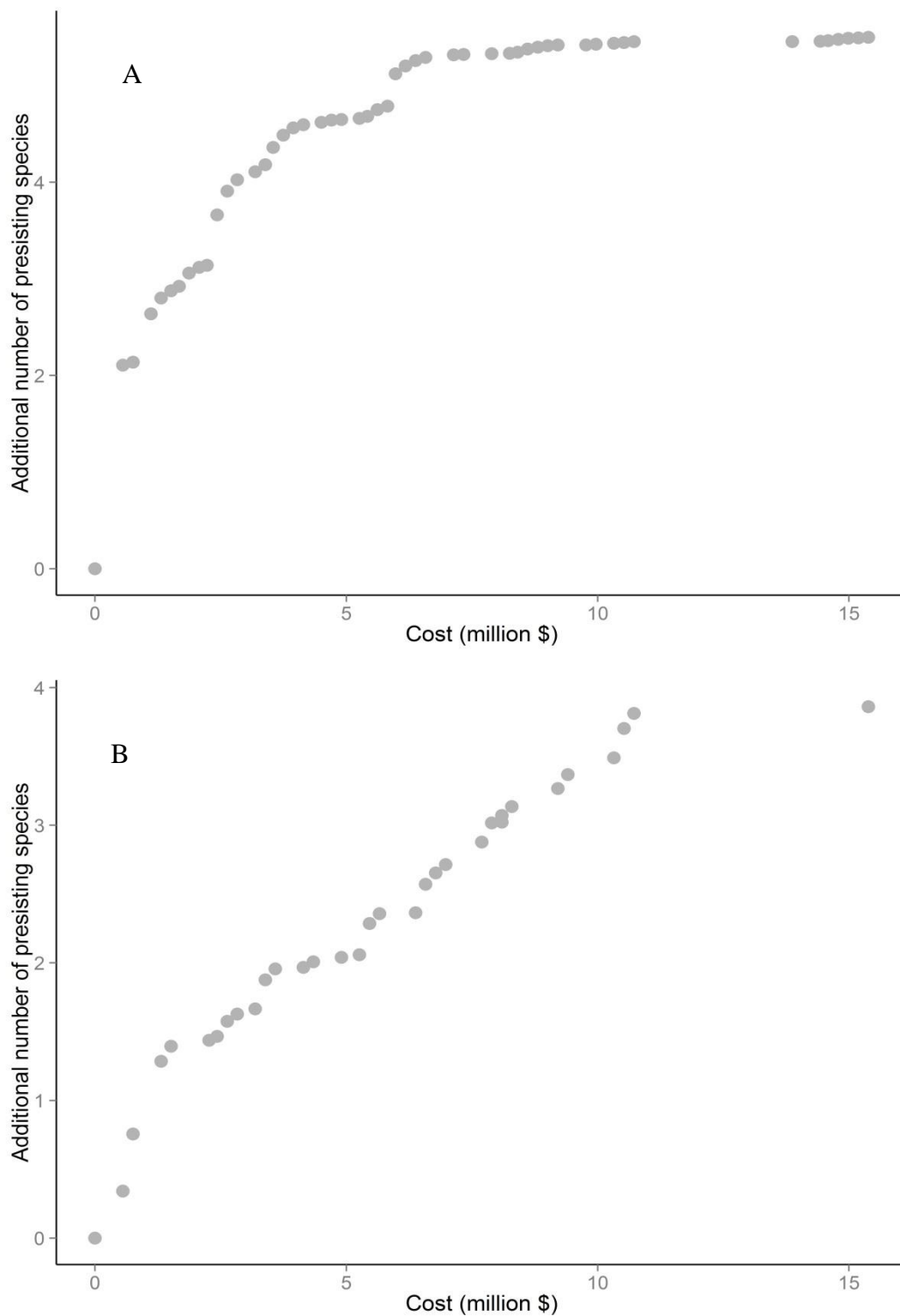


Figure 3.3: Efficiency frontier for the expected number of persisting species, in the multispecies analyses for the Australian species database (A) and the European species database (B). The frontier represents the non-dominated solutions of mitigation combination at different costs. The solutions are the ones that perform the best along both the number of persisting species (y-axis) and mitigation costs (x-axis). The light grey dots are the non-dominated solutions that are the best for their cost.

We found no life history traits among species that were consistently the most similar to the multispecies scenario. In the European species set, the same species (the European rabbit) was the most similar to the multispecies scenario for both fences and wildlife passages (Figure S3.1C-D). In the Australian species set, two different species exhibited the most similarity, depending on the mitigation (sacred kingfisher and red-browed treecreeper for fences and wildlife passages, respectively; Figure S3.1A-B). Out of these three species only the red-browed treecreeper was one of our predetermined focal species (largest home range).

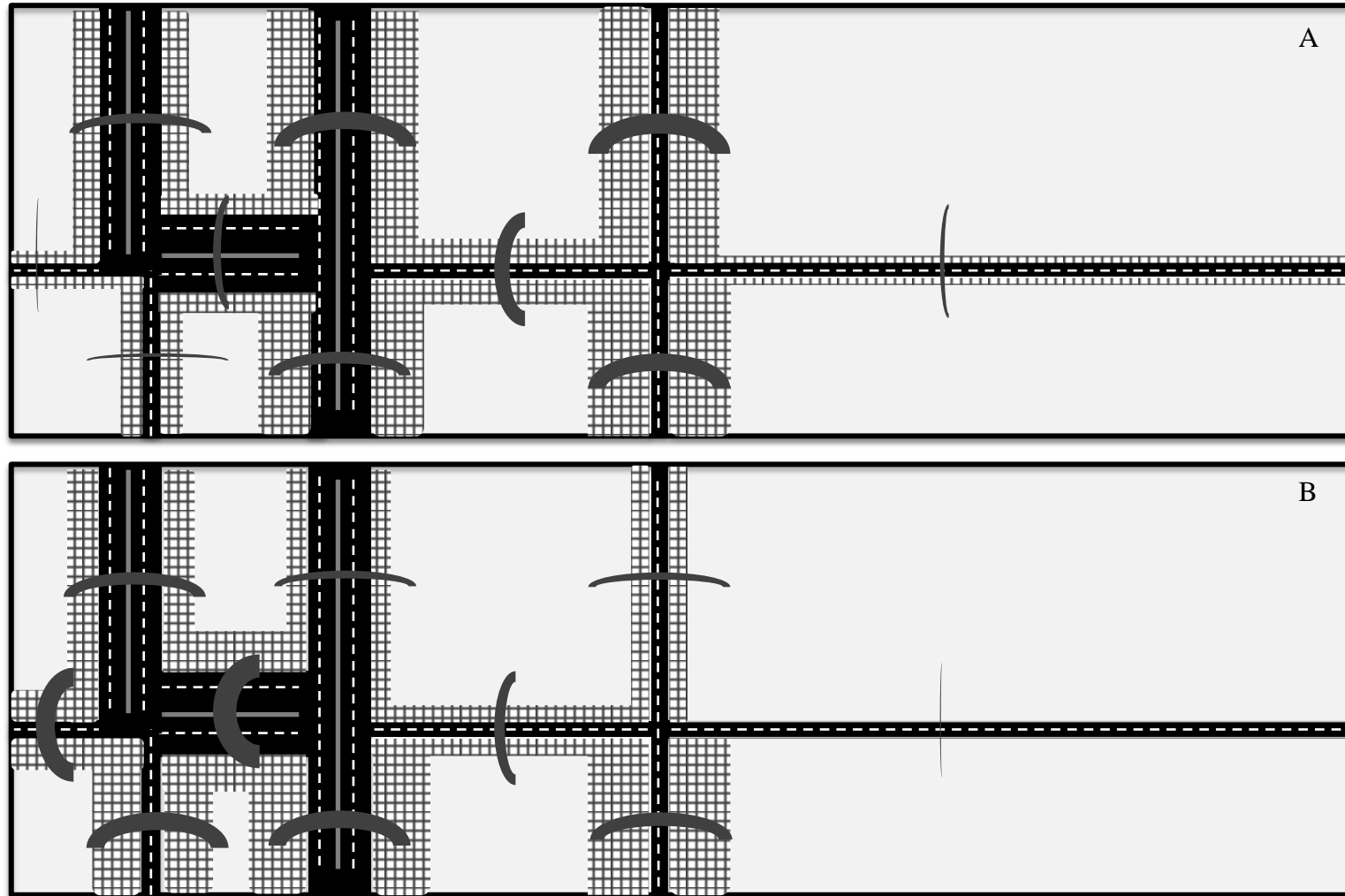


Figure 3.4: Fences and wildlife passages frequencies along the efficiency frontier of the multispecies analysis for the A) Australian and B) European species sets. Gridded areas represent fences and dark grey arches represent wildlife passages. The thicker the grid or the arch, the higher the frequency the fence appeared on this road, indicating the importance of applying this mitigation on that road.

3.4.4. Cost-effectiveness of planning scenarios

Each of the scenarios we tested had a different spatial configuration of mitigation measures (Table S3.6). For both species sets the multispecies scenario was considerably cheaper than both single species and single species accumulative scenarios. For the Australian species set the multispecies scenario was 8-25 million dollars cheaper than the single species accumulative and single species scenarios, respectively (Figure 3.5A). For the European species set the multispecies scenario was 4.8-20 million dollars cheaper than these two scenarios (Figure 3.5C).

From the two focal species, the species with the lowest fecundity provided the lowest number of persisting species for both species sets, while the focal species with the largest home range had the higher number of expected species for the Australian species set and the second lowest for the European species set (Figure 3.5A, C). However, at the same benefit (number of persisting species) the multispecies analysis has a lower cost than both of the focal species. The multispecies analysis was cheaper by \$200,000 and \$557,825 than the largest home range focal species for the Australian and European species sets, respectively, while for the lowest fecundity species the multispecies scenario was over a million dollars cheaper for the Australian species set and had a similar cost for the European species set (Figure 3.5A,C).

In addition, the multispecies analysis that provides a similar benefit (number of persisting species) to that of the focal species with the lowest fecundity provided a higher benefit/cost ratio, and thus the highest value for money for the Australian species set. For the European species set, the benefit was the same as the lowest fecundity species. The largest home range focal species had intermediate value for money at both species sets. Again, the multispecies analysis at the same benefit as that focal species was even better or the same for the European and the Australian species sets, respectively. Lastly, the two single species scenarios provided the lowest benefit/cost ratio in both species sets (Figure 3.5B, D).

When we added the information from species to the cost-effectiveness analysis we could not find any obvious focal species (Figure S3.2). In addition, the species that was the closest to the multispecies scenario in the European species set was the red squirrel and not the European rabbit, as in the frequency similarity results (Figure S3.1). This means that we cannot get a clear indication for a better focal species than the two species we chose ad-hoc.

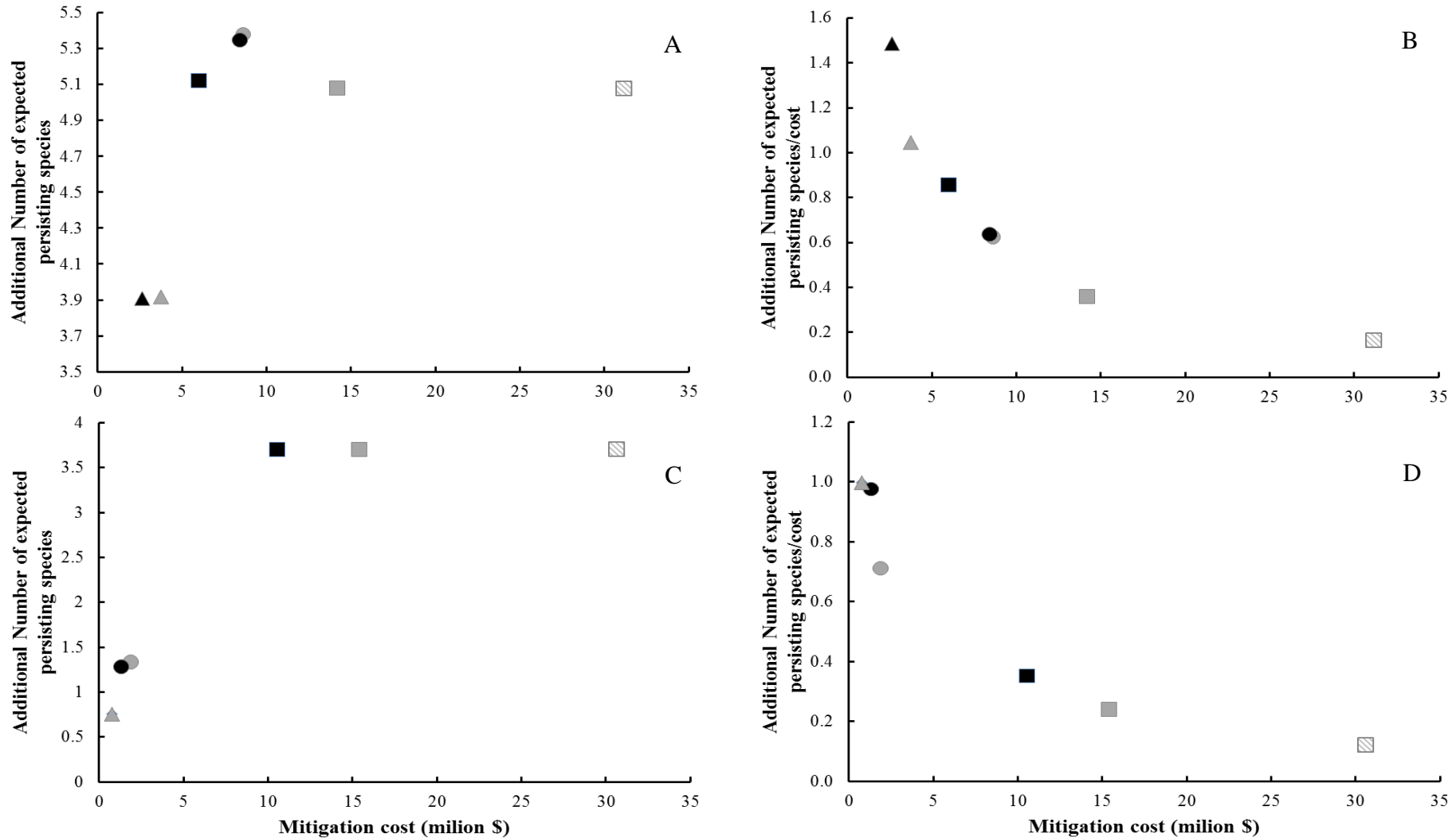


Figure 3.5: Comparing cost efficiency and value for money between the different planning scenarios and the multispecies analysis. The additional number of expected species was plotted against cost in millions of dollars. The plots on the left side are the additional number of persisting species, for the Australian species (A) and the European species (C). The plots on the right side are the additional number of persisting species/cost (value for money) with cost in millions of dollars as the x-axis, for the Australian species (B) and the European species (D). Squares represent single species analysis: Dashed filled square – single species; grey square – single species accumulative and black square – multispecies analysis at a similar benefit to the previous scenarios. Circles represent focal species with the largest home range: grey circle – largest home range focal species and black circle – multispecies analysis at a similar benefit to that of the focal species. Solid triangles represent the focal species with fecundity: grey triangle – largest home range focal species and black triangle – multispecies analysis at a similar benefit to that of the focal species. If a black symbol does not appear it means that it has the exact same parameters (benefit and cost) as the scenario it is compared to.

3.5. Discussion

The majority of terrestrial species on earth are negatively affected by roads (Rytwinski and Fahrig 2012) and every species has a unique reaction to a road. In this study, we present a novel method for systematic, cost-effective planning of mitigation for multiple species, focussing on species' persistence. We found that planning wildlife mitigation measures taking into account every species simultaneously will provide the most cost-effective planning strategy. Our findings correspond to studies that suggest multispecies planning provides better results than single species planning (Roberge and Angelstam 2004a). Yet, our finding contradicts Cullen et al. (2005), who argued that multispecies management projects for recovery of threatened species in New Zealand were not more cost-effective than single species projects. That said, the projects tested by Cullen et al. (2005) were focused on conservation actions than on mitigation (as was tested here), the benefits from these actions are expected to be more species specific than generic road mitigation. We found that planning road mitigation options for each species separately does not deliver very efficient solutions, but in the two cases of focal species we explored, planning only for the species with the largest home range is reasonably efficient but with mixed results.

Moreover, for both species sets the multispecies scenario not only provided the overall highest value for money but also had a value that was higher than or the same as each of the planning scenarios we compared (Figure 3.5B, D). Consequently, from all the planning strategies, the multispecies scenario can be deemed the optimal strategy when planning road mitigation for a multispecies system. When information on local species attributes is available, road mitigation planners should examine the results along the multispecies' efficiency frontier when considering which mitigation measures to use and where to place them.

Moreover, the frequencies of mitigation measures (fences and wildlife passages) that we extracted from the multispecies' efficiency frontier can indicate which roads are more important to mitigate (Figure 3.4). Here, again, we can see that there are similarities and differences between the species sets since, while the simulated landscape is the same for both species sets, there are some differences between them. Both species sets require fencing between the city and the suburbs and the suburbs and the country (roads four and seven). However, the Australian landscape requires higher mitigation in the country than the European landscape; this is because road nine exhibits high fencing frequencies in the Australian landscape. On the other hand, the European species sets require stronger mitigation in the city, because road two had higher fencing frequencies (Figure 3.4, Table S3.5). Moreover, the Australian landscape has higher wildlife passages frequencies, these again between the suburbs and the country. Indicative of a need to conserve connectivity in the countryside, this does not appear in the European landscape for this set of species. This might be connected to the fact that some of the species in the Australian species set have long dispersal distances (Table S3.2), which derive the need to protect the larger open patches to maximize the metapopulation probability of persistence. These mitigation frequencies can provide decision makers with

more flexibility in their decisions if there is a problem achieving the exact mitigation combinations recommended by the efficiency frontier (e.g. budget, stakeholder interests, etc.).

However, when information on local species attributes is not available, there are two options: 1) collect more data and 2) use focal species. Our second finding supports some of the findings of Cullen et al. (2005), as we also determined that a species with the largest home ranges is a somewhat effective focal species. We prefer the home range focal species over the fecundity focal species, because even though the former was less cost-effective and provided a lower value for money than the latter, it has the potential to deliver high benefit (as in the Australian species set). The fecundity focal species always delivered the lowest number of persisting species so we do not recommend following it. This is because we are not dealing with commodities but with living species, and unless mitigation is completely impossible or useless and other measures are needed, we should not simply forgo the species to fall into extirpation.

Therefore, we see that some life history traits can make a species as useful focal species for road mitigation planning. In our case, home range was a key feature while fecundity was not. Home range is also one of the major traits that makes species more vulnerable to the effects of roads (Rytwinski and Fahrig 2012), corresponding with the umbrella/focal species approach (Lambeck 1997). Such species can be studied and planned for in isolation when time or budget constraints prevent collecting data on the entire species community in the management area. Nonetheless, we acknowledge that the largest home range focal species delivers mixed results (it did not provide good results for the European species set).

From the cluster analysis we found a few species that presented higher similarity to the multispecies scenario (than the focal species). Although there were no strong patterns, all the species that exhibited strong similarity to the multispecies solution had a relatively large home range (sacred kingfisher, European rabbit, red-browed treecreeper and red squirrel). If information is not available and there are time or funding limitations in collecting the necessary data, it may be feasible to conduct a smaller multispecies analysis on only a few (two to three) species that have larger home ranges relative to the other species expected to live in the focal system.

There are some sensitivity issues that one needs to consider with this combination of road formulation and metapopulation model. The metapopulation model is sensitive to changes in home range, which means that the species tested should have a home range that will be in scale with the smallest patch in the system (i.e. for our system, between 0.5 and 10 ha). Also, Nicholson and Possingham (2007) showed that decisions will change with information uncertainty, especially in the two parameters which are hardest to estimate – the extinction–area exponent x_k and the species' dispersal distance d_k . In the context of roads and their mitigation, because the metapopulation model is rate-based, colonization rate is a crucial variable in the model, thus mitigation measures cannot be perfect and some movement should be allowed even when roads are fenced off. Lastly, while the species' movement element in the model is affected by which mitigation actions we take, the proximity to roads can also have a daily impact on the quality of the patch (similar to an edge effect) and affect both the survivorship and the recruitment within the patch. We can refer to this as the

sensitivity of the species to the road; in our model, this is $\beta_s(x_s, y_s)$ and we chose to use the maximum effect value of $\beta_s(x_s, y_s)=1$. The reason that we decided to focus on results when the magnitude is at its maximum is because we consider it a conservative estimate meant to avoid unnecessary losses of species due to underestimation of species' road sensitivity. However, we also showed that reducing this value will reduce the magnitude of mitigation measures needed. Thus, the effect of the road on patch quality in the form of decreasing patch size will impact the choice of optimal mitigation configuration. This means that this value should be considered carefully as underestimation can lead to insufficient mitigation measures and overestimation might waste funds that can be invested elsewhere.

3.6. Conclusions

van der Ree et al. (2011) addressed the need for larger scale and higher order road research focusing more on the mitigation that will benefit communities and regions rather than single species. Nonetheless, multispecies studies are still a rarity in the road ecology literature and, to our knowledge, so far none has focused on cost-effective mitigation planning for more than one species. Moreover, only a few studies incorporate cost-effectiveness at all into their mitigation planning (Putman et al. 2004, Ascensão et al. 2013, Polak et al. 2014). Multispecies systematic planning is a common practice in other fields of conservation. The most common example is protected area planning (Brooks et al. 2004, Nicholson and Possingham 2006, Polak et al. 2015). Other examples include identifying important biodiversity areas (Root et al. 2003) and management programs (Cullen et al. 2005). Our work will help to integrate multispecies systematic planning into road mitigation planning, making it a common practice in this field as well.

Our research is one of the first studies that provides support to focal species in road mitigation studies (Jaeger and Fahrig 2004a, Lesbarreres and Fahrig 2012, van der Grift et al. 2013). While we showed that single species research will not provide cost-effective solutions for a multispecies system, single species research might be adequate if there are limitations in monitoring time or costs. Using the largest home range focal species may provide adequate results for the entire system. However, using a few species with larger (compared to the other species in the system) home ranges in a multispecies analysis will likely provide an ever better result. As such, while we still believe that multispecies planning is optimal, there may be a paucity of either funds or information to use such a strategy. In addition, using a focal species or a set of focal species as a starting point and then improving at a later time if necessary may also be effective when there is a need for fast decision making and there is simply not time to collect the required data on all the species in the system.

In a world of growing roads (Laurance and Balmford 2013), declining biodiversity and reduction of conservation funds, cost-effectiveness tools are essential. We believe that we have provided an important and robust tool that can help practitioners and decision makers in making cost-effective management decisions

regarding road mitigation. Moreover, our method is not only robust but is also flexible and can be adapted to any system and species combination and provide cost-effective solutions at any budget by using the efficiency frontier of non-dominated solutions. Either by performing a multispecies analysis or by selecting the right indicator, using our method may provide more protection and save more valuable conservation funds than other road mitigation planning strategies in place today.

Chapter 4: Efficient expansion of global protected areas requires simultaneous planning for species and ecosystems

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4.1. Abstract

The Convention for Biological Diversity (CBD)'s strategic plan's Target 11 supports the use of environmental surrogates, such as ecosystems, as a basis for planning where new protected areas should be placed. However, the efficiency and effectiveness of this ecosystem-based planning approach to adequately capture threatened species in protected area networks is unknown. We tested the application of this approach in Australia according to the nation's CBD-inspired goals for expansion of the national protected area system. We set targets for ecosystems (10% of the extent of each ecosystem) and threatened species (variable extents based on persistence requirements for each species) and then measured the total land area required and opportunity cost of meeting those targets independently, sequentially and simultaneously. We discover that an ecosystem-based approach will not ensure the adequate representation of threatened species in protected areas. Planning simultaneously for species and ecosystem targets delivered the most efficient outcomes for both sets of targets, while planning first for ecosystems and then filling the gaps to meet species targets was the most inefficient conservation strategy. Our analysis highlights the pitfalls of pursuing goals for species and ecosystems non-cooperatively and has significant implications for nations aiming to meet their CBD mandated protected area obligations.

4.2. Introduction

Protected areas are pivotal for conserving both ecosystems and threatened species (Rodrigues and Brooks 2007). While the persistence of biodiversity often requires a suite of management strategies, protected areas provide a buffer from a myriad of threatening processes (Margules and Pressey 2000, Boyd et al. 2008). Gap analyses of the current global coverage of protected areas (~12% of Earth's land surface), highlight that many ecosystems and most threatened species are not well represented (Rodrigues et al. 2004b, Dietz and Czech 2005, Jenkins and Joppa 2009, Cantú-Salazar et al. 2013, Venter et al. 2014, Watson et al. 2014). In most countries a lack of systematic planning has given rise to significant biases in the location of protected areas (Joppa and Pfaff 2009, Barr et al. 2011). Typically conservation land was selected in locations that were not required for other, more lucrative, land uses (Joppa and Pfaff 2009). Systematic conservation planning approaches have sought to redress these biases by using spatial data on species distributions and ecosystems to prioritize locations for new protected areas (Moilanen et al. 2009). The expansion of current protected area networks has the potential to overcome these biases and improve ecosystem protection and the survival of threatened species populations, helping to avoid biodiversity loss and species extinctions (Rodrigues et al. 2004a, Rodrigues et al. 2004b, Chape et al. 2005, Dietz and Czech 2005).

Over the past decade, there has been a major shift towards ecosystem-based planning for the expansion of protected area networks (Margules et al. 2002, Silva 2005, CBD Secretariat 2010, Government of South Africa 2010). Ecosystem-based targets use environmental surrogates at various scales (e.g. bioregions, ecoregions) with the intention of efficiently representing biodiversity as a whole, including species and processes (Margules et al. 2002, Hoekstra et al. 2005). Ecosystem-based planning is used as an approach to avoid the often challenging need for unbiased, high resolution information on the spatial distributions of species (Ferrier 2002, Lombard et al. 2003, Brooks et al. 2004). Much of the existing species data have sparse or patchy distributions biased by survey effort, causing species-driven conservation planning to fail in representing biodiversity as a whole (Neel and Cummings 2003b). Ecosystem data is typically spatially contiguous and coarser than species data; thereby providing more flexibility for locating new protected areas and more options for avoiding conflicting land uses (Venter et al. 2014).

Critics of ecosystem-based targets argue that they are too coarse to effectively represent biodiversity, allowing many species to fall through the cracks (Ferrier and Watson 1997, Araújo et al. 2001, Brooks et al. 2004, Rodrigues and Brooks 2007). For example, both Araújo et al. (2001),

and Lombard et al. (2003), found that environmental surrogates perform relatively well for plants but fail to adequately represent vertebrates, while Rodrigues and Brooks (2007) found that environmental surrogates were poor at representing species. Further, the effectiveness of environmental surrogates decreases for species that are rare, have patchy or historically driven distribution, and/or are data deficient, which is the case for many threatened species (Ferrier 2002, Lombard et al. 2003).

The global goals stated within the Convention on Biological Diversity (CBD) strategic plans in both 2004 and 2010 are a primary reason for the shift from species-based to ecosystem-based planning for future protected area acquisitions (CBD Secretariat 2010). Specifically, in the 2010 CBD's Aichi target 11, there is a clear goal to conserve 17% of terrestrial and inland waters and 10% of marine and coastal ecosystems (CBD Secretariat 2010). The CBD states that networks should be ecologically representative, but gives no specific stipulation for how much habitat for threatened species should be protected (CBD Secretariat 2010). The achievement of threatened species protection under Aichi target 11 is therefore open to interpretation by nations considering the expansion of their protected area estate.

There are 195 parties part of the CBD treaty, each with the opportunity to translate these goals to a national level in ways that may result in various outcomes for biodiversity represented in protected areas. For example, ecosystems are the base unit of the South Africa National Protected Area Expansion Strategy (NPAES), which plans to achieve the 17% representation by targeting different proportions of ecosystems depending upon their diversity and protection requirements (Government of South Africa 2010). Similarly, Australia's National Reserve System's primary goal at the time of research was to protect 10% of each of its 85 bioregions (Commonwealth of Australia 2009) by representing at least 80% of the different types of ecosystems within each bioregion by 2015, with a secondary goal to represent core areas for threatened species by 2030 (Commonwealth of Australia 2009). This plan is an example of a coarse/fine scale approach, which advocates planning for ecosystems and then filling the gaps for species (TNC 1982, Noss 1987), which is also applied in North America (Alberta Parks , TNC 1982).

The use of ecosystem-based targets, both in global protected area guidelines and country-level protected area expansion policy has occurred in the absence of scientific analyses on how efficiently the ecosystem-based surrogates represent threatened species. While several studies (Neel and Cummings 2003a, Carmel and Stoller-Cavari 2006, Rodrigues and Brooks 2007) have examined the comparative benefits of both approaches, none have investigated their efficiency in protecting both species and ecosystems in the context of the CBD's strategic plan and country-level priority setting. Full implementation of the 2010 CBD strategic plan across all signatory countries is

likely to take considerable time and resources, but would represent to one of the greatest expansions of the global protected area estate in modern times (Venter et al. 2014). An improved understanding of how an ecosystem-based approach is likely to impact conservation outcomes is therefore timely and will assist countries in translating the CBD goals into protected area expansion that efficiently and effectively conserves threatened species as well as ecosystems.

Here we conduct a novel assessment of the impact of ecosystem-based planning and the global CBD goals on protected area outcomes for threatened species at the country level upon which they are implemented. We assess the potential for efficiency and effectiveness in threatened species and ecosystem coverage in the expanding protected area network across Australia, arguably the first country to fully embrace a systematic planning approach using ecosystem-based targets to design the protected area estate (Watson et al. 2008, Commonwealth of Australia 2009, Steffen et al. 2009). A recent continent wide analysis by Watson et al. (2011) found that despite this relatively systematic approach, threatened species coverage in the protected area estate (which covered 11.6% of the terrestrial surface) is still inadequate, with ~12% of threatened species completely absent from the protected area network. The commonwealth of Australia's plan to expand their reserve system (known as the National Reserve System, or NRS; (Natural Resource Management Ministerial Council 2004, Commonwealth of Australia 2009) follows the guidelines and ecosystem-based approach suggested by the CBD.

Specifically we investigate (i) how well threatened species are likely to be captured in the resultant protected area network if Australia aims to meet its 10% targets for all ecosystems most efficiently (as current policies suggest) by minimizing the area required; (ii) how well ecosystem-based targets are likely to be met if Australia's protected area network is designed to meet targets for threatened species only; and finally (iii) the efficiency and effectiveness of planning for both sets of targets simultaneously versus sequentially (e.g. meeting ecosystem targets first and species targets later or vice versa). We define efficiency as the amount of area required to meet a given set of targets, and effectiveness as the level of representation of a target in a given protected area network.

4.3. Methods

4.3.1. Ecosystem spatial data and targets

At the time of this research Australia was divided into 85 bioregions, hereafter ‘ecosystems’, based on the Interim Biogeographic Regionalization of Australia (IBRA bioregions. Steffen et al. 2009, version 6.1), at a spatial resolution of approximately 10km². These ecosystems were derived by compiling geographic information on continental scale gradients and patterns in climate, substrate, landform, vegetation, and fauna, and each bioregion is considered a distinct ecologically and geographically defined area (Natural Resource Management Ministerial Council 2004). The Australia’s National Reserve System strategy uses Bioregions as the unit to represent ecosystems (Commonwealth of Australia 2009). Other countries may use different types of data to represent ‘ecosystems’ in their protected area expansion. As such we refer to the unit used in this analysis as ‘ecosystems’ to facilitate transference between nations. The Commonwealth of Australia (Natural Resource Management Ministerial Council 2004, Commonwealth of Australia 2009) has set a target of at least 10% representation in each of ecosystem in the protected area estate for the NRS, which is the ecosystem target adopted in this study.

4.3.2. Threatened species data and targets

We considered distributions of 1320 species from the total of 1737 species listed under the Environmental Protection and Biodiversity Conservation Act (EPBCA). We used maps of species’ distributions at a resolution of approximately 10km², developed for extant terrestrial and freshwater threatened species available in the Species of National Environmental Significance (SNES) database (Commonwealth of Australia 2012b). We excluded 95 extinct species and 367 species that are marine, freshwater or migratory, or whose distributions are only estimated with low certainty. The species we considered, hereafter referred to as ‘threatened species’ are listed as Critically Endangered, Endangered or Vulnerable (Commonwealth of Australia 2012b) (note that the definitions of these categories as applied within Australia differ slightly from those employed globally by the IUCN Red List, and also that there are species on the IUCN Red List that are not listed nationally, and vice versa).

Following Watson et al. (2011) and building on a method developed by Rodrigues et al. (2004a) and Kark et al. (2009), we set a series of adequacy targets for these 1320 threatened species

based on geographic range size and level of endangerment. This method develops area-based targets that scale with geographic range size, requiring species with smaller ranges to be increasingly well protected (Pressey et al. 2003, Rodrigues et al. 2004a, Rodrigues et al. 2004b, Carwardine et al. 2008a, Klein et al. 2010). A target of complete coverage (i.e. 100% of remaining extent) by protected areas was set for those species considered Critically Endangered and those species with a geographic range size of $< 1,000\text{km}^2$. Conversely, for those species with large range sizes ($>10,000\text{ km}^2$) the target was set to cover 10% of current range. For species with geographic ranges of intermediate size (between $1,000\text{km}^2$ and $10,000\text{ km}^2$) the target was linearly interpolated between these two extremes, with decreasing representation targets (smaller percentage of their range) set for species with larger range sizes (Figure S4.1).

4.3.3. Spatial prioritization analyses

We determined the amount of each of the 85 ecosystems and 1307 threatened species already covered by the current protected area estate by intersecting the ecosystem maps and threatened species distribution maps with the map of the Australian protected area estate (Commonwealth of Australia 2006; this includes IUCN management categories I-VI). For both ecosystems and species we masked out distributions that occurred in cleared areas (i.e. are not potential for conservation). For some species the area of remaining available intact habitat was smaller than their set target. In such cases, we reduced the target for these species to represent 100% of remaining available intact habitat. Thirteen of our 1320 species had none of their distribution within areas that were considered intact and available for conservation and were counted as gap species and their targets were set to zero. This left 1307 species as our threatened species target set.

We created a planning unit layer of $10\times 10\text{ km}$ grid cells covering Australia, which was the smallest resolution computationally feasible and approximately matches the scale of the maps of threatened species (Watson et al. 2011) and ecosystems (Fuller et al. 2010). We intersected the planning unit layer with the protected area layer, such that each existing protected area was a separate planning unit. We determined the amount of each species and ecosystem type in each planning unit based on their spatial overlap.

We used the systematic conservation planning software Marxan (Ball et al. 2009) to identify solutions for the expansion of Australia's protected area network to meet the above targets for ecosystems and threatened species coverage. Marxan uses a simulated annealing algorithm to select multiple alternative sets of areas that meet pre-specified biodiversity targets whilst minimizing

overall cost (Ball et al. 2009). It has been used for identifying proposed conservation areas in Australia and throughout the world (e.g. Carwardine et al. 2008b, Smith et al. 2008, Klein et al. 2009). When investigating spatial options for expansion, we locked in the current protected area estate and assumed that targets for all species and ecosystems were of equal importance to meet. We set the cost of each planning unit as the total area potentially suitable for conservation within the planning unit, i.e. we assumed that only areas of native vegetation would be suitable for inclusion in the protected area estate and we used area as a universal surrogate for the costs of protected area management (Ball et al. 2009).

We used Marxan to identify 500 solutions for each of five scenarios (Table 4.1). First, we identified the additional area required to protect all the ecosystem-based targets (by being added to the current network) and assessed how well the selected network covered the adequacy targets for the 1307 threatened species (Table 4.1, scenario 1). Next we determined the minimum amount of newly protected land needed to meet the range-based targets for threatened species, and assessed how well this solution met the representation targets set for ecosystems (Table 4.1, scenario 2). In our third and fourth scenarios (Table 4.1) we investigated how much additional land area would be required to be added to the network formed in scenarios one and two to achieve all targets for both species and ecosystems, i.e. achieving 100% of all targets in a stepwise way. Lastly, for scenario five, we established the minimum amount of land needed to create a protected area network for both ecosystems and species targets when planning simultaneously (Table 4.1).

All five scenarios were evaluated by: 1) the total number and percentage of targets that were fully met; 2) average proportion of coverage for each set of targets (species and ecosystems) in the top solution for each scenario (coverage was calculated per target, and if more than 100% of a target was met, it was capped at 100% when averaging across all targets in the set). We compared the dissimilarity between scenarios (1-5) using Jaccard distances for both the added protected areas only and the entire network including the existing protected areas (Table S4.1).

We also investigated the sensitivity of our results: 1) the measure of cost we used (area) by comparing with a cost based on forgone agricultural opportunities (Marinoni et al. 2012); 2) the possible impact of the reserve expansion being driven by current location of protected areas, by testing a scenario where protected areas were not locked in. First, we re-ran scenarios one through five (Table 4.1) with the cost of protecting a planning unit based on its current agricultural profitability, instead of its area (higher profitability values represent higher opportunity costs). We used a GIS agricultural profit map (\$/ha) from Marinoni, Navarro Garcia (Marinoni et al. 2012) to calculate a per planning unit annual profitability value in \$/ha and multiplied it by the area of the planning unit potentially suitable for conservation, and used this value as the planning unit cost.

Negative values were rounded to zero and a transaction cost of \$10,000 was added proportionally to the planning size as the minimum land value (Carwardine et al. 2008b). Second, we re-ran the analysis without locking in existing protected areas, thus capturing a scenario where no fixed current protected areas network exists and all non-cleared areas are available for conservation. Third, we tested if the additional area that was selected for protected areas was able to meet the target better than if that same amount of area was conserved by randomly selecting available planning units.

4.4. Results

There is a large degree of variation in the coverage of ecosystems (bioregions) and threatened species in the current protected area network (Table 4.1). Forty-eight (56.5%) ecosystems have achieved their target of 10% protected; however, some ecosystems are poorly represented, and on average ecosystems have attained 72.6% of their target level of protection. The protected area estate is performing worse for threatened species, with only 284 (21.5%) threatened species reaching their range-based target. On average across all species 47.3% of the target area is covered in the current network (Table 4.1).

We found that a minimum of 29.5 million ha must be added to the existing protected area network to achieve 10% representation of each ecosystem. The solution with the sole target of achieving 10% of each ecosystem in the smallest amount of area requires approximately 15.4% (Table 4.1) of terrestrial Australia to be in protected areas (Figure 4.1A). One of the main reasons that the required national level coverage is greater than the 10% target is because some ecosystems, mostly arid ecosystems (Pressey 1994), have been protected to a level above 10%. Another reason is that many planning units are selected to meet targets for ecosystems which only occur in a small portion of the unit. Expansion aimed solely at increasing ecosystem representation would incidentally increase the number of threatened species adequately captured by 3.2% and increase the average proportion of adequacy targets met across all species from 47.3% up to 52.2% (Table 4.1).

Expanding the current protected area network to represent all threatened species adequately without considering ecosystem targets would require an additional 54.9 million ha. This equates to a protected area system that is approximately 144 million ha in size (or 18.7% of Australia; Table 4.1, Figure 4.1B). In this scenario, the number of ecosystems protected to a 10% level would increase from 48 to 60.

If the protected area network is expanded to meet ecosystems and threatened species targets simultaneously, an additional 72 million ha would require protection (approximately 21.0% of Australia's land surface; Figure 4.1C, Figure 4.2). Planning to meet these same goals sequentially, starting with ecosystems targets and then adding areas to meet threatened species targets, would require 79.5 million ha (21.9% of the land; Table 4.1, Figure 4.2) to be added to the existing network, which is approximately seven million ha more than the most efficient scenario which integrated these targets. Planning sequentially, starting with threatened species targets and then

adding areas to achieve the 10% ecosystems representation target will require a similar amount of land as planning simultaneously (Table 4.1, Figure 4.2).

Table 4.1: Scenario results: Area of proposed protected areas and amount of species and ecosystem targets that are adequately protected

	Current situation	Scenario 1 Achieving 10% ecosystem targets	Scenario 2 Achieving threatened species coverage	Scenario 3 Achieving 10% ecosystem targets then adding species	Scenario 4 Achieving threatened species coverage targets then adding 10%	Scenario 5 Achieving both threatened species and ecosystem targets
Land covered in protected areas in ha	89,115,652 (11.59%)	118,629,670 (15.43%)	143,988,700 (18.73%)	168,574,630 (21.93%)	161,689,810 (21.03%)	161,191,100 (20.96%)
<i>Threatened species coverage</i>						
Number of species adequately protected	284 (21.5%)	323 (24.7%)	1307 (100%)	1307 (100%)	1307 (100%)	1307 (100%)
Average proportion ^ of species target met*	47.8%	52.2%	99.9%	99.9%	99.9%	99.9%
<i>Ecosystems coverage</i>						
Number of ecosystems with 10% coverage	48 (56.5%)	85 (100%)	60 (70.6%)	85 (100%)	85 (100%)	85 (100%)
Average proportion ^ of 10% ecosystems coverage achieved	72.6%	100%	85.1%	100%	100%	100%

^Some features had more than 100% of their target met but for the analysis reported in this table we only allowed a maximum of 100% coverage.

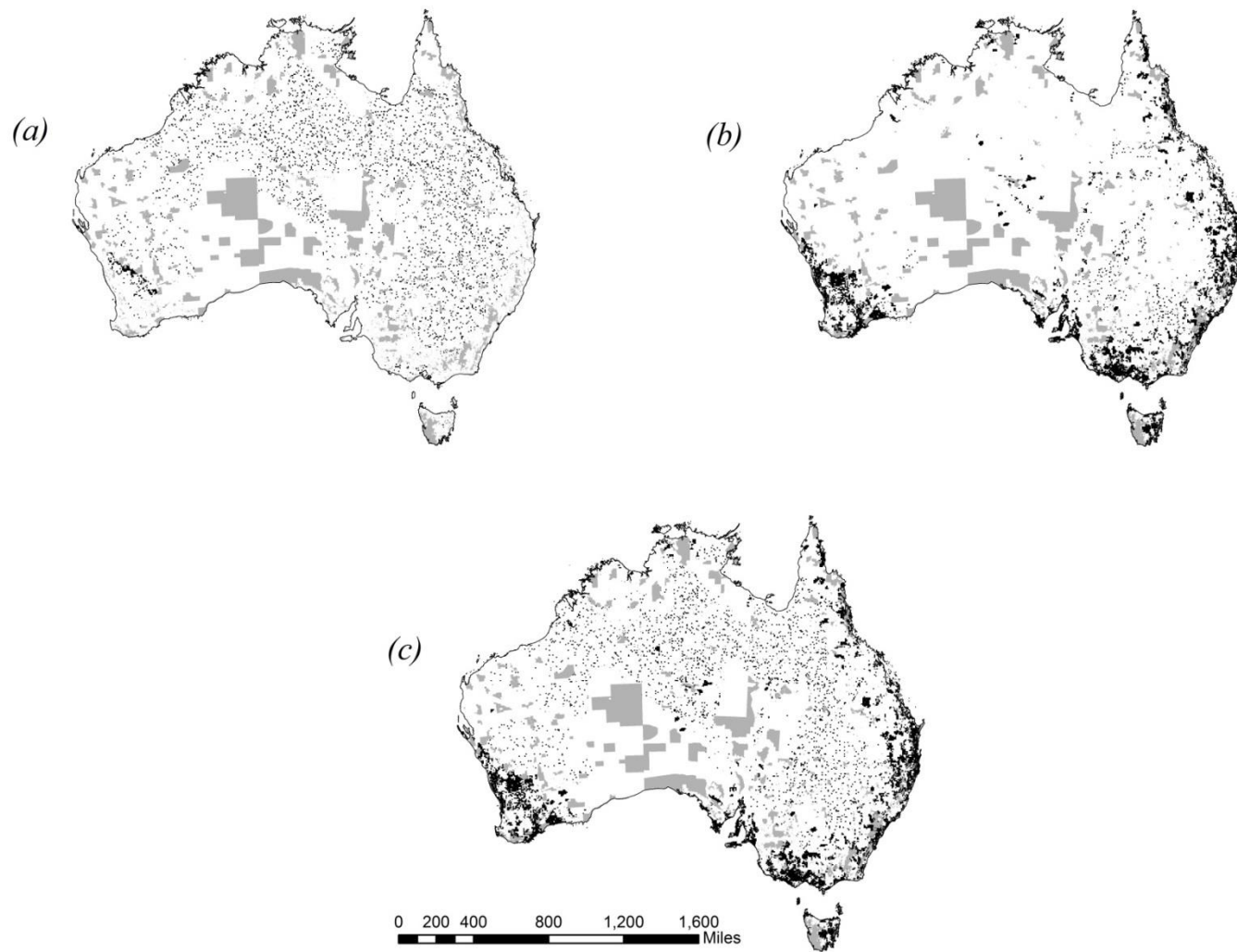


Figure 4.1: Spatial distribution of proposed protected areas and existing protected areas for each of the planning scenarios. Grey areas represent the current protected areas; black areas represent the proposed additional protected areas for each scenario's best solution. A-Achieving 10% ecosystem targets; B-Achieving threatened species coverage targets; C- Achieving both threatened species and ecosystem targets simultaneously.

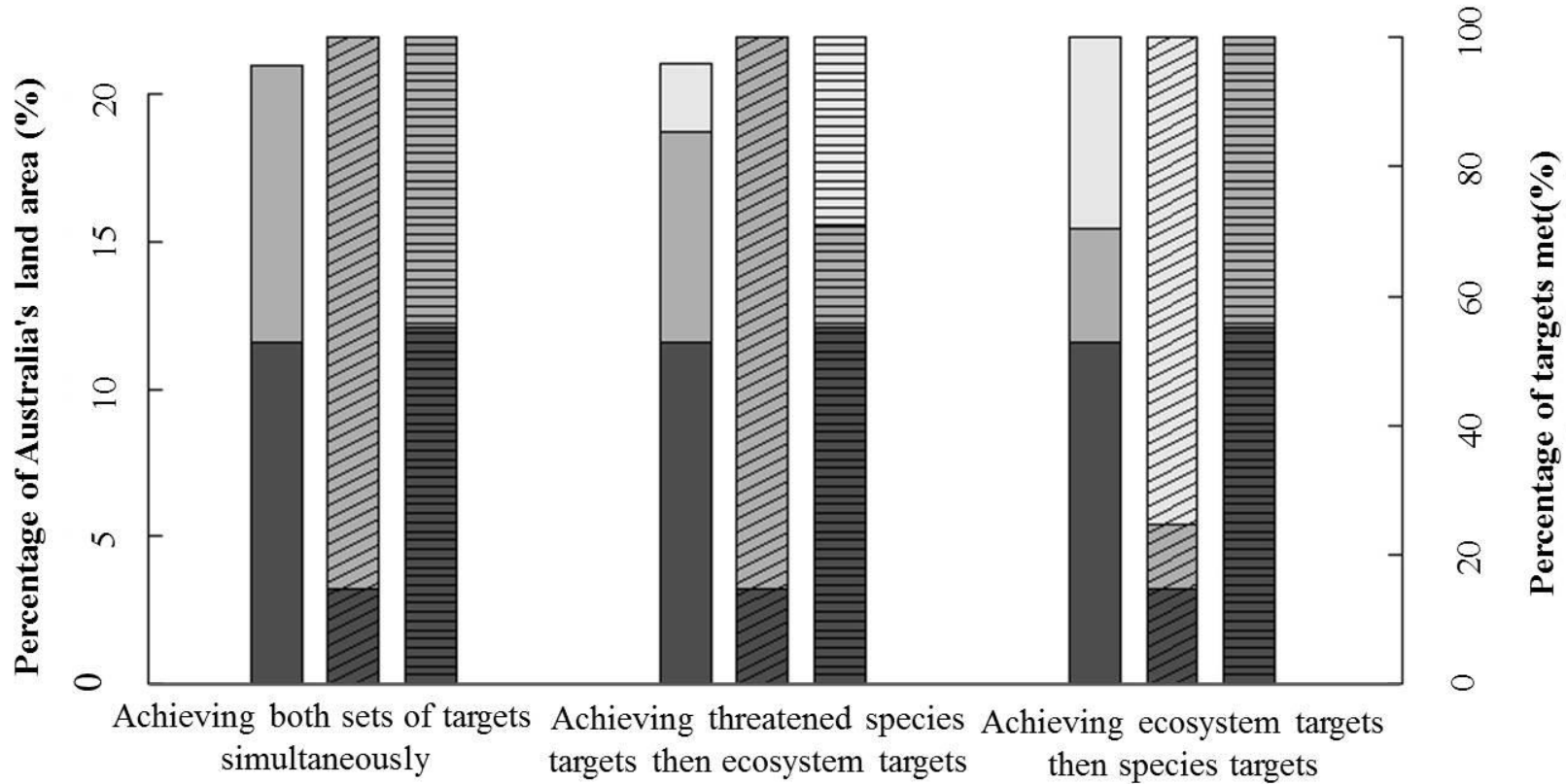


Figure 4.2: Comparing the efficiency of the two step-wise scenarios and the simultaneous scenario (scenarios 3 -5): from the existing protected areas network (black) to the first step of protected areas selection, (light grey) to the second step (dark grey) of filling the gaps for the opposite target-type (ecosystem or species). The plain bars (left y-axis) show the increase in land area (as % of Australia's land area). The diagonally striped bars represent percentage of species targets met (right y-axis). The horizontally striped bars represent percentage of ecosystem-based targets met (right y-axis).

There are substantial differences in the spatial configuration of the protected areas network expansion between the five scenarios (Table S4.1). The majority of the difference lies between scenarios one and two (selection for ecosystems or selection for species, Figure 4.1A-B, Jaccard dissimilarity distance of added protected areas $d_j=0.982$). When planning for ecosystems only (Figure 4.1A) we get a map of protected areas which are arranged relatively evenly throughout Australia as a result of the nature of the ecosystems which are large non-overlapping spatial features. When planning for threatened species (Figure 4.1B) the resulting network is concentrated around the coastline reflecting the fact that species distributions are usually small dynamic units affected by internal and external processes and reflect past land use changes (Kirkpatrick and Brown 1994). Larger protected areas might be more effective in promoting persistence for biodiversity and might be more robust to climate change (Mackey et al. 2008, Watson et al. 2013). However, a species-based approach is likely to protect more areas that are threatened by habitat loss and valuable for recreational use by society (Taylor et al. 2011).

The same pattern of cost-effectiveness holds when using agricultural profits as the cost layer instead of land area, indicating that our analysis was robust to using either of these costs surrogates (Figure S4.2). Planning for ecosystems only marginally improves protection for threatened species and filling the gaps to reach 100% of species targets delivered the most costly scenario (Table S4.2). Planning for both targets simultaneously again proved the most cost-effective approach, followed by sequentially planning first according to species targets and then adding areas to achieve ecosystem targets (Table S4.2).

When performing the same analyses but assuming that no current protected area network exists, scenarios follow the same overall pattern, with simultaneous planning (scenario 5) being the most cost-effective closely followed by sequential planning starting with species (scenario 4). Again, sequentially planning starting with ecosystems (scenario 3) was the least cost-effective option (Table S4.3). Planning according to ecosystems only (scenario 1) required less area than the current protected area network but only protected 9% of the species while planning according to species achieved 60% of the ecosystems targets (Table S4.3).

Lastly, All of the best solutions in scenarios 1-5 (Table 1) produced protected areas networks that performed significantly better than random (one-sample t-test, $p<0.0001$, Table S4.4).

4.5. Discussion

If implemented by signatory nations, the CBD 2010 strategic plan will lead to the largest increase in global protected area establishment in history (Venter et al. 2014, Watson et al. 2014). Importantly, national protected area plans adopted by governments often follow the global CBD guidelines which have explicitly promoted an ecosystem-based approach to achieve the expansion (CBD Secretariat 2010). We tested whether an ecosystem-based approach, by itself, would be effective in adequately conserving threatened species, using Australia as a case study. We found that prioritizing future protected areas based on representing the 85 major ecosystems is likely to fall well short of capturing adequate amounts of many (~75%) threatened species' ranges.

We found that planning for the expansion of protected area networks to meet targets for ecosystems and species at the same time will achieve both sets of targets with fewer resources and less land. This result contrasts with the stepwise coarse/fine scale approach, which we show is likely to be a less efficient way to achieve targets for both species and ecosystems together. Our results concur with other analyses that show if the goal is to protect species and ecosystems, a dual approach is most effective (Kirkpatrick and Brown 1994, Ferrier 2002, Lombard et al. 2003). Simultaneous planning is most efficient because the planning units that collectively meet both goals most efficiently can be identified and avoiding the selection of planning units that become redundant once a secondary goal is added.

The efficiencies gained by simultaneous planning on a continent the size of Australia are modest, but could become enormous once multiplied up to a global scale. Assuming the same patterns hold, the efficiencies gained by planning for threatened species and ecosystems together across the world would equal an area the size of a third of all EU countries. Our results have significant implications for how nations should interpret the CBD strategic plan. Implementation of the ecosystem-based targets alone is likely to mean future protected areas will not be optimal to meet each countries commitment to protecting threatened species, nor the overall aim of the CBD. Considering the biodiversity crisis most nations currently face (Olson et al. 2002) and the limited amount available for conservation (Sanderson et al. 2002), future acquisitions of protected areas need to be efficient in achieving ecosystem and threatened species representation.

The disparity between protected area network expansion for threatened species targets versus ecosystem-based targets is due to the differences in the spatial resolution of the two types of features. Ecosystems are large and non-overlapping, permitting flexibility in which planning units are selected for conservation and promoting a spatially even spread of protected areas.

Alternatively, species distributions are often smaller, can overlap, are spatially aggregated and reflect land use history (Kirkpatrick and Brown 1994, Taylor et al. 2011). As such the areas still available to these species are spatially skewed and usually small compared to the large and widely distributed ecosystems (Kirkpatrick and Brown 1994, Lawler et al. 2003). While many nations do not have extensive spatial data on their threatened species, the IUCN red list assessments make this freely available when it does exist (IUCN 2014).

We do not attempt to present a future plan for Australia's protected area network, which would entail the inclusion of further social, economic and biological considerations. We assume all areas are available for protected area expansion, but in reality factors such as opportunities for landholder engagement, public accessibility and feasibility would impact on this availability (Knight et al. 2006, Carwardine et al. 2008a, Watson et al. 2009). Further, while a well-managed, well-placed protected area network provide a key component required to facilitate the persistence and recovery of threatened species (Bruner et al. 2001, Kalamandeen and Gillson 2007, Taylor et al. 2011, Wilson et al. 2011), many threatened species require a more intensive management program than gazetting of protected areas alone (Leverington et al. 2010, Woinarski et al. 2011). The full costs of protecting and managing areas include the opportunity costs of not developing a site, direct costs such as infrastructure, maintenance and salaries, and the costs of planning and implementing management programs (James et al. 1999, Bruner et al. 2004).

Additional ecological considerations required in a real world protected area expansion task also include the consideration of species distributions under climate change, minimum protected area size and connectivity and corridors, which may be important for improving the likelihood that species will persist in reserves over the long term. Future research will need to consider the dynamic nature of threats such as land use change and climate change, presenting a need to assess both species and ecosystem range shift to these changes. Moreover, given the role of biodiversity-driven ecosystem services such as pollination, pest control and recreation (Ingram et al. 2012), it may be important for real-world planning to consider ecosystem-services. Data and targets for threatened species, ecosystems and protected areas is regularly updated but the minor changes that have recently occurred are not likely to affect the conclusions of our analyses (Commonwealth of Australia 2010, 2012b, a).

We found that expanding the protected area network to meet the targets used in this study would result in forfeiting (or shifting the locations for generating) almost five billion dollars in annual potential agricultural profit. Due to the simplifications we made in our analysis, it is likely that a real-world comprehensive protected area network in Australia would require a larger total area being needed to meet ecosystem and species targets, as the most 'efficient' options may not be

available nor sufficient to ensure species persistence. We also note that protected areas can provide alternative sources of income by creating jobs, helping to develop rural areas and tourism revenues and providing benefits for human health and wellbeing while helping to protect the intrinsic values of nature (Balmford et al. 2002). Regardless of the cost and size of the resultant protected area estate, an efficiency approach such as the one we present serves to minimize the costs of providing these benefits to society.

Biodiversity loss is a global problem. However, the expansion of protected area networks is typically planned at a national level. In countries such as Australia, where ecosystem and species databases exist, planning for both ecosystems and species can occur simultaneously to deliver the most efficient solutions. Countries with protected area expansion plans inspired by interpretations of the CBD guidelines (Silva 2005, Commonwealth of Australia 2009, Government of South Africa 2010), need to consider the best available data on both species and ecosystems if both are to be efficiently protected.

Chapter 5: Balancing ecosystem and threatened species representation in protected areas and implications for nations achieving global conservation goals

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5.1. Abstract

Balancing the representation of ecosystems and threatened species habitats is critical for optimizing protected area (PA) networks and achieving the Convention on Biological Diversity strategic goals. Here we provide a systematic approach for maximizing representativeness of ecosystems and threatened species within a constrained total PA network size, using Australia as a case study. We show that protection of 24.4% of Australia is needed to achieve 17% representation for each ecosystem and all threatened species habitat targets. When the size of the PA estate is constrained, trade-off curves between ecosystem and species targets are J-shaped, indicating potential “win-win” configurations. For example, optimally increasing the current PA network to 17% could protect 9% of each ecosystem and ensure that all threatened species achieve at least 78% of their targets. This method of integrating species and ecosystem targets in PA planning allows nations to maximize different PA goals under financial and geographical constraints.

5.2. Introduction

Systematically planned protected Areas (PAs) aim to ensure representative samples of ecosystems are protected and threatened species' habitats are retained (Barr et al. 2011; Butchart et al. 2015; Watson et al. 2014), yet global and national level analyses indicate that neither of these biodiversity conservation goals has yet been achieved (e.g. Rodrigues et al. 2004b; Dietz and Czech 2005; Venter et al. 2014). Gaps in PA coverage occur because of past biases in PA placement towards remote and unproductive areas with low land use conflicts, coupled with a more recent focus on achieving areal targets without considering the underlying conservation objectives (Rodrigues et al. 2004a; Watson et al. 2011; Watson et al. 2016a). Future expansion of PAs can only fill these gaps if fine resolution data on species and ecosystem distributions are systematically included (Moilanen et al. 2009; Polak et al. 2015).

The Convention on Biological Diversity (CBD)'s strategic plan (CBD Secretariat 2010) provides systematic guidance for a global expansion of PAs. The 2010 CBD's Aichi Target 11 stipulates a quantitative goal to protect 17% of terrestrial and inland water area and 10% of marine and coastal ecosystems in areas of particular importance for biodiversity. These PAs should be ecologically representative, effectively managed and connected. The CBD advocates the use of ecosystems as the primary targets for the placement of PAs to achieve ecological representation (CBD Secretariat 2010; Woodley et al. 2012) and the phrase 'areas of particular importance for biodiversity' has often been operationalized as protecting threatened species' habitats (CBD Secretariat 2010; Watson et al. 2014; Butchart et al. 2015). In addition, Aichi Target 12, which refers specifically to preventing the extinction of threatened species, also refers to protecting habitat as one of the means to achieving this goal.

While the CBD plays an important role in bringing nations together to secure global biodiversity, its guidance is somewhat open to interpretation regarding the exact amounts of each ecosystem and threatened species range that should be protected. A common interpretation of the representation element of Target 11 is that 17% of each terrestrial ecosystem should be represented in PAs (Woodley et al. 2012; Venter et al. 2014). The guidelines for threatened species under Target 12 are even less specific (Butchart et al. 2015; Watson et al. 2016b). More quantitative guidance would assist countries in expanding their PAs in a way that provides maximum protection for threatened species as well as ecosystems.

As PA networks across the world continue to expand in response to the CBD targets, it is crucial that we understand the trade-offs between targets focused on ecosystem representation

(Target 11) and those focused on threatened species habitat requirements (Target 12; Marques et al. 2014; Venter et al. 2014; Di Marco et al. 2015). Here, we address this challenge and provide a systematic approach for simultaneously maximizing representation of threatened species and ecosystems within fixed-size PA networks, using Australia as a case study. We start with a set of area-based targets for the country's 85 major ecosystems and 1,320 listed threatened species, following Polak et al. (2015). We use trade-off curves and cost-effectiveness analysis to explore the possible representation of ecosystems and threatened species as PA coverage expands. For each of four PA network sizes (15%, 17%, 19% and 21% of Australia's total terrestrial area) we identify the optimal combination of ecosystem and species target sizes that can make the best use of limited conservation resources, offering key insights for PA expansion.

5.3. Methods

5.3.1. Biodiversity datasets and targets

We divided Australia into 85 bioregions, based on the Interim Biogeographic Regionalization of Australia (Figure 5.1, IBRA bioregions, version 6.1, Steffen et al. 2009), using a spatial resolution of approximately 10 km². Australia's bioregions were derived by compiling geographic information on continental scale gradients and patterns in climate, substrate, landform, vegetation, and fauna, and each bioregion is considered a distinct ecologically- and geographically-defined area (Natural Resource Management Ministerial Council 2004). Bioregions are the unit used by Australia's National Reserve System strategy (Commonwealth of Australia 2009) to represent ecosystems as referred to by the CBD, whereby the goal is to represent 17% of each bioregion to meet the CBD's ecosystem representation goal (Commonwealth of Australia 2015). Other types of data may be used to best represent 'ecosystems' in other national contexts. We refer hereafter to our selected units as 'ecosystems' to allow for a more universal interpretation. Each ecosystem received an upper target representing 17% of its area, and a range of smaller target sizes was also explored.

We considered the distributions of 1,320 extant terrestrial species listed under the Environmental Protection and Biodiversity Conservation Act (EPBCA). We used maps of species' distributions at a resolution of approximately 10 km², developed for extant threatened species available in the Species of National Environmental Significance (SNES) database (Commonwealth of Australia 2012). Species-specific targets for each of the 1,320 threatened species were set based on geographic range size and level of endangerment (Watson et al. 2011; Polak et al. 2015). These targets scale with geographic range size, requiring species with smaller ranges to be increasingly

well protected (Rodrigues *et al.* 2004a). Critically endangered species and/or those with a geographic range size of $<1,000 \text{ km}^2$ were set a target of complete coverage (i.e. 100% of remaining distribution area). For species with large range sizes ($>10,000 \text{ km}^2$), the target was set to cover 10% of current range. For species with geographic ranges of intermediate size (between $1,000 \text{ km}^2$ and $10,000 \text{ km}^2$), the target was linearly interpolated between these two extremes (see Polak *et al.* 2015 for details).

For both ecosystems and species we masked out distributions that occurred in cleared areas devoid of native vegetation. Approximately 7% (0.5 million km^2) of Australia is covered by 'cleared areas' which are largely developed for urban or intensive agricultural land use (using a cleared land layer at 100 m^2 resolution in Arc GIS 10.2.2; ESRI 1996). These areas are not currently suitable for conservation through PAs and we were not able to consider the opportunity and financial costs and feasibility of improving their conservation value. For some species, the area of remaining available intact habitat was smaller than their representation target. In such cases, we reduced the target for these species to represent 100% of remaining available intact habitat. Thirteen of our 1,320 species had none of their distribution within areas that were considered intact and available for conservation. These were counted as gap species and their targets were set to zero. This left 1,307 species as our threatened species target set.

We created a planning unit layer of $10 \times 10 \text{ km}$ grid cells covering Australia, and intersected it with the Collaborative Australian Protected Area Database using PAs with IUCN categories I-IV. This resolution approximately matches the scale of the maps of threatened species (Watson *et al.* 2011) and ecosystems (Fuller *et al.* 2010). We intersected the planning unit layer with the PAs, species distribution and ecosystems layers, to determine the amount of each biodiversity feature in each planning unit and the amount already protected based on spatial overlap.

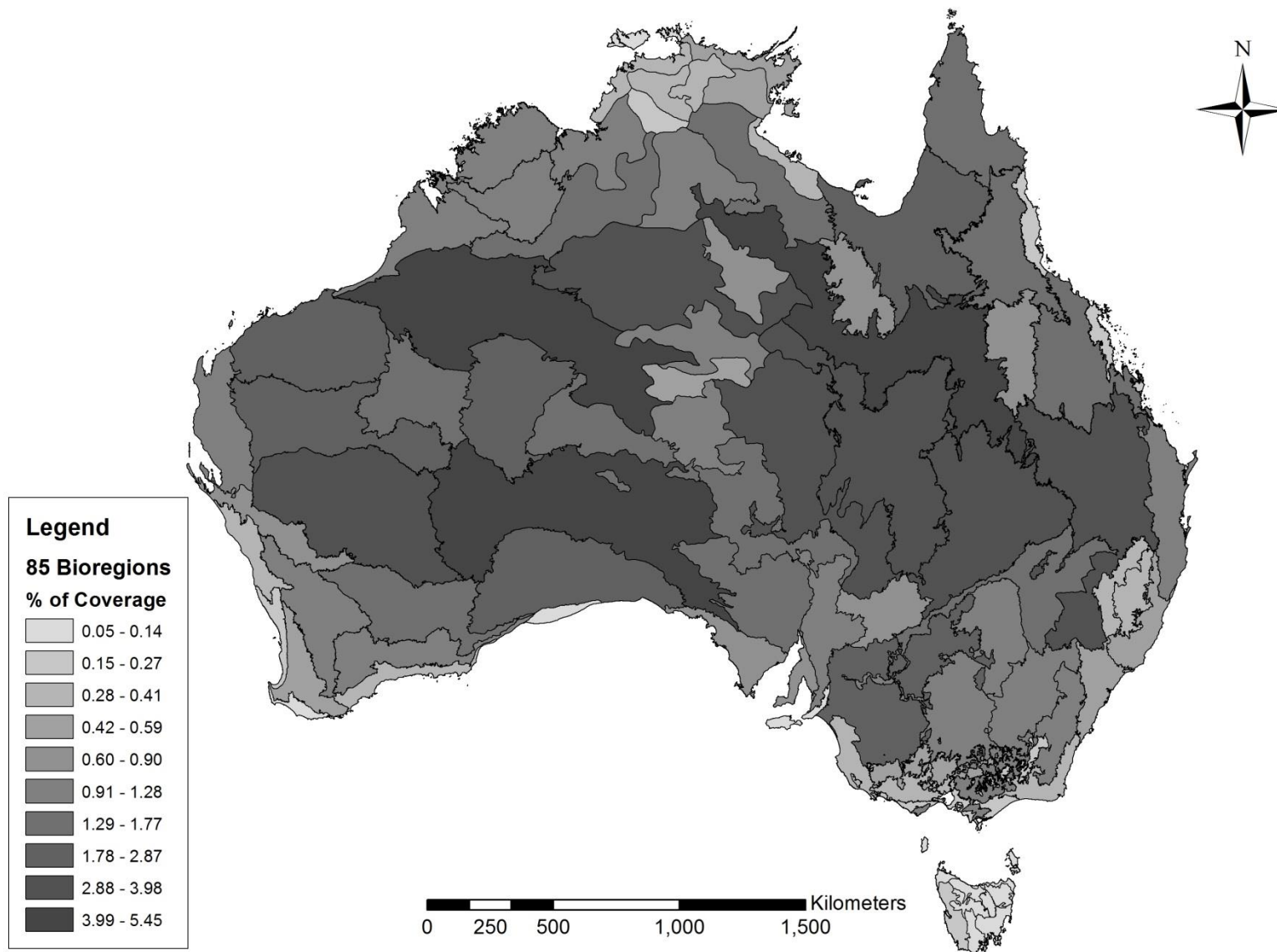


Figure 5.1: The spatial distribution and cover of Australia's 85 bioregions based on the Interim Biogeographic Regionalization of Australia (IBRA bioregions, version 6.1, Steffen et al. 2009).

5.3.2. Trade-off and cost-effectiveness analyses

We used the systematic conservation planning software Marxan (Ball et al. 2009) to identify the efficiency frontier for the trade-off between representation targets for ecosystems and threatened species coverage when expanding Australia's PA network. Marxan is typically used to select multiple alternative sets of areas that meet pre-specified biodiversity targets whilst minimizing overall cost (e.g. Carwardine et al. 2008; Smith et al. 2008; Klein et al. 2009). When investigating trade-offs between the two sets of targets, we locked in the current PA estate (Watson et al. 2011; Polak et al. 2015) and set the cost of each planning unit as the total area potentially suitable for conservation within the planning unit. We assumed that only non-developed areas would be suitable for inclusion in the PA estate and we used area as a surrogate for the costs of PA management (Ball et al. 2009).

To test the trade-off between the target of each ecosystem and threatened species that could be represented, we varied the size of target selected for each feature from 1 to 100% of the original target size, in 1% increments, for all features of the same type (ecosystem or threatened species). We evaluated all combinations of target percentages (e.g. 50% of the original target size for the ecosystem and 10% of the original targets size for the species), giving us 10,000 combinations of target size for the two kinds of features. These percentages of target size are only the minimum level of protection for each run, as Marxan will allow for more protection if it comes at no extra cost. Since there are ~1,300 biodiversity features, many with overlapping distributions, representation above a target level is common because some planning units containing an over-represented feature are critical for meeting targets for other features. Lastly, for ease of interpretation of the results, we translated the percentage of target size for ecosystems to percentage of ecosystem area (i.e. 60% of the 17% target is 10.2% of the size of the ecosystem). We did this for ecosystems only as their target is uniform (17% of each ecosystem's area), while species targets are species-specific (see above).

For each of the target combination runs we identified 100 alternative PA networks and used the most efficient solution (i.e., the one that meets all targets at the lowest cost) in our analysis. We built trade-off curves between the protection of ecosystems and threatened species under four scenarios based on differing sizes of PA networks: 15%, 17%, 19% and 21% of the land area of Australia. For each scenario we only recorded the unique combinations (out of 10,000) of target percentages that met the scenario's area constraints. Of those, we recorded how many of the targets for each set were met to 99.9% or above for each unique combination of target percentage. These results created a trade-off curve that provides the efficiency frontiers of the non-dominated

solutions: all points on the top edge of the curve cannot be out-performed by any other point. We also tested how much area of terrestrial Australia is needed to reach every target in full for both kinds of conservation features.

A J-shaped trade-off curve can indicate the existence of a “win-win” solution, where we can achieve relatively high percentages of both targets within the limitation of the set reserve area. To find the points that represent the most cost-efficient “win-win” solutions, we calculated the cost-efficiency of each point, which is the benefit (sum of the two percentages of targets met for species and ecosystems) divided by the area-based cost (i.e. the percentage of Australia’s terrestrial area that was used to limit the analysis). Although each point on the efficiency frontier is optimal for the set of targets it meets, the most cost-efficient points provide the greatest feature coverage per unit area protected. The most cost-efficient points were compared within and between the scenarios. We plotted the benefit/cost value of each point along each efficiency frontier against the area constraint of each scenario to compare each area constraint in terms of overall value for investment.

5.4. Results

Expanding Australia's current PA network to meet 100% of all species and ecosystem targets requires 24.4% of the total land area, which is much higher than the minimum 17% recommended by the CBD and the area constraints we tested (15-21%). We identified clear trade-offs between target sizes for threatened species and ecosystems, for all four area-constrained scenarios. For each scenario only a few hundred (out of the 10,000) runs met both the area constraints' restrictions and all their targets (Figure 5.2a-d).

All scenarios displayed J-shaped efficiency frontiers, indicating the potential for finding win-win combinations of target sizes for ecosystems and threatened species (Figure 5.3a). When the analysis was limited to 15% of Australia's land area, the most cost-efficient points corresponded to protecting between 7.14-7.8% of the area for each ecosystem and 54-58% of each species' area target. When following a common interpretation of Aichi Target 11's areal goal of protecting 17% of terrestrial area, the most cost-efficient points corresponded to ecosystem protection of at least 8.7-9.5% of the area for each ecosystem and threatened species protection of at least 75-80% of each species' target. A higher total PA network size of 19% of Australia improves representation of features to at least 81-82% of each species' area target and 12.5-12.8% of the area for each ecosystem. Finally, when the size constraint is at 21% of the land area of Australia, 88-90% of species targets could be met along with the coverage of 15-15.3% of the total extent of each ecosystem.

The cost-effectiveness of the optimal points along each efficiency frontier varied with the area constraint and the combination of target percentages represented (Figure 3b). The area constraint that gives the point with the highest cost-effectiveness ratio is 21% of Australia, at the point of representing ~15% of the ecosystems. While a PA of 24.4% could meet all targets, the targets met per unit PA were slightly lower.

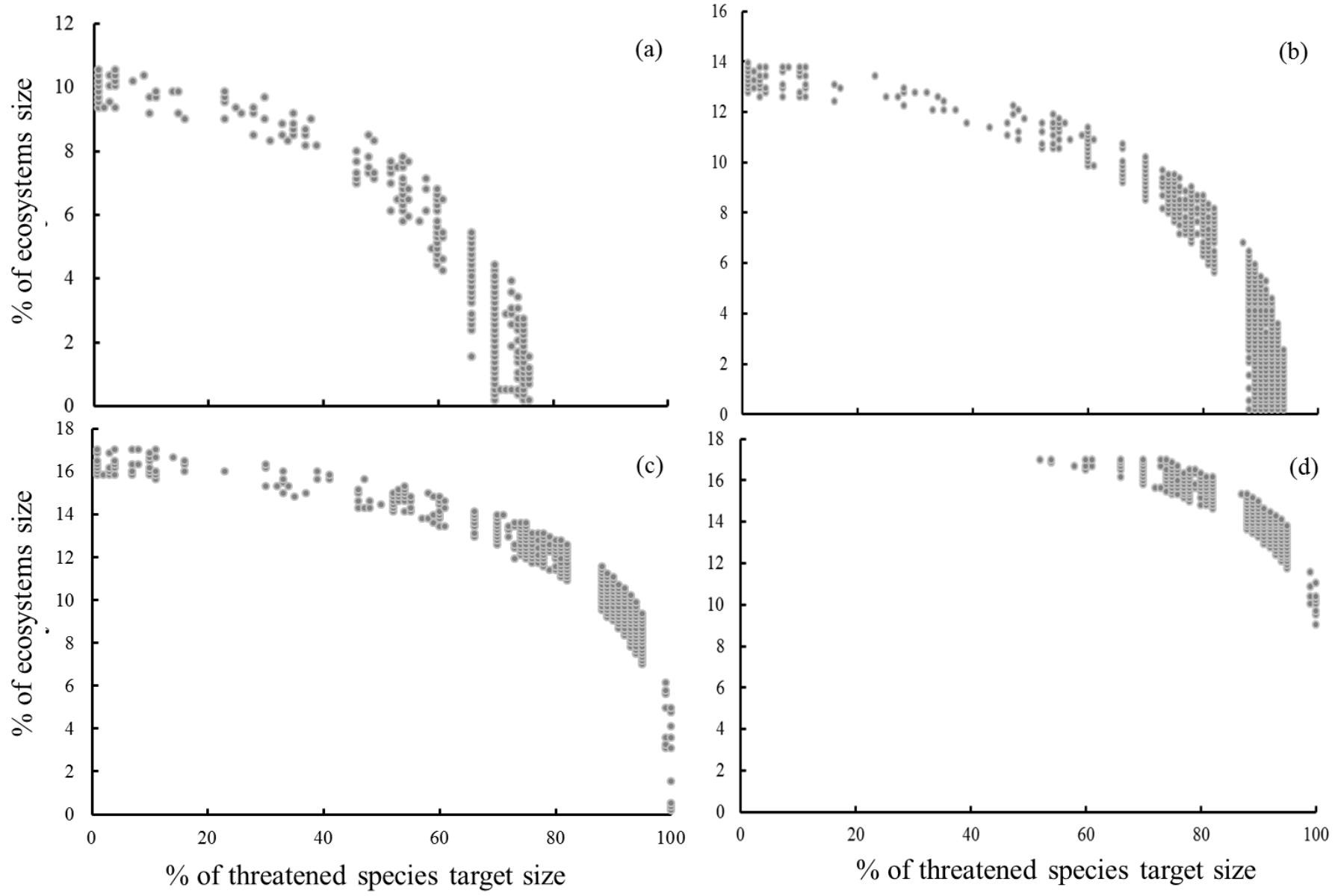


Figure 5.2: Trade-off curves between target size of species versus target size of ecosystems in a protected area network the size of: a) 15%, b) 17%, c) 19% and d) 21% of Australia’s land area. Grey points represent solutions that met the area constraints and met all their targets to a level of 99.9%.

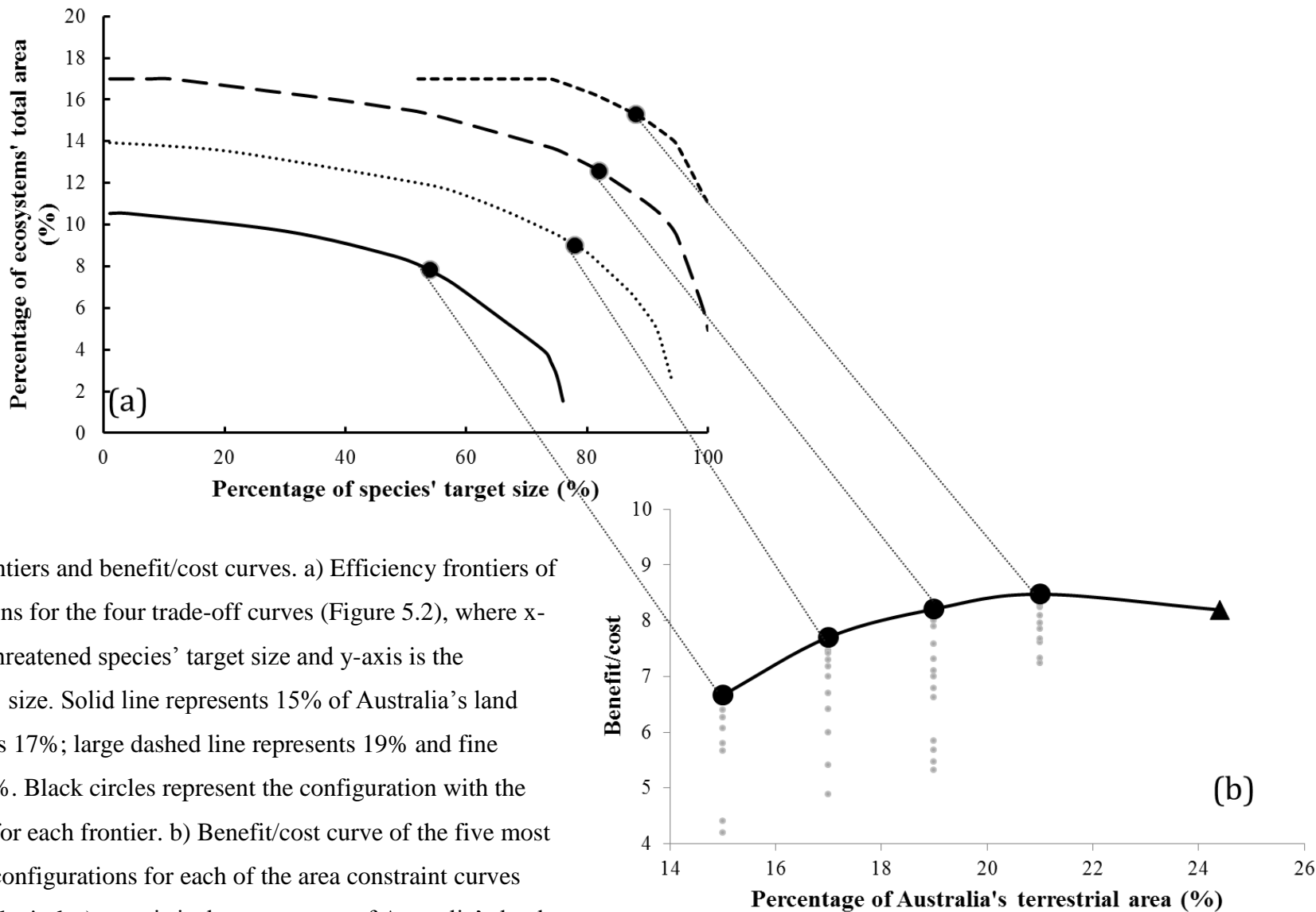


Figure 5.3: Efficiency frontiers and benefit/cost curves. a) Efficiency frontiers of the non-dominated solutions for the four trade-off curves (Figure 5.2), where x-axis is the percentage of threatened species' target size and y-axis is the percentage of ecosystems' size. Solid line represents 15% of Australia's land area; dotted line represents 17%; large dashed line represents 19% and fine dashed line represents 21%. Black circles represent the configuration with the highest benefit/cost ratio for each frontier. b) Benefit/cost curve of the five most cost-efficient percentage configurations for each of the area constraint curves from Figure 5.3a (the black circles): x-axis is the percentage of Australia's land area and y-axis is the combined target size percentages over the percentage of Australia's land area. Small light grey circles below each of these represent the benefit/cost values of the rest of the points along the efficiency frontier. Black triangle represents the point where both sets of targets are at 100% (24.4% of Australia's land area).

5.5. Discussion

We provide a clear and systematic approach to show how to maximize both ecological representativeness and threatened species' coverage in a PA network within a constraint on the total size of the PA system within a country. This enables decision makers to operationalize the dual goal of adequately protecting important habitats for threatened species and achieving ecosystem representation in the global PA network, which is at the heart of the CBD strategic plan (CBD Secretariat 2010). Our approach provides trade-off curves for a wide range of optimal solutions (Polasky et al. 2005) allowing decision makers to choose between different configurations of target sizes within the constraints they set on the size of their PA network. For example, placing 17% of terrestrial Australia in PA can at best achieve 9% representation of all ecosystems and at the same time achieve at least 78% of each threatened species' habitat target. This is well short of what is needed to meet Australia's obligations under the CBD, but maximizes the benefits of a size-limited total PA estate.

We found that amongst the multiple solutions along the efficiency frontier for each area-constrained scenario, there was a large range of cost-efficiency in terms of how many targets can be met in a limited area. Within each area-constrained scenario, the most cost-efficient points are the ones nearest the inflection point of the J-shaped frontiers, and cost-efficiency declines away from these win-win points (Polasky et al. 2005). When comparing between the different area-constraint scenarios (Figure 3b), we can see that the maximum cost-effectiveness increases slightly as more area is available for PA expansion, up to 21%, and then declines. This is likely because as more area becomes available there is more opportunity to select efficient areas that can protect multiple biodiversity features. Once the PA is above 21%, the more efficient and compact options for meeting targets will already be protected and gaining the remaining land required to meet the final parts of targets will require larger areas, resulting in less efficient PA networks.

Although the work we present here is based on information from one country, many of the same challenges faced by land management agencies in Australia occur in other countries (Waldron et al. 2013; Venter et al. 2014; Di Marco et al. 2015). This is because countries are challenged by the goals of meeting their current CBD and country-level PA targets (Waldron et al. 2013; Walsh et al. 2013). There is a clear need for systematic thinking around targets for species and ecosystem representation, and transparent analysis of the likely compromises between species-based and area-based objectives (Di Marco et al. 2015). The overall lesson from our study is that even when countries cannot reach full protection, it is still possible to make progress toward the targets

logically and efficiently. Our approach can assist countries in deciding where and how to focus PA expansion efforts given a particular set of geographical and financial constraints.

Where possible, countries should employ spatial information on both ecosystems and threatened species to create their country-specific trade-off curves. If the two sets of targets (Targets 11 and 12) are relatively well aligned, the shape of the curve will exhibit a strong J-shape, making both targets easier to meet. However, if the two sets are relatively discordant, the curves will be closer to linear, and it will be more challenging and area-intensive to represent both sets of targets in a PA network. In many countries, distributions of threatened species reflect current and past land-use histories (Taylor et al. 2011). This may lead to spatial alignments between the two target types, where remaining threatened species' habitats overlap with the remnants of heavily impacted ecosystems. However, the financial and/or opportunity costs of PA networks in these cases may be relatively high due to the fact that heavily impacted ecosystems are often productive for other uses. In such cases it may be useful to investigate trade-off curves that consider costs as well as area.

Protecting threatened species typically requires a range of management actions, including PA establishment. Decisions on allocating resources amongst threatened species should consider how important PAs are for ensuring threatened species' persistence. For example, in New Zealand the highest priority action to conserve threatened species is predator control (Dowding and Murphy 2001; McGuinness and Carl 2001). Expanding PA's alone will not adequately protect threatened species unless resources for predator control are built into PA management plans. As such, when planning PA expansion, New Zealand may prioritize the representation of ecosystems in PAs to meet Target 11 (i.e. points on the upper left of the efficiency frontier in Figure 5.3), while constructing separate threatened species management plans to meet the goals of Target 12.

We have addressed the trade-off between two of the fundamental goals of the CBD, the representation of ecosystems and threatened species through PA expansion. Further trade-offs also exist in the protected area planning process. For example, a potential trade-off exists within Target 11 between representing ecosystems and 'areas of importance for biodiversity and ecosystem services'. Further, a synergy exists between protecting threatened species (Target 12) and reducing the rate of loss of natural habitat (Target 5), as identified by Di Marco et al. (2015). There is also a trade-off between protecting existing habitat and restoring some currently unsuitable habitat, especially for species with very limited suitable habitat remaining. Understanding and incorporating multiple trade-offs will improve the effectiveness of implementing the CBD targets. Our approach can be modified to include additional criteria for making informed and optimal decisions when reality demands compromises among various biodiversity goals in PA estates.

Planning for PAs is a dynamic process. The CBD targets have adjusted with time - between 2004 and 2010, CBD targets for global PA's increased from 10% to 17% - and are likely to continue to change, along with countries' capacity to meet them (Noss et al. 2012). Changes in species' conservation status will occur and better data on species distributions and their responses to management are likely to become available in the future. For example, there is currently a taxonomic bias in threatened species listing, with many invertebrates missing (Walsh et al. 2013). The inclusion of more invertebrate species targets is likely to increase the area or resources required for their protection; however, further research is required to determine how well aligned the important areas for invertebrates with existing priority areas. Countries can use our approach to accommodate such changes, by re-evaluating the progress of protected areas against new goals and information as they arise.

Chapter 6: Discussion

In this thesis, I tested the cost-effectiveness of moving between fine- and coarse-scale features in conservation planning. To do that, I examined two common conservation problems: 1) mitigating the effects of roads on wildlife (**Chapters 2-3**); and 2) protected area network planning (**Chapters 4-5**). Specifically, I tested how moving from the fine- to the coarse-scale conservation features used in the planning process affect the outcome's cost-effectiveness. Since the two conservation problems presented in this thesis are quite different, I will use this chapter to discuss the common understanding gained from the results of both problems. I will also deliver a synthesis on how this research can be carried forward to continue filling the many gaps in our understanding of the cost-effectiveness of up-scaling in conservation.

6.1. Common understandings

As discussed above both problems presented in this thesis are quite different but there are some similarities. First and foremost is the fact that these two problems are both related to conservation planning and how to optimize the utilization of resources (e.g. funds, land, etc.) to achieve maximum biodiversity benefit. This is a vital concern in conservation, because resources are limited and biodiversity loss is still accelerating (Game et al. 2013). As such, deciding how to spend scarce conservation resources becomes all the more important. Due to the limitation in time and resources, scientists are trying to find shortcuts and rules of thumb in order to make the best decision possible. Therefore, the first common point I discuss is a theme that cuts across this thesis: Will moving to coarse-scale conservation efforts be more cost-effective than fine-scale conservation? Indeed, one common point between the two conservation problems I analysed is that both do not fully (or at all) support the cost-effectiveness of coarser-scale conservation. This is more pronounced in the protected areas' planning problem, whereby planning according to the needs of threatened species appears to be more cost-effective than the ecosystem-based planning suggested by the CBD (Chapter 4). In the problem of optimal road mitigation this is less pronounced but still apparent, because while planning for multiple species was more cost-effective than planning for individual species separately, the focal species I chose were only weakly supported.

In my opinion, information (and its availability) is the chief reason that my results did not support the cost-effectiveness question of coarser-scale conservation. One advantage of coarser-scale features is that it is relatively cheaper and quicker to gain information on coarser features than finer ones. When fine-scale information is lacking, up-scaling might be more cost-effective because collecting new information requires time and money (Runge et al. 2011, Runting et al. 2013, Maxwell et al. 2015), which may not be available within the timeframe and/or budget allocated for a project. For example, when a new road is built there is limited time for consultants to give their recommendations on mitigation measures. Thus, conducting the necessary population research on all the local wildlife might not be feasible, making the multispecies method I suggested in Chapter 3 often impractical.

However, while that may be true when information is lacking, the scientific world has gathered an enormous amount of information that can and should be used in conservation planning. The PanTHERIA database for life histories of mammals (Jones et al. 2009) and the IUCN red list for threatened species (IUCN 2014) are two examples of freely available information. Notably, for both the conservation planning problems presented in this thesis there was no *in situ* information gathering, and while data assembly still requires time and money (in this case, in the form of a PhD scholarship), it is considerably less expensive than collecting the actual empirical data itself. In both situations, it is worthwhile using all available information – there are no shortcuts. Again, this is more apparent in the second problem of protected area planning (Chapters 4-5), where the main recommendation was to use both species and ecosystem datasets simultaneously (Chapter 4). This is also true for the optimal road mitigation problem, where one of my main recommendations is to use information about as many species as possible (i.e. the multispecies approach, Chapter 3). While there were some focal species that may represent the needs of the community, I found that these should only be used in situations where there are limitations in time and/or money (i.e. when information is lacking and there is not enough time or funds to collect it).

That said, there are many situations where new data are needed in order to sufficiently plan conservation actions (Runge et al. 2011, Runting et al. 2013). In these cases, using coarser-scale features might be more cost-effective. However, in the two examples I presented in this thesis this avenue was not explored. So, I can state that from my own work, up-scaling from fine- to coarse-scale features is probably not cost-effective (Chapter 4) or is only partially cost-effective (Chapter 3). I recognize that additional work is necessary on how information gathering affects the cost-effectiveness of this form of up-scaling from fine to coarser features. Using value-of-information approaches, which assess how the benefit will increase by collecting more data (Yokota and Thompson 2004, Maxwell et al. 2015), are particularly promising avenues to consider.

Road mitigation planning is one area where information and problem solving methods need to be made available globally soon. Roads are often built quickly, and scientists and consultants are often requested to deliver swift recommendations about future mitigation measures before the new road is built, meaning that time and money are of the essence. As such, acquiring new information about local biodiversity that will affect decision-making might not be possible. Hence, while I did recommend using data on multiple species to plan mitigation measures (Chapter 3), I did not take into account the investment needed to acquire the information required for the model. Rather, I used the literature to acquire that information, but in some cases we may need further empirical research. This will probably increase the cost of the multispecies approach and hence reduce its cost-effectiveness, maybe to the point where other strategies (i.e. focal species) are preferred. Indeed, I identified a possible focal species (i.e. the species with the largest home range) that is not as cost-effective (as the multispecies approach) but can be used when time or money is limited.

Another common theme between the two problems discussed in this thesis is that both examine optimal planning through the creation of cost-effective decision making tools. In Chapter 2, I presented a way to optimally plan cost-effective mitigation measures to reduce the impact of roads on wildlife. For this, I used a single threatened population of koala, for which road kill is the second largest cause of death (Rhodes et al. 2011). I was able to use this tool in Chapter 3 to determine the cost-effectiveness of up-scaling to coarser-scale conservation when planning road mitigation measures for multiple species and focal species, whereas in the problem for protected areas' network, I did the reverse and first tested the cost-effectiveness of up-scaling (Chapter 4). Later, I looked at providing a set of trade-off curves that may be used as planning tools for countries that are struggling to find the budget and/or area to meet the CBD's targets (Chapter 5).

Like many other studies that introduce new methods and ideas in conservation biology, the case studies I selected were simplified (e.g. Nicholson et al. 2006, Maxwell et al. 2015). In Chapter 2, I present an optimization method that is new in road ecology. To present the method I had to simplify it to a small area and a small population of koalas. However, the method can be adapted to fit other systems and species. In Chapter 3, I used a simulated landscape and a metapopulation model of mean time to extinction (Frank and Wissel 2002), which was different from the population simulation model used in Chapter 2. However, this model had shortcomings as well, again in the relatively small spatial scale of the simulated landscape. These were dictated by the requirements of the metapopulation model, which did not allow for a large distinction between patch size and home range size of the tested species. This is because the model determines the population size (which will reflect on the probability of persistence) by the number of territories that can fit in a patch. Thus, if a species has a very small home range compared to the patch size, it will never have a

chance to go extinct or venture from the patch to the others in the system, because the in-patch population is large enough. On the other hand, if a species has a very large home range compared to the size of the patches in the system, it will always go extinct because in the whole system there will be room for maybe one or two individuals. Hence, all species in the system had to have a home range that was at a similar scale (i.e. 0.5-10 ha) to the smallest patch in the system. Migration from outside the system, age-based dispersal, species-specific mitigation measures and real-set landscape were not incorporated into this model.

A new method can be a model or a tool, such as the problem formulation presented in Chapters 2-3, but it can also be presented in a more abstract way in order to convey ideas and understanding to decision makers. For example, in the protected areas planning problem I state that simultaneously planning using both species-based and ecosystem-based conservation features will provide the most cost-effective results for the expansion of Australia's protected areas network (Chapter 4). However, when planning the protected areas expansion I did not include other elements such as stakeholders, connectivity, labour, actual land costs (area and agricultural opportunity costs were used as surrogates), planning and implementation costs. Nonetheless, the cost-effectiveness insights delivered from this chapter are important for the implementation of the CBD targets. Moreover, in Chapter 5, I presented an approach that will allow countries to reach compromises and still remain within the limitation of their budget. This approach uses existing tools (in this case, Marxan) to create trade-off curves to assist decision makers. While Australia's trade-off curves probably cannot be used as rules of thumb for other countries, the method itself can create country-specific trade-off curves according to the available biodiversity information and budget limitations.

In addition, a common problem that arises from trying to determine cost-effectiveness in conservation actions is the problem of accurate costing. In my thesis, I use infrastructure costs (Chapters 2-3) that are incomplete, and substitutes that represent costs (i.e. land area or agricultural miss opportunity costs in Chapter 4-5). Cost surrogates can influence the accuracy of the results (Carwardine et al. 2008b). Some problems arise due to lack of data, while others are due to incomplete reporting of bottom line dollar figures (Lindsey et al. 2005). Dollar figures are difficult to transfer among locations and systems. For example, in Australia, labour costs are amongst the highest in the world. A dollar figure from a particular action taken in the Amazon will not be transferable to Australia. The optimal road mitigation is a good example of this, as the only information available was the total dollar value of each mitigation measure infrastructure and a maintenance cost. However, as these costs went across all mitigation configurations (Chapters 2-3) and were used to compare between these configurations, I am confident that the comparative cost-effective results are accurate, even if the actual costs are not usable for actual planning. When

testing cost-effectiveness of protected area expansion I used a less accurate cost surrogate: land area. The use of land area as a cost surrogate is very common in conservation, although I acknowledge it as a potential limitation (Naidoo et al. 2006, Carwardine et al. 2008b).

6.2. Future directions

6.2.1. Optimal road mitigation

The impact of roads on wildlife is a growing problem, which is expected to increase (Laurance and Balmford 2013). Finding how best to utilize resources for mitigating the effects of roads on wildlife is a crucial conservation problem. In this thesis, I developed a method that allows decision makers to choose the most cost-effective road mitigation option to reduce impacts on wildlife populations. While this method worked well for single and multiple species, the spatial scale of the problem was small; only a few kilometres of roads were managed in the analysis due to the exponential increase in planning possibilities when the number of roads in the system increases. This means that there is a need to incorporate this problem into an algorithm that can deal with a greater number of possibilities. One example is simulation annealing, which is used by Marxan to assist in spatial planning (Ball et al. 2009). Simulated annealing is able to address large numbers of possibilities and find a good approximate to the optimal solution (Ball et al. 2009). Using this or a similar algorithm might be necessary in order to make this method into a tool that can produce recommendations on a larger spatial scale than the one I presented here.

In addition, while I did solve the problem of planning mitigation for multiple species (Chapter 3), the limitation in the metapopulation model that I used dictated using species with small-to-medium body size and relatively similar home ranges and dispersal distances. However, in the real world, roads affect species with diverse life history traits (Rytwinski and Fahrig 2012) and planning will have to take all species into account. This means that to follow my recommendation on multiple species planning there is a need to develop a more robust model that can calculate the biological benefit while accounting for a larger variety of species with different life histories.

6.2.2. Protected areas planning

There are 193 member nations in the CBD that are obligated to meet the CBD's targets, which, if implemented, will lead to an historic increase in protected areas (Venter et al. 2014, Watson et al. 2014). Moreover, this will probably be the largest establishment of protected areas to use systematic planning. In this thesis, I used Australia as a case study (Chapters 4-5) to test the cost-effectiveness of protected area expansion when considering Aichi Target 11 (ecosystem approach; CBD Secretariat 2010, Woodley et al. 2012) and Target 12 (halting the decline of threatened species; CBD Secretariat 2010). While Australia is a large continental country and I believe that it can reflect similar patterns in other countries, if not globally, I have not tested this. Thus, an additional up-scaling should be in the spatial scale of the problem, to see if these cost-effectiveness patterns will hold for different countries and globally. Future research may be able to determine a typology of countries by their available data, existing protected area system and remaining land available for conservation. If one size does not fit all there might be several types of cost-effectiveness relationships between these targets that may be revealed.

In addition, in this thesis I provided insights as to how to increase the effectiveness of the expansion of protected areas to meet two of the CBD's targets – Target 11 and Target 12. However, the CBD has 20 targets of which six require setting aside areas for protection or restoration. For example, Target 15 is aimed at enhancing ecosystems that retain high carbon stocks and Target 5 is aimed at reducing the loss of natural ecosystems (CBD Secretariat 2010). While there have been a few publications recently that tested the feasibility and cost-effectiveness of different elements of the CBD, including some synergy analysis between several targets (Di Marco et al. 2015), to date none has considered the plan as a whole. Since these targets are not mutually exclusive, there is a high probability that some targets will support each other (Marques et al. 2014, Di Marco et al. 2015), while others may cause us to take very different actions. As 2020 approaches, it is becoming clear that the CBD's targets are not going to be met (Tittensor et al. 2014); moreover, it is becoming clearer that new and ambitious targets are expected (Di Marco et al. 2015). Given these trajectories, there is a need to increase the efficiency and cost-effectiveness of the CBD's strategic plan (CBD Secretariat 2010). One way of achieving this is to continue looking for synergies and trade-offs between targets (Di Marco et al. 2015, Chapter 4-5). This can also be viewed as a type of up-scaling in conservation because we increase the number of targets and try to find a cost-effective solution that will address the requirements of all targets.

Lastly, protected areas, while important, are not the only action that can or should be taken. Indeed, Wilson et al. (2007) found that applying multiple actions can be more cost-efficient than

land acquisition alone, while Barr (2012) found that ~26% of Australia's threatened species are not affected at all by protected areas. Restoration, invasive species eradication, fire management, pest management, reintroduction, and translocation are some of the actions that can be taken. Some features (especially species but some ecosystems as well) may benefit more from actions combining several conservation practices rather than land acquisition alone. As such, it is possible to expand the analysis presented in Chapter 4 to include multiple conservation actions for both targets (Wilson et al. 2007).

6.2.3. Moving from fine- to coarse-scale in conservation

As I stated previously, I believe that one of the reasons I did not find up-scaling from fine to coarse features cost-effective is the fact that I used available information. Conservation of coarser features is believed to be more cost-effective due to the fact that it is relatively easier and cheaper to gain information. However, it was found by myself (Chapters 3-4) and others (Runting et al. 2013) that easier, cheaper information might not provide the best output. However, the cost and the time needed to obtain more information may outweigh this. Runting et al. (2013) is the first study I have found that used value-of-information to test the cost-effectiveness of gathering new data to solve a conservation planning problem. Here, as well, they found that using less complex data and models were not cost-effective even when there are high costs of information gain. However, I believe that there is still much more to learn on this subject to see how the value of perfect information (EVPI) and expected value of perfect partial information (Yokota and Thompson 2004) can change the cost-effectiveness of moving from fine- to coarse-scale conservation. For example, what fraction of the ecological community is enough to provide a good representation for the multispecies analysis? Will gaining additional information on more species increase the cost-effectiveness of conservation, or is there a point at which gaining more information will not increase cost-effectiveness?

6.3. Final remarks

Biodiversity loss increases every day and human population growth demands more and more resources, meaning that conservation biologists need to find fast and smart solutions to reduce this decline. However, to make smart decisions we need information, which also requires time and money, necessitating some shortcuts. Up-scaling from fine to coarser target features can be thought

of as a way to look for shortcuts for both information gathering and implementation (e.g. protecting an ecosystem will protect species and processes: one action to achieve many goals). While in my own work I did not find that these shortcuts worked well, there may be many situations where shortcuts are necessary. Using a bad shortcut can be more wasteful (Chapter 4) than spending the necessary time and funds to collect the correct data and work at the right scale (Runting et al. 2013). This thesis represents one of the first works on cost-effectiveness of up-scaling fine- to coarse-scale features in conservation and it is just a small step in our understanding of this subject.

Lastly, this thesis is about moving between fine and coarse features in conservation and the cost-effectiveness of planning for either. However, there might be a middle way to achieve conservation goals. Indeed, in some cases a combined approach of coarse- and fine-scale working together is appropriate (Noss 1987, Tracy and Brussard 1994, Poiani et al. 2000, Lindenmayer et al. 2007). My own work is an example of that, with simultaneously planning being the most cost-effective for reserve expansion or multispecies planning being optimal for road mitigation. While both problems still required complete information for both fine and coarse scales, that information was not empirically collected. This means that if we find a way that reduces the amount of effort in collecting the information needed while still maintaining similar outcomes, there can truly be a middle way, =a compromise and a shortcut.

Chapter 7: Reference List

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8. Appendixes

8.1 Chapter 3 appendix

Table S3.1: Model system road attributes.

Road #	Length (m)	Traffic density (Average hourly)	# of lanes	Between patches	Type of road
1	316.2	2000	2	1-3	City road
2	316.2	2000	2	1-2	City road
3	632.5	2000	4	2-4	Highway
4	316.2	1500	4	3-5	Highway
5	632.5	1500	4	3-4	Highway
6	632.5	1000	4	4-6	Highway
7	316.2	500	2	5-7	Suburban road
8	1264.9	500	2	5-6	Suburban road
9	632.5	500	2	6-8	Country road
10	2529.8	200	2	7-8	Country road

Table S3.2: Model parameters for the study species

Species common name	Species scientific name	Home range Ha (H_k)	Fecundity (γ_k)	Dispersal distance km (d_k)	Extinction- area exponent (x_k)	Road edge effect m (h_k)	Species length m (l_k)	Species velocity mhr ⁻¹ (v_k)	Continent	Source
Australian species										
Greater glider	<i>Petaurus volans</i>	3 ^a	0.15 ^a	2 ^a	0.87 ^a	188.4	0.43	6126.9 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
Mountain brushtail possum	<i>Trichosurus cunninghami</i>	4 ^a	0.12 ^a	5 ^a	1.00 ^a	251.2	0.5	7561.9 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
Common ringtail possum	<i>Pseudocheirus peregrinus</i>	2 ^a	0.4 ^a	0.85 ^a	0.78 ^a	125.6	0.35	5993.5 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
Common brushtail possum	<i>Trichosurus vulpecula</i>	4 ^a	0.45 ^a	1 ^a	1.30 ^a	251.2	0.4	7561.9 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
Red-browed treecreeper	<i>Climacteris erythrops</i>	10 ^a	0.55 ^a	1 ^a	1.20 ^a	628	0.15	8289.6 ^c	Australia	^a (Nicholson et al. 2013) ^c (Alerstam et al. 2007)
White throated treecreeper	<i>Cormobates leucophaea</i>	5 ^a	0.41 ^a	5 ^a	1.40 ^a	314	0.1	7863.9 ^c	Australia	^a (Nicholson et al. 2013) ^c (Alerstam et al.

Laughing kookaburra	<i>Dacelo novaeguineae</i>	5 ^a	0.35 ^a	20 ^a	1.60 ^a	314	0.45	9071.2 ^c	Australia	2007) ^a (Nicholson et al. 2013) ^c (Alerstam et al. 2007)
Sacred Kingfisher	<i>Todiramphus sanctus</i>	7.5 ^a	0.7 ^a	15 ^a	1.15 ^a	471	0.23	8605.2 ^c	Australia	^a (Nicholson et al. 2013) ^c (Alerstam et al. 2007)
Bush rat	<i>Rattus fuscipes</i>	0.2 ^a	1.25 ^a	0.1 ^a	0.72 ^a	12.56	0.4	4612.8 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
Agile antechinus	<i>Antechinus agilis</i>	1 ^a	1.20 ^a	5 ^a	0.45 ^a	62.8	0.2	3094.0 ^b	Australia	^a (Nicholson et al. 2013) ^b (Garland 1983)
<hr/>										
European species										
<hr/>										
European rabbit	<i>Oryctolagus cuniculus</i>	4 ^d	0.42 ^e	1.4 ^f	0.25 ^g	225.7	0.4 ^d	20000 ^h	Europe	^d (Jones et al. 2009) ^e (von Holst et al. 2002) ^f (Bowman et al. 2002) ^g (Hone 1999) ^h (Rabbit webpage)
European hedgehog	<i>Erinaceus europaeus</i>	7 ^d	0.92 ⁱ	3.78 ^j	1.61 ⁱ	298.6	0.24 ^d	795 ^k	Europe	^d (Jones et al. 2009) ⁱ (Kristiansson 1990) ^j (C Patrick et al.

Red squirrel	<i>Sciurus vulgaris</i>	5 ^l	0.32 ^m	1.57 ^f	0.30 ^m	252.4	0.21 ^d	5625 ^o	Europe	2001) ^k (Hof 2009) ^d (Jones et al. 2009) ^f (Bowman et al. 2002) ^l (Wauters and Dhondt 1992) ^m (Wauters et al. 2004) ^o (Center) ^p (Emys home website) ^q (Rivera and Fernández 2004) ^r (Ficetola and De Bernardi 2006) ^s (Cordero-Rivera et al. 2010) ^t (Aresco and Russell 2005) ^v (Brito 2003) ^u (Brito et al. 2003) ^w (Pleguezuelos et al. 2007) ^x (Miras et al. 2009)
European pond turtle	<i>Emys orbicularis</i>	0.5 ^p	0.23 ^q	1 ^r	1.22 ^s	97.8	0.2 ^p	3 ^t	Europe	
Lataste's viper	<i>Vipera latastei</i>	0.24 ^v	0.26 ^{u,w,x}	0.26 ^v	0.15 ^y	55.3	0.46 ^u	146.8 ^z	Europe	

^y(Andrén and
Nilson 1983)
^z(Heckrotte 1967)

Table S3.3 – Model parameters

Parameter	Description
$q_k(\mathbf{S}, T, \mathbf{r})$	Probability of persistence of species k
n	Number of species
k	Individual species
S	A suit of all road segments
s	Individual road segments
r	Combination of road mitigation
t	Terminal run time
B	Monetary budget
x_s	Fence on road segment s
y_s	Wildlife passages on road segment s
$T_k(\mathbf{r})$	Mean time to extinction
M	Number of patches
V_{agg}	Effective local extinction rate
Z	Aggregation of the effective colonization abilities of the subpopulations
v_i	Local extinction rate for patch i
c_{ij}	Colonization rate between patches i and j
A_i	Area of patch i (in ha)
H_k	Species' k home range size
ϵ_k	Extinction-area exponent
h_{ik}	Species-patch specific local road effect
$\beta_s(x_s, y_s)$	Magnitude of the effect in relation to the mitigation actions
l_s	Length of road segment s
d_{ij}	Distance between the centres of patches i and j ,
d_k	Species k dispersal distance
γ_k	Species' k fecundity
p_{ij}	Probability of crossing successfully all the

	roads between patches i and j
$p_s(x_s, y_s)$	Probability of safely crossing road segment s
μ	Hourly traffic volume
W	Width of the road
l_k	Length of species k
δ_k	Velocity of species k

Table S3.4- Individual species' lowest cost mitigation combination that provided 0.9 probability of persistence.

Species name	Road #										Cost (\$)
	1	2	3	4	5	6	7	8	9	10	
Agile antechinus	N	N	N	N	N	N	N	N	N	N	0
Bush rat	N	N	N	N	N	N	N	N	N	N	0
Common brushtail possum	F	F	F	F	F	F	F	F	F	F	13,387,819
Common ringtail possum	N	N	N	N	N	N	N	N	N	N	0
Greater glider	N	N	N	F	N	N	FP	N	N	N	1,315,652
Laughing kookaburra	N	N	N	N	N	N	F	N	N	N	557,825
Mountain brushtail possum	F	F	N	F	N	N	FP	N	FP	N	3,746,955
Red-browed treecreeper	N	N	FP	F	F	FP	F	FP	FP	N	8,609,561
Sacred kingfisher	N	N	N	N	N	F	F	N	FP	N	2,989,129
White throated treecreeper	N	N	N	N	N	N	F	N	N	N	557,825

European rabbit	FP	FP	FP	FP	FP	N	F	N	N	N	5,462,606
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European hedgehog	N	N	N	N	N	N	F	N	FP	N	1,873,477
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Red squirrel	FP	FP	N	FP	N	FP	FP	N	FP	N	5,662,606
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European pond turtle	N	N	N	N	N	N	N	N	FP	N	1,315,652
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Lataste's viper	N	FP	FP	N	N	N	F	FP	N	FP	9,725,212
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The top part (above the dashed line) is the Australian database and the lower half is the European database. N – No mitigation; F – Fence, FP – Fence and a wildlife passage.

Dark grey – largest home range indicator, light grey – smallest fecundity rate indicator

Table S3.5 – Frequency of fences and wildlife passages from the solutions along the efficiency frontier of the two multispecies objective functions

Objective function	Frequency of	Road 1	Road 2	Road 3	Road 4	Road 5	Road 6	Road 7	Road 8	Road 9	Road 10
Expected number of persisting species	Fences	0.36	0.24	0.43	0.84	0.41	0.75	0.98	0.49	0.80	0.14
	Passages	0.14	0.04	0.39	0.47	0.25	0.69	0.69	0.49	0.80	0.14
Expected number of persisting species	Fences	0.77	0.63	0.49	0.91	0.74	0.31	0.97	0.34	0.29	0.03
	Passages	0.71	0.60	0.49	0.69	0.74	0.31	0.54	0.34	0.29	0.03

The top part (above the dashed line) is the Australian database and the lower half is the European database. Dark grey mark roads with a high frequency (≥ 0.8) of fences on that road along the efficiency frontier and light grey represents a high frequency of wildlife passages on the road.

Table S3.6: Mitigation configuration for the five scenarios tested in the cost-effectiveness analysis for each species set and the configurations that provided 0.9 probability of persistence at the lowest possible cost.

Scenario/Species Name	Road										Cost (\$)	Expected number of persisting species
	1	2	3	4	5	6	7	8	9	10		
Multispecies	N	N	N	F	N	F	F	FP	FP	N	5,978,258	8.63
Red-browed treecreeper	N	N	FP	F	F	FP	F	FP	FP	N	8,609,561	8.89
Mountain brushtail possum	F	F	N	F	N	N	FP	N	FP	N	3,746,955	7.43
Single species accumulative	F	F	FP	F	F	FP	FP	F	FP	F	14,187,819	8.59
Single species	F	F	FP	F	F	FP	FP	F	FP	F	31,164,766	8.59
Greater glider	N	N	N	F	F	F	FP	N	N	N	1,315,652	6.31
Common ringtail possum	N	N	N	N	N	N	N	N	N	N	0	3.51
Common brushtail possum	F	F	F	F	F	F	F	F	F	F	13,387,819	5.46
White throated treecreeper	N	N	N	N	N	N	F	N	N	N	557,825	5.62
Laughing kookaburra	N	N	N	N	N	N	F	N	N	N	557,825	5.62
Sacred kingfisher	N	N	N	N	N	F	F	N	FP	N	2,989,129	7.47
Bush rat	N	N	N	N	N	N	N	N	N	N	0	3.51
Agile antechinus	N	N	N	N	N	N	N	N	N	N	0	3.51
Multispecies	FP	FP	FP	FP	FP	FP	F	FP	FP	N	10,525,213	4.32
European hedgehog	N	N	N	N	N	N	F	N	FP	N	1,873,477	1.94
European pond turtle	N	N	N	N	N	N	FP	N	N	N	757,825	1.37

Single species accumulative	FP	FP	FP	FP	FP	FP	FP	FP	FP	FP	15,987,819	4.32
Single species	FP	FP	FP	FP	FP	FP	FP	FP	FP	FP	30,617,812	4.32
European Rabbit	FP	FP	FP	FP	FP	FP	F	N	FP	N	8,093,909	3.63
Red Squirrel	FP	FP	FP	FP	FP	FP	FP	FP	FP	N	10,725,212	4.42
Latastes' viper	N	N	FP	N	N	N	N	FP	N	FP	9,167,987	1.91

Top half – the Australian database; bottom half – the European database. N – No mitigation; F – Fece, FP – Fence and a wildlife passage.

Dark grey – largest home range indicator, light grey – smallest fecundity rate indicator

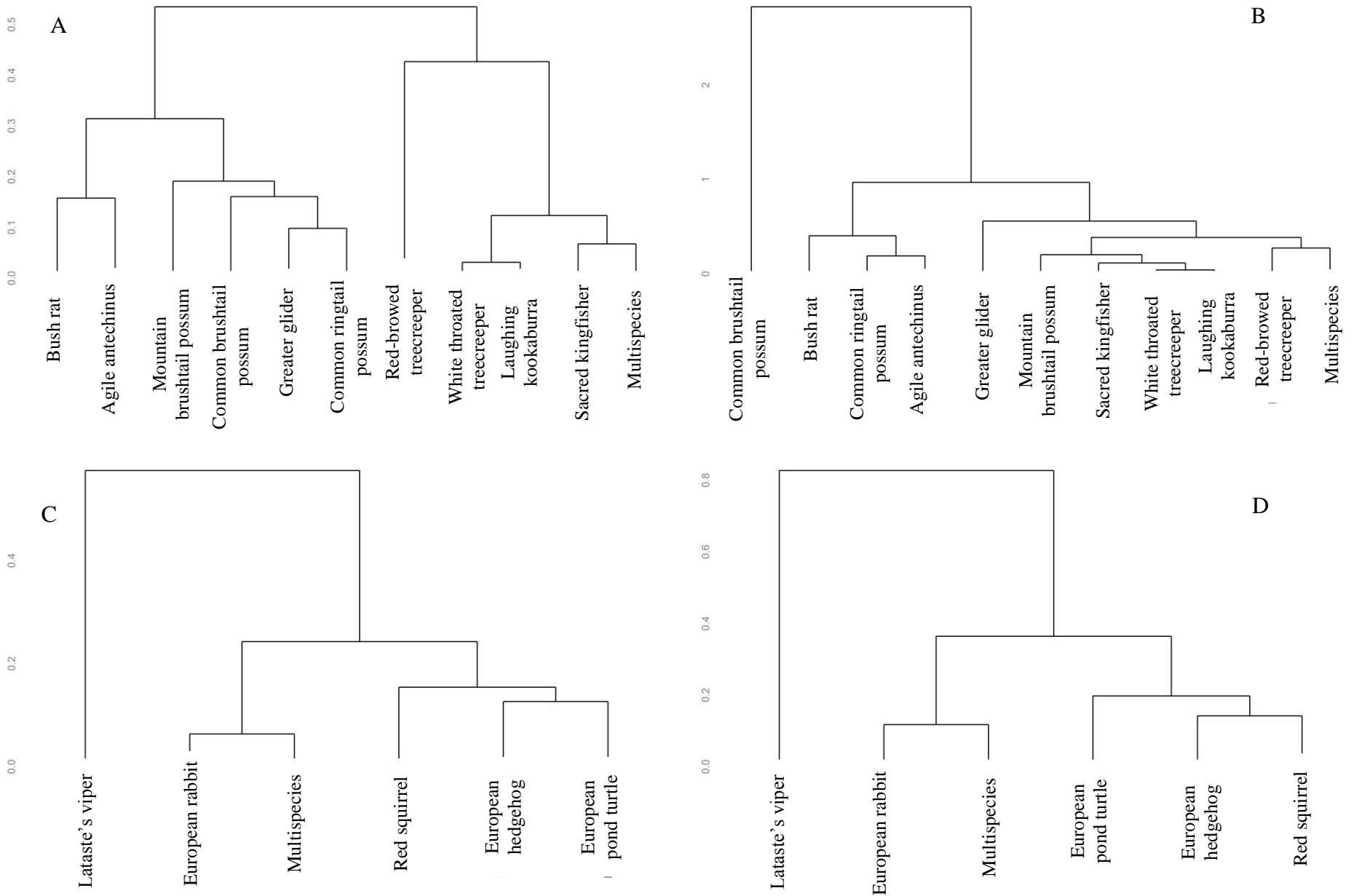


Figure S3.1 – Mitigation frequencies' similarity analysis results between the different species and the multispecies analysis. A) Similarity between fencing frequencies for the Australian species set; B) Similarity between wildlife passage frequencies for the Australian species set; C) Similarity between fencing frequencies for the European species set; D) Similarity between wildlife passage frequencies for the European species set. The closer two species are the similar the frequencies of their mitigation measures along each species' efficiency frontier.

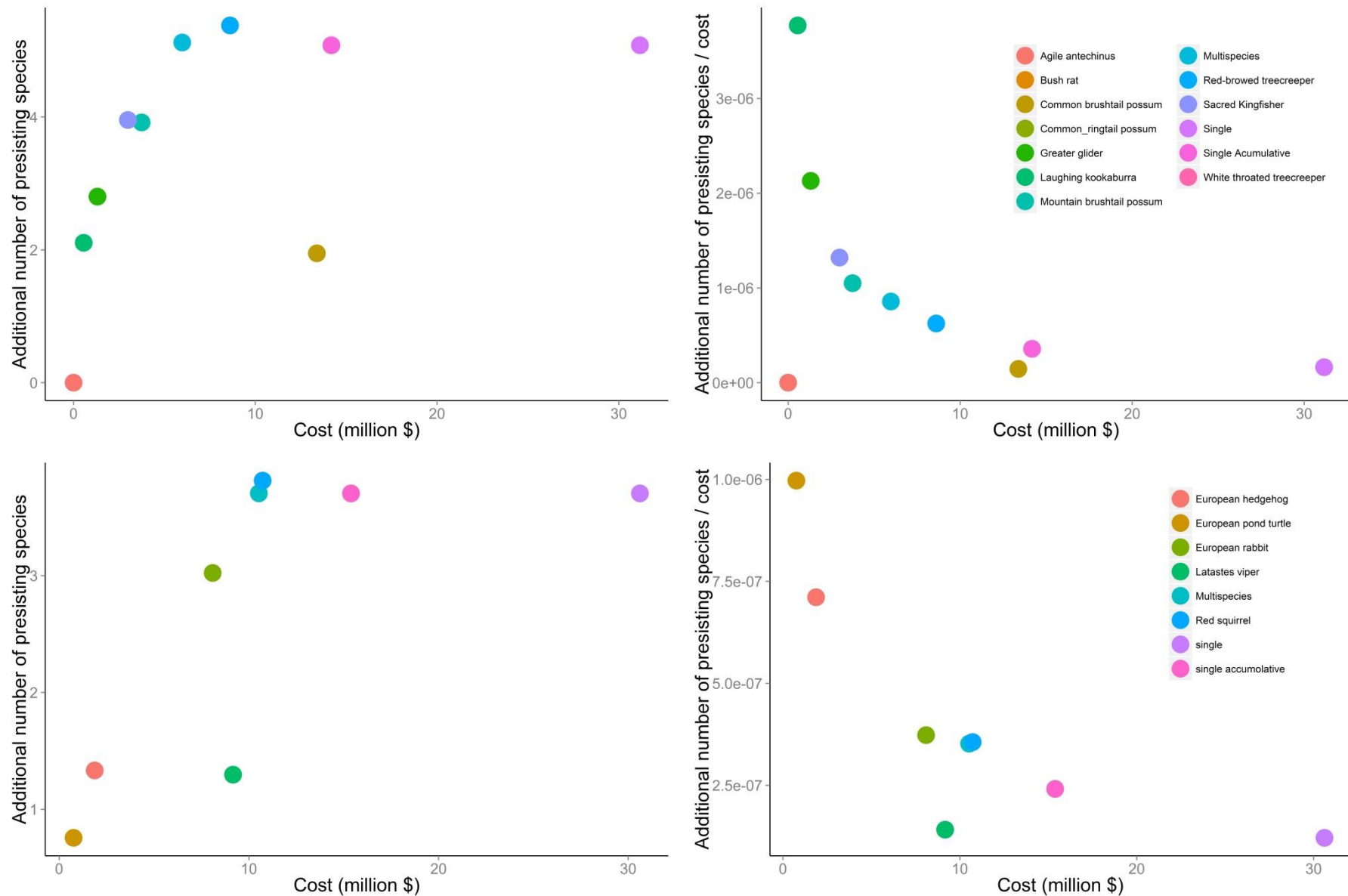


Figure S3.2 – Cost- effectiveness of different planning scenarios and all individual species. The benefit – the additional number of expected species which was extracted from each species and scenario selected mitigation configuration (the mitigation configuration which provided probability of persistence 0.9 at the lowest cost) – was plotted against its cost as: A) Additional number of persisting species for all species for the Australian species set; B) Additional number of persisting species/cost for all species for the Australian species set; C) Additional number of persisting species for all species for the European species set; D) Additional number of persisting species/cost for all species for the European species set. Colours represent the different planning scenarios and species.

8.2. Chapter 4 appendix

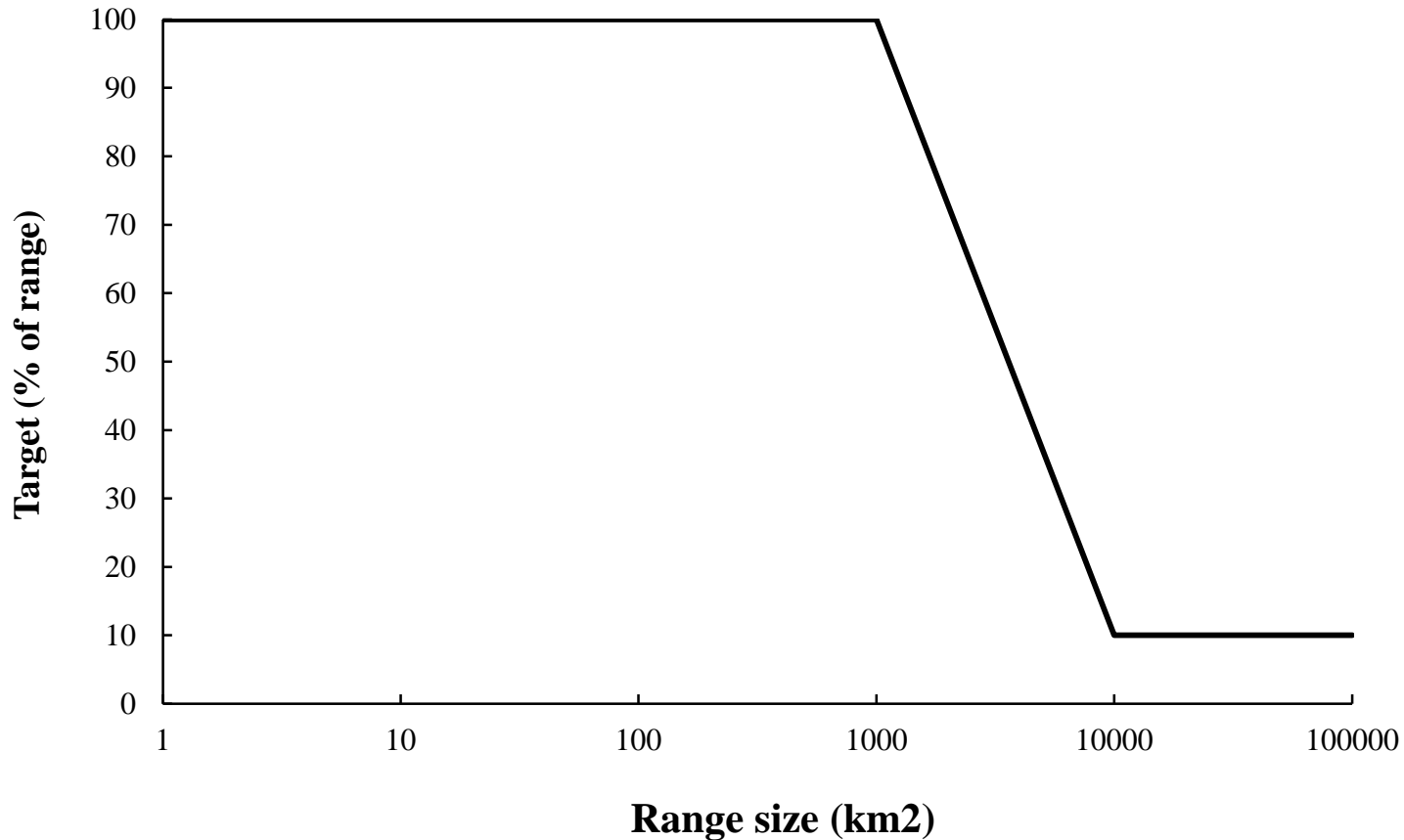


Figure S4.1: Target calculation diagram provided from unpublished data related to Watson and colleagues. For species with a range size smaller than 1000 km² a target of 100% of their range was set (upper horizontal line). For species with a range size larger than 10,000 km² a target of 10% of their range was set (lower horizontal line). For species with an intermediate range size of 1,000-10,000km² a target was interpolated between the upper and lower values (along the diagonal line)

Table S4.1- Comparing between scenarios using Jaccard Dissimilarity index. The numbers above the diagonal represent the distances between the scenarios for the new protected areas only and the numbers below the diagonal represent the distances between the scenarios for the entire network, including the existing protected areas.

	Scenario 1 Achieving 10% ecosystem targets	Scenario 2 Achieving threatened species coverage targets	Scenario 3 Achieving 10% ecosystem targets then achieving species targets	Scenario 4 Achieving threatened species coverage targets then Achieving 10% ecosystem targets	Scenario 5 Achieving both threatened species and ecosystem targets simultaneously
Scenario 1 Achieving 10% ecosystem targets	0	0.98	0.71	0.95	0.95
Scenario 2 Achieving threatened species coverage targets	0.33	0	0.56	0.26	0.38
Scenario 3 Achieving 10% ecosystem target then achieving species targets	0.27	0.22	0	0.55	0.56
Scenario 4 Achieving threatened species coverage target then Achieving 10% ecosystem targets	0.35	0.08	0.23	0	0.45

Scenario 5						
Achieving both threatened species and ecosystem targets simultaneously	0.35	0.12	0.23	0.16	0	

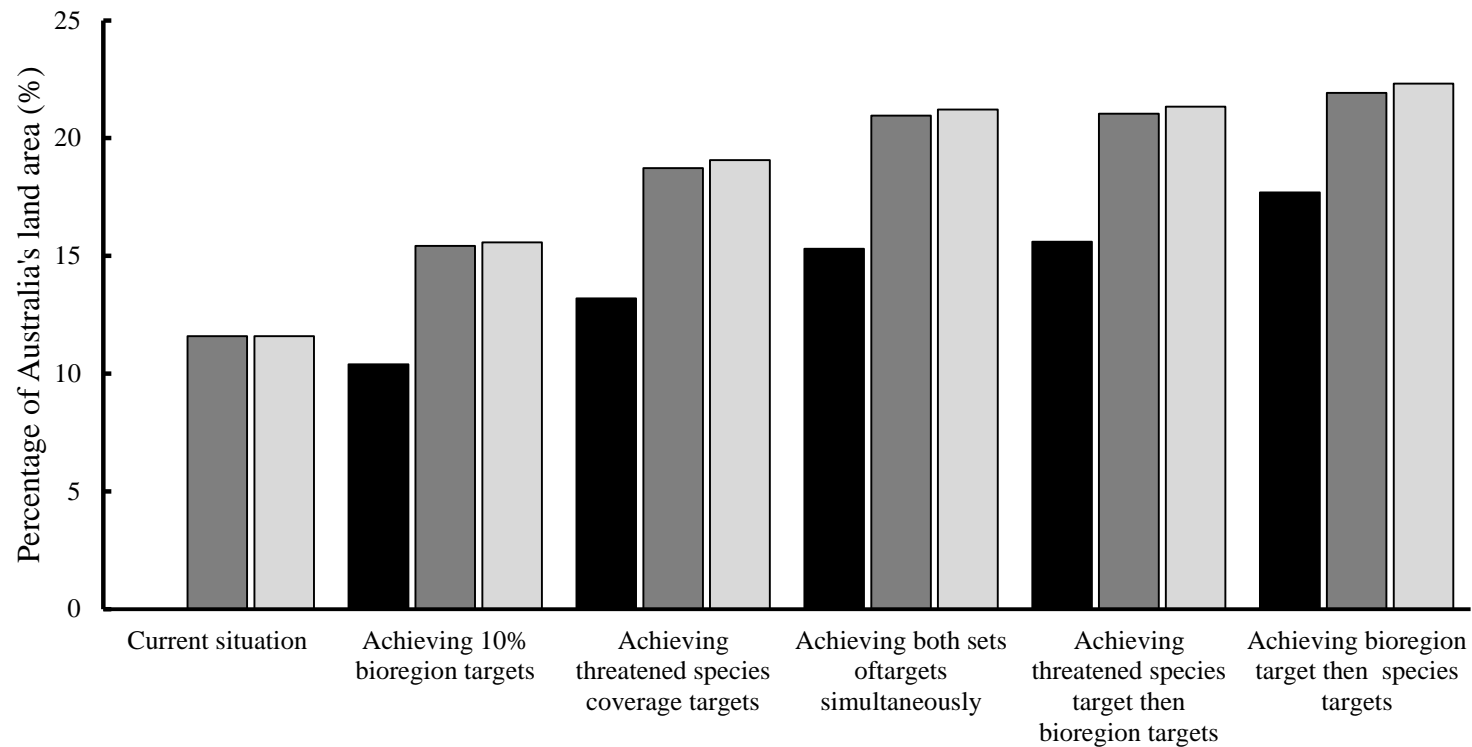


Figure S4.2: Comparison of land area required for the protected area network for each scenario (represented in percentages of Australia's land area) when planning to minimize land area (dark grey); when planning to minimize agricultural losses (light grey) and when current protected areas are ignored (i.e. not locked in to the solution - black).

Table S4.2: Scenario results: Area of proposed protected areas and amount of species and ecosystem targets that are adequately protected – Agricultural costs

	Current situation	Scenario 1 Achieving 10%	Scenario 2 Achieving threatened	Scenario 3 Achieving 10% ecosystem targets	Scenario 4 Achieving threatened species coverage	Scenario 5 Achieving both threatened species
Cost in agricultural profits (\$)	399,155,453	433,157,482	4,866,346,856	4,892,078,578	4,884,714,984	4,882,251,716
Land Area (ha)	89,115,652	119,686,896	146,548,225	171,563,300	163,991,556	163,108,658
<i>Threatened species coverage</i>						
Number of species adequately protected	284 (21.5%)	331 (25.3%)	1307 (100%)	1307 (100%)	1307 (100%)	1307 (100%)
Average proportion [^] of species target met	47.8%	52.5%	99.8%	99.8%	99.8%	99.8%
<i>Ecosystems coverage</i>						
Number of ecosystems with 10% coverage	48 (56.5%)	85 (100%)	61 (71.8%)	85 (100%)	85 (100%)	85 (100%)
Average proportion [^] of 10% ecosystems	72.6%	100%	85.4%	100%	100%	100%

[^]Some features had more than 100% of their target met but for the analysis reported in this table we only allowed a maximum of 100% coverage.

Table S4.3: Scenario results: Area of proposed protected areas and amount of species and ecosystem targets that are adequately protected without an existing protected areas network

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
	Achieving 10% ecosystem	Achieving threatened species	Achieving 10% ecosystem targets then	Achieving threatened species coverage targets	Achieving both threatened species and ecosystem
Land covered in protected areas in ha	79,749,870 (10.4%)	101,807,550 (13.2%)	136,600,920 (17.7%)	120,000,460 (15.6%)	117,565,970 (15.3%)
Efficiency from expanding current PA ^{\$}	38,879,800	42,181,150	32,572,710	41,689,350	43,553,130
<i>Threatened species coverage</i>					
Number of species adequately protected	120 (9.2%)	1307 (100%)	1307 (100%)	1307 (100%)	1307 (100%)
Average proportion [^] of species target met	28.6%	99.9%	99.9%	99.9%	99.9%
<i>Ecosystems coverage</i>					
Number of ecosystems with 10% coverage	85 (100%)	51 (60%)	85 (100%)	85 (100%)	85 (100%)
Average proportion [^] of 10% ecosystems	100%	84%	100%	100%	100%

[^]Some features had more than 100% of their target met but for the analysis reported in this table we only allowed a maximum of 100% coverage.

^{\$}Protected area network

Table S4.4: Random analyses results: Ability to meet targets when the selected area is chosen randomly for each scenario.

Scenario	Parameter tested	n	One-sample t-test	P-value
Achieving 10% bioregion targets	Number of species adequately protected	85	-1266.01	P<0.0001 for all results
	Average proportion $\hat{\alpha}$ of species target met*		-2233.6	
	Number of bioregions with 10% coverage		-1859.18	
	Average proportion $\hat{\alpha}$ of 10% bioregional coverage achieved		-195.0	
Achieving threatened species coverage targets	Number of species adequately protected	96	-4034.81	
	Average proportion $\hat{\alpha}$ of species target met*		-386.66	
	Number of bioregions with 10% coverage		-1511.28	
	Average proportion $\hat{\alpha}$ of 10% bioregional coverage achieved		-355.87	
Achieving 10% bioregion target then achieving species targets	Number of species adequately protected	100	-1579.76	
	Average proportion $\hat{\alpha}$ of species target met*		-122.45	
	Number of bioregions with 10% coverage		-1118.86	
	Average proportion $\hat{\alpha}$ of 10% bioregional coverage achieved		-126.5	
Achieving threatened species coverage target then Achieving 10% bioregion targets	Number of species adequately protected	100	-2121.1	
	Average proportion $\hat{\alpha}$ of species target met*		-213.09	
	Number of bioregions with 10% coverage		-1440.06	
	Average proportion $\hat{\alpha}$ of 10% bioregional coverage achieved		-226.22	
Achieving both threatened species and bioregional targets simultaneously	Number of species adequately protected	100	-2333.28	
	Average proportion $\hat{\alpha}$ of species target met*		-192.84	
	Number of bioregions with 10% coverage		-1350.84	
	Average proportion $\hat{\alpha}$ of 10% bioregional coverage achieved		-184.0	