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Addressing new challenges in dynamic conservation planning

PhD thesis submitted by Piero Visconti BSc(Hons)
in June 2011

For the degree of Doctor of Philosophy
in the School of Marine & Tropical Biology
James Cook University, and the School of Animal Biology,
Department of Biology and Biotechnologies, Sapienza Università
di Roma

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Thesis committee:

- Professor Robert L. Pressey, Australian Research Council, Centre of Excellence for Coral Reef Studies, James Cook University
- Dr. Carlo Rondinini, Global Mammal Assessment program, Department of Biology and Biotechnology, La Sapienza Università di Roma
- Dr. Natalie Ban, Australian Research Council, Centre of Excellence for Coral Reef Studies, James Cook University

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Prof. Robert L. Pressey
Dr. Natalie Ban
Dr. Carlo Rondinini
Prof. Atte Moilanen
Mr. Daniel Segan
Dr. Toby Gardner
Dr. Michael Bode
Dr. Luigi Maiorano
Dr. Brendan Wintle
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"The goal of working with scenarios is not to predict the future, but to better understand uncertainties in order to reach decisions that are robust under a wide range of possible futures".
Peter Schwartz. "The art of the long view" Doubleday 1991.

Abstract

The available resources for biodiversity conservation are so chronically limited that conservation agency must choose what to protect immediately and what to leave for the future, understanding that some of what they leave remains at risk. This implies not only the choice of areas or species requiring protection, but also what to protect first, that is, designing a conservation schedule. Scheduling is the coordination of actions over time and space depending on the urgency for intervention, the spatial options for protecting features, the availability of funds, and other factors. Because most of these factors are poorly known, several simplifications are commonly made when setting priorities. These simplifications, or assumptions, concern both the socio-economic and the ecological aspects of biodiversity conservation. The uncritical use of assumptions reduces the effectiveness of conservation actions and prevents further progresses towards best practice in conservation. In this regard, I set four objectives for my thesis the achievement of which would may foster the progress in the field of systematic conservation planning:

1. Providing a framework to identify influential assumptions in dynamic conservation planning and testing their effects on the spatial pattern of conservation priorities and on the effectiveness of a proposed plan;
2. Explicitly incorporate biodiversity processes (habitat fragmentation) and variable site costs in dynamic conservation planning;
3. Identifying the planning contexts in which habitat vulnerability needs to be accounted for in dynamic conservation planning;
4. Assessing the utility of future global change scenarios, for conservation planning by applying them to predict the future conservation status of terrestrial mammals.

The first, introductory chapter, provides the context for the thesis by retracing the history of systematic conservation planning with a focus on dynamic conservation planning.

The second chapter (first research chapter) investigates the influence of assumptions on

conservation-decision making with a focus on proactive and reactive approaches to priority setting. In this chapter I propose that the process of making assumptions explicit and testing them with scenarios and sensitivity analyses can help in reconciling apparently contrasting approaches to prioritization, and find an informed and more effective balance between proactive and reactive conservation. I find that assumptions regarding the irreplaceability of areas under threat, the viability of species in habitat fragments, and the relationship between costs and threats can significantly affect the spatial allocation of conservation efforts by shifting priorities in different ways with respect to the South American deforestation frontier. These assumptions should be critically evaluated before choosing an approach to priority setting, from the local to the global scale.

In the third chapter I test the implications for conservation effectiveness (persistence of three forest-dwelling species) of two assumptions when scheduling conservation actions: 1) that populations are viable in small fragments; and 2) that costs are homogeneous in the study area. I do this by incorporating realistic estimates of acquisition cost of private land and simulating the species-specific effect of fragmentation on the distribution of three forest-dwelling species in coastal New South Wales (Australia). I tested two approaches to scheduling Maximizing short term gain of biodiversity in reserves (MazGain) and Minimizing short term loss of biodiversity in the planning region (MinLoss). This is a local scale application respectively of a proactive and reactive approach to conservation. I find that, although accounting for fragmentation and variable site cost reduces the cost-effectiveness of MinLoss, this approach remains the most effective with respect to MaxGain.

In the fourth chapter I identify the conditions in which it is useful to incorporate information about habitat vulnerability (probability of development) in prioritization algorithms. I use computer simulations to investigate the role of various parameters in determining the best choice between three options: 1) using available vulnerability estimates when setting priorities; 2) investing in data collection to improve the accuracy of vulnerability estimates before selecting priority areas; or 3) discarding vulnerability altogether and selecting priority areas based only on biodiversity value and cost. I find that uncertainty in vulnerability estimate can alter the balance between proactive and reactive investments. In fact, when vulnerability estimates are on average wrong by at least 50%, discarding vulnerability and taking a proactive approach is best. Improving vulnerability estimates is the most effective choice when vulnerability variance is high and uncertainty is between 20% and 50%, otherwise, using existing vulnerability estimates with a reactive approach is best.

In the fifth chapter I explore the implications for the conservation of terrestrial mammals in four global scenarios of human development from the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005b) and identify the future hotspots of global mammal conservation. I find that, across all scenarios, Mexico, most of South America and Sub-Saharan Africa will experience large losses of suitable habitat for many terrestrial mammals. Projected agricultural expansion both for food and energy crops will pose a severe threat to mammals in the coming decades.

This thesis has contributed to the theoretical advancement of the field by shedding light on the relative performance of different conservation planning approaches and testing their sensitivity to approximations in data and models. My research has also provided an empirical framework to evaluate the role of assumptions in conservation planning. The first step is to frame a conservation planning problem using decision-theory to identify conservation objectives, actions, benefits, costs, and constraints. Then a series of questions related to the validity of the data and models available to solve the problems is used to identify the parameters and processes (ecological and socio-economic) for which more uncertainty exists. Different assumptions and different approaches to solve the conservation planning problem are then tested with different scenarios, each reflecting a different assumption about parameters and models. Combining the structured approach to problem-solving of decision-theory with the flexibility and foresight of scenario planning allows planners to make and learn from false assumptions without paying the consequences of real world mistakes. This, in turn, can provide insights on the approach to conservation that is most robust to future uncertainties.

This thesis might also contribute to advancing conservation practice. The rules of thumb and recommendations on optimal priority setting for conservation practitioners stemming from my research can have important practical consequences for conservation decisions at local to global scales.

Publications associated with this thesis

This thesis is based on the following manuscripts published or in preparation which have been edited here to reduce redundancy and ensure a consistent terminology

- Visconti P., Pressey R.L., Ban N.C. Gardner T.A. Bottrill M.C., Watson J.E.M., Balancing proactive and reactive conservation approaches: the role of assumptions. *In preparation*
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Chapter 1: Introduction

1.1 Global biodiversity loss and conservation biology

The present and projected rate of species extinction and habitat degradation is such that some argue that we have entered a new era, the "Anthropocene", in which humans exert such a powerful influence on the physical aspects of the planet as to bring it into new stable states (Crutzen 2002; Rockström et al. 2009). Despite progress where conservation actions have been implemented (Hoffmann et al. 2010), most biodiversity indicators point to a steady decline of biodiversity (Butchart et al. 2010) caused by habitat loss and degradation, direct killing and harvesting, invasive species, and climate change, among other factors (www.iucnredlist.org). Conservation biology is the discipline tasked with providing the scientific knowledge to address the human-induced biodiversity crisis (Soule 1985). Within conservation biology, conservation planning is the body of knowledge that addresses the problem of identifying and managing priority areas and species for conservation to protect them from threatening processes (Margules & Pressey 2000).

Setting conservation priorities is necessary because the financial resources available are largely insufficient to protect all areas of high biodiversity value from current and future threats. Globally, it is estimated that the expansion and management of a comprehensive network of conservation areas would cost US$18-28 billion annually over the next 30 years (James et al. 2001). This is far in excess of current expenditure, estimated at around US$6 billion per year (Balmford et al. 2003). Conservation planning is tasked with finding methods that identify areas for protection that advance the most towards set conservation objectives at the least cost or within budgetary constraints (Margules & Pressey 2000).

This thesis expands on the existing body of knowledge in conservation planning, with a focus on the allocation of conservation priorities over space and time: i.e. scheduling conservation actions, or dynamic conservation planning. In particular, I address some of the major challenges of adding a dynamic component to systematic conservation planning by considering biodiversity responses to habitat loss and fragmentation and understanding the role of threat estimates in setting priorities at the landscape or seascape scale. I investigate the effect of adding these real-world complexities in the light of different approaches to priority setting: proactive conservation which avoids threatened areas and reactive conservation that prioritize them. My thesis also provides advancement to the broader discipline of conservation planning by investigating the effects of assumptions underlying decisions about conservation priorities, and the utility of using scenario planning to set priorities. Below I explain the necessity of dynamic conservation planning by briefly summarizing the history of systematic conservation planning.

1.2 Introduction to systematic conservation planning

1.2.1 *Ad hoc* conservation planning

Humans have set aside land for the preservation of natural values for millennia. Royal hunting forests (Kanowski et al. 1999) and sacred sites are clear examples of this (Chandrashekara & Sankar 1998). The year 1872 signaled the birth of the world's first national park: Yellowstone National Park in the United States. The first national parks were established for their aesthetic and wilderness values, not primarily for protecting biodiversity. As a result, they did not represent all components of biodiversity, but rather were biased towards protecting large, conspicuous and charismatic species (Pressey 1994). Additionally, much of the land set aside for conservation was of little economic value (Pressey 1994) and was typically located in steep, infertile areas, or areas otherwise inhospitable for humans (e.g., areas infested by tsetse flies in Zambia (Leader-Williams & Harrison 1990)). This form of opportunistic reservation has inspired terms to describe protected areas[1] such as “worthless land” (Runte 1979), “the land nobody wanted” (Shands & Healy 1977), “high and far” (Joppa & Pfaff 2009), and "rock and ice". Reserves were, and often still are, selected opportunistically, commonly by relying on expert judgement.

1.2.2 The rise of systematic conservation planning

In recognition that protected areas left much of biodiversity unprotected, more recent designations included biodiversity protection as a rationale for establishment, and methods of

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[1] I use interchangeably the terms protected area, conservation area and reserve throughout the thesis.

prioritization have become more explicit. The first explicit method to select nature reserves emerged in the 1970s, which identified sites of conservation interest in the UK (Ratcliffe 1971; Ratcliffe 1977). Criteria like naturalness, richness (of species and habitats), rarity, vulnerability, connectivity and representation were for the first time explicitly accounted for in the selection of nature reserves. According to Justus and Sarkar (2002), these principles came about because the rapid increase in protected areas during the 1960s still left much of biodiversity unprotected while threats to biodiversity were increasing, and, therefore, explicit criteria for selecting areas to reserve were needed.

A new generation of scientific methods to select reserves emerged out of the recognized need for reserves to protect biodiversity. The first reserve selection algorithm was developed in 1980 in Tasmania, where Jamie Kirkpatrick was working to identify a minimum set of reserves to complement existing ones in protecting some of the island's endemic and endangered plants. He devised an iterative heuristic algorithm (decision rules iteratively used to select sites to add to the conservation portfolio) that, for the first time, included the concept of complementarity (although it was not explicitly defined so). Complementarity reflects "the need for reserves to complement, rather than unnecessarily duplicate, other areas according to unachieved targets for the features they contain" (Pressey 2002). Kirkpatrick's seminal work (Kirkpatrick 1983) laid the groundwork for a new algorithmic approach "in which the criteria invoked were applied mechanically to remove any residue of intuitive judgment" (Justus & Sarkar 2002).

Around the same time as Kirkpatrick's work, a number of researchers independently realized that selecting reserves based on ranked lists developed by earlier explicit scoring methods was not the most efficient way to represent all species in a reserve network (Ackery & Vane-Wright 1984; Margules et al. 1988; Rebelo & Siegfried 1990). A limitation of ranked lists is that, if two areas are both rich in species (and are consequently ranked highly) but share a large number of species, they would simply duplicate each other. Therefore, the next best option would be the area that adds the most species that have not already been represented. This is what was later called the principle of complementarity (Vane-Wright et al. 1991). The inception and evolution of complementarity-based conservation planning algorithms is reviewed in Justus and Sarkar (2002).

1.2.3 Conservation planning algorithms

The concept of complementarity, together with the use of explicit, quantitative objectives is common to all systematic conservation planning algorithms. The first iterative heuristics relied on complementarity, often coupled with richness and rarity to solve the problem of representing certain species in the smallest number of reserves; this is a conservation application of the minimum set problem of operation research (Possingham et al. 1993)
However, while iterative heuristics are more efficient than *ad hoc* methods or scoring approaches, they cannot guarantee an optimal solution (i.e., the most efficient solution). Because complementarity is an emergent property of a set, it can only be fully assessed if a whole set of candidate reserves is evaluated together rather than making iterative selections of the best-ranking site according to the chosen criteria (Possingham et al. 2000). Global search methods such as simulated annealing (Kirkpatrick et al. 1983) and genetic algorithms (Goldberg 1989) can approximate optimal solutions by making random changes to an entire set of candidate reserves and gradually improving the overall efficiency of the proposed reserve network (note that optimality is not guaranteed because global search methods, despite the name, do not sample the entire solution space). They can quickly find solutions close to a global optimum of a minimum set problem and would typically outperform iterative heuristics, especially when spatial configuration is one of the objectives (Moilanen 2005; Possingham et al. 2000). In fact, spatial processes such as fragmentation and connectivity are emergent properties of a system, similarly to complementarity; as such they can be addressed more effectively when the entire set of proposed reserves is evaluated. There are many ecological and practical reasons why one would want a reserve system to be more compact rather than fragmented. One way to achieve this is to reduce the overall boundary of the reserve system (Possingham et al. 2000), thereby favouring compact reserves over thin, elongate ones and few large reserves over many small ones. This in turn would reduce edge-effects and isolation while improving manageability of the network.

To find global optimal solution to a conservation planning problem, one need to use algorithms that can solve the problem as a mathematical function, for example linear programming (Haight & Snyder 2009) or stochastic dynamic programming (Costello & Polasky 2004; Possingham et al. 1993). While these algorithms can guarantee to find an optimal solution, they can only solve problems defined by a limited number of planning units (individual areas assessed in the prioritization process) and number of biodiversity features. In the case of stochastic dynamic programming, the planning units are normally less than 20. Linear programming can deal with larger problems (tens of thousands of planning units) but can only solve linear problems, thus excluding cases in which the benefits of incorporating any planning unit are not additive, for example when connectivity is taken into account (Moilanen 2008). Therefore, there exist two options for approaches that do not guarantee optimality. The first is based on a major simplification of a conservation planning problem into a problem solvable with optimal algorithms. This solution would be the most efficient for the simplified problem, and might involve substantial progress in the development of computational methods, but would be suboptimal or simply fail if evaluated with a more realistic model system. The second option is based on the solution of the more realistic and complicated problem, not solvable with optimal algorithms but with suboptimal heuristics. The latter solution would not be the most efficient but certainly more realistic (Moilanen 2008), and therefore I use this option in the chapters that follow.

1.2.4 Recent evolution of systematic conservation planning

Systematic conservation planning has been evolving rapidly in the last decade. It began as a discipline focused on finding the most efficient, adequate and representative set of reserves to achieve a set of explicit objectives. While retaining those capabilities, it is broadening into socio-economic and political considerations that assist the whole process of defining priorities, designing conservation plans and implementing conservation actions. Conservation planning algorithms have evolved to address more complex theoretical and practical planning needs. During the 90s and early 2000s, systematic conservation planning algorithms incorporated more complex theoretical issues such as economic costs (Ando et al. 1998; Naidoo et al. 2006; Polasky et al. 2001) measures of biodiversity such as abundance of a species (Rodrigues et al. 2000), probability of occurrence (Araujo & Williams 2000; Cabeza et al. 2004; Wilson et al. 2005b), and spatial aspects such as level of aggregation and minimum sizes of protected areas (Ball & Possingham 2000; McDonnell et al. 2002; Nicholls & Margules 1993; Possingham et al. 2000). In the late 2000s, systematic conservation planning evolved to address the needs of real-world conservation problems, including bridging the gap between planning and implementation

(Knight et al. 2006; Pressey & Bottrill 2008). Consequent advances in problems and algorithms included the consideration of multiple conservation costs (Watts et al. 2009), multiple conservation actions and zoning (Watts et al. 2009), species-specific benefit functions (Arponen et al. 2005; Moilanen 2007), species-specific connectivity measures (Moilanen & Wintle 2007), probability of success of conservation (Guerrero et al. 2010; McBride et al. 2007), and species interactions (Rayfield et al. 2009). The advances in algorithms have been mirrored by the emergence and evolution of a more comprehensive operational framework for conservation planning. The 11 stages of conservation planning (Pressey & Bottrill 2009) elaborate on the 6 proposed by Margules and Pressey (2000) later expanded by Margules and Sarkar (2007). The new framework emphasizes the importance of goal-setting and stakeholder involvement to ensure maximum implementability of a conservation plan.

1.3 Dynamic conservation planning

Conservation plans in general, including those developed using a systematic approach are rarely implemented all at once because of limited funding, staff and implementation opportunities (Meir et al. 2004). Regional and local conservation plans are therefore implemented over a period of time during which new opportunities and threats commonly arise. For example, some of the areas flagged as priorities for conservation might lose their value before being protected because of conversion to agricultural land or urban development (Pressey & Taffs 2001). Such ongoing losses highlight the need for planners to prioritize conservation actions within the planning region according to the immediacy of threats to areas and species, their biological value, alternative options for protection, and implementation opportunities and costs. This prioritization process is called conservation scheduling, and the body of research addressing it comes under the area of research of Dynamic Conservation Planning (Costello & Polasky 2004). Scheduling conservation actions requires planners to anticipate future spatial patterns of threats, such as deforestation, and to evaluate how these patterns may change depending on the sequence of conservation actions implemented. This is done by modelling threats such as land-use change in parallel with reservation and letting the competing processes interact during the planning period (the period over which scheduling occurs). The best reservation strategy would be the one yielding the highest biodiversity value retained at the end of the planning period.

Conservation scheduling is not only a theoretical exercise. It is implicitly or explicitly done in practical conservation every time choices are made about what to protect first and what to leave for later. Conservation NGOs, for example, use scoring methods to identify priorities within priorities, such as those within the Ecoregional Planning framework of TNC and WWF (The Nature Conservancy 2002; The Nature Conservancy and World Wildlife Fund 2006).

As with the minimum set problem, scheduling can be solved with heuristics (Moilanen & Cabeza 2007; Pressey & Taffs 2001; Pressey et al. 2004; Spring et al. 2007; Turner & Wilcove 2006; Wilson et al. 2006), or optimal algorithms such as Integer Linear Programming (Snyder et al. 2004) or Stochastic Dynamic Programming (Drechsler 2005; Spring et al. 2007; Strange et al. 2006; Wilson et al. 2006). Two heuristic approaches define the extreme of a spectrum of possible approaches to scheduling conservation actions: maximizing short-term gain and minimizing short-term loss (Murdoch et al. 2007; Wilson et al. 2006). Maximizing short-term gain (MaxGain) has been also called “pre-emptive” (Spring et al. 2007), benefit/cost targeting (Newburn et al. 2005) and “myopic” (Costello & Polasky 2004). Minimizing short-term loss (MinLoss) has been called, “fire-fighting” (Spring et al. 2007), benefit loss/cost targeting (Newburn et al. 2005), and “informed myopic” (Costello & Polasky 2004). MaxGain aims to maximize biodiversity benefit in conservation areas at a given cost (maximal coverage problem) or achieve conservation objectives in conservation areas at a minimum cost (minimum set problem). Benefit can be measured as richness, representation, abundance of species/habitats, or in other ways. MaxGain assumes that everything outside conservation areas will eventually be lost and therefore effective conservation will need to represent all the valued biodiversity in a network of conservation areas. On the other hand, MinLoss aims to minimize biodiversity loss in the entire planning region. This is equivalent to maximizing the retention of biodiversity value in the region and requires planners to account for the different levels of vulnerability of areas and biodiversity features to the threats being addressed. MaxGain is a proactive approach to conservation because it ignores threats and would tend to protect species where it is cheapest to do so, often in remote areas that are not immediately threatened (Newburn et al. 2005). MinLoss is a more reactive approach because it focuses on areas and species that are threatened now or at least within the planning horizon.

1.4 Emerging issues in dynamic conservation planning

Dynamic conservation planning is arguably 18 years old - the first formulation of a dynamic conservation planning problem dates to 1993 (Possingham et al. 1993). However, most of the research in the field has been carried after 2004 following the publication of three key papers (Costello & Polasky 2004; Meir et al. 2004; Pressey et al. 2004). This is therefore a very young discipline and, as such, has explored only little of the complexity of real world scheduling problems – a limitation that I try to address in my thesis. Below are some gaps in knowledge and methodology that are relevant for this thesis. Other major gaps that were not specifically addressed in my thesis are discussed in the last chapter.

1.4.1 Conservation costs

Conserving biodiversity with limited budgets stresses the need to be cost-efficient and requires allocating resources to actions that give the biggest return on investment (Ando et al. 1998; Carwardine et al. 2008; Murdoch et al. 2007; Naidoo et al. 2006; Polasky 2008; Polasky et al. 2001). Conservation costs can vary by many orders of magnitude across candidate areas for protection and this variation can be the main factor influencing conservation priorities based on return on investment (Bode et al. 2008). The need for accurate estimates of conservation costs at the appropriate scale applies to all conservation planning applications, but here I focus on dynamic conservation planning where the use of costs has been quite limited to date.

Some dynamic conservation planning studies have applied global datasets of conservation costs at the country-level (Wilson et al. 2006), others have used area as a surrogate for cost (Nicholson et al. 2006; Pressey et al. 2004), while others have ignored costs altogether (Cabeza 2003; Cowling et al. 2003). Ignoring costs is unsatisfactory from a theoretical point of view as the spatial variation in conservation costs can differ from that of threats and biodiversity values. Ignoring costs is also unsatisfactory from a practical point of view as unnecessarily expensive solutions are less likely to be implemented. Using coarse-resolution cost estimates with unknown accuracy is also inappropriate as these estimates are blind to variation in costs within planning units and can potentially misplace conservation actions in areas that are not cost-efficient. Fine-resolution and accurate estimates of conservation costs are therefore ideal for cost-efficient conservation spending (Polasky 2008). Techniques for estimating costs at fine resolutions are now available for both marine and terrestrial environments (Adams et al. 2011; Carwardine et al. 2008; Naidoo & Adamowicz 2006). Their incorporation into dynamic conservation planning is necessary to bridge the gap between research and implementation as well as to advance the theoretical understanding of optimal scheduling of conservation actions. I advance the thinking on conservation costs by including fine-scale estimates of costs, investigating the spatial relationship between cost and urgency to act and its implication for conservation scheduling (chapters 2-4).

1.4.2 Biodiversity processes

Biodiversity is generated and maintained by long-term processes such as evolution, and faster processes such as population dynamics, dispersal, migration, species interaction and patch dynamics. These processes occur at all spatial scales, including regional and continental. At these scales they cannot be captured by a single conservation area but can only be maintained and managed by entire networks; ergo the value of reserve networks is more than the sum of their parts (individual reserves). These emergent properties of reserve networks are only evident when one looks at processes such as evolution (gene flow among populations and genetic isolation of distinct populations), population dynamics (metapopulation dynamics, source-sink dynamics), and patch dynamics (fire regimes, coral bleaching, nutrient upwelling). During the protracted time over which reserve networks are expanded, these emergent properties can be disrupted unless their persistence is explicitly considered among the conservation objectives (Pressey et al. 2007). Because the persistence of biodiversity processes requires large areas to be protected and managed, these can often only be maintained in remote areas, where the conflict with alternative uses is lower and so is the opportunity cost for conservation; this is often raised as an argument for proactive conservation (Laurance, 2005, Cantú-Salazar & Gaston 2010).

Only very few studies have accounted for processes in conservation planning. Static conservation planning studies have recently started to incorporate biodiversity processes such as diversification of lineages (Rouget et al. 2003), metapopulation dynamics (Nicholson et al. 2006), species interactions (Rayfield et al. 2009), climatic stability (Carroll et al. 2010), patch dynamics (Game et al. 2008), terrestrial inter-patch connectivity (Cerdeira et al. 2005; Moilanen & Wintle 2007; Van Teffelen et al. 2006), freshwater connectivity (Linke et al. 2008; Moilanen et al. 2008), and inter-realm connectivity (Beger et al. 2010). Little has been done on scheduling conservation actions while accounting for biodiversity processes and this has been limited to the incorporation of connectivity to minimize the level of isolation between reserves (Harrison et al. 2008; Sabbadin et al. 2007; Spring et al. 2010) and climatic stability (Iwamura et al. 2010). Other factors affecting local population persistence, such as the effects of fragmentation, have been so far neglected in dynamic conservation planning. I contribute towards filling this gap in chapter 3 by accounting for species-specific habitat fragmentation effects during simulated incremental protected area network expansion.

1.4.3 Methods to deal with uncertainty in biodiversity data, costs and threats

Conservation planning, like any other scientific discipline, relies on models of the real world. These can approximate more or less well the complex ecological and socio-economic dynamics underpinning conservation decision-making. When testing and comparing conservation planning strategies, it is often forgotten that these tests reflect the apparent performance of prioritization methods based on models and simulated or estimated data, not on real and observed data (Grand et al. 2007; Halpern et al. 2006; Langford et al. 2009; Moilanen & Cabeza 2005; Moilanen et al. 2006a; Moilanen & Wintle 2006; Moilanen et al. 2006b). However, it is known that the relative performance of conservation planning strategies can be influenced by the accuracy of data and models (Langford et al. 2009; Moilanen & Wintle 2006). Because uncertainty is pervasive, it is therefore important to account for uncertainty in systematic conservation planning theory, if this is to be relevant to conservation practice (Regan et al. 2009).

Investigations of the sensitivity of conservation plans to inaccurate data have considered cost estimates (Carwardine et al. 2010), measures of biodiversity value (Grantham et al. 2008; Moilanen et al. 2006a; Moilanen et al. 2006b), land and funding availability (Meir et al. 2004) and likelihood of success (McBride et al. 2007), but there is no published study that investigated the effects of uncertainty about threatening processes. Vulnerability to threats underpins the difference between proactive and reactive conservation and between MaxGain and MinLoss conservation approaches. Thus it is intuitive that uncertainty about threats might affect the relative performance of one approach over the other. Therefore, understanding this relationship would be key to determining the best prioritization approach in a given conservation context.

Robustness of the spatial location and effectiveness of conservation priorities to uncertainty in data and models is crucial to give planners, donors and other stakeholders the required confidence to defend and implement a conservation plan. There are several possible methods to deal with uncertainty in ecology and conservation (reviewed in Regan et al. 2009). The main ones are sensitivity analyses, info-gap theory and conservation scenarios. Sensitivity analyses, consist in perturbing the input data (cost, biodiversity data, threats) and assessing the variation in outputs (spatial priorities) and outcomes (e.g. biodiversity representation or persistence, Regan et al. 2009). This allows identification of the conservation approach most robust to uncertainty as well as the input parameters that most influence priorities and effectiveness of a proposed plan. Unless the entire possible parameter space is tested, sensitivity analyses require prior knowledge or assumptions about the likely distribution of parameter values to be used. I use this approach in my thesis to test which factors influence the most the choice between MaxGain and MinLoss conservation strategies (chapter 4). Another option is to use info-gap theory (Ben-Haim 2006). This approach flips the problem of robustness on its head because it estimates how wrong can one be and still get an acceptable result rather than, with sensitivity analysis, perturbing the input data and observing their influence on outcomes. Because info-gap theory explores the entire horizon of parameter's uncertainty, it is useful when there is little knowledge of the distribution, bias and magnitude of potential errors in data and models and when, therefore, sensitivity analyses are not feasible (Adams & Pressey 2011; Ben-Haim 2006; Nicholson 2007; Regan et al. 2005).

A third option to addressing uncertainty explicitly is to use scenarios to model a few plausible conditions in which conservation has to take place, that is, a few combinations of parameters and models. The outcomes of a conservation portfolio are then tested in each scenario. Scenarios are useful when there are many parameters to test at once and sensitivity analyses and info-gap become infeasible because of the required number of simulations to test all parameters interactions within the bounds of the sensitivity analysis or info-gap simulations. Scenarios are used to test a few plausible parameter combinations and learn about the effects of different factors with a limited, but representative, number of simulations. Scenarios represent individual points in the hypervolume defined by all parameter combinations of the model system and are chosen based on specific assumptions about parameters and models. These assumptions make the exploration of uncertainty of several parameters at a time tractable.

While the use of scenarios has been advocated in conservation to identify conservation strategies more likely to be successful in a dynamic and uncertain future (Peterson et al. 2003), their use in dynamic conservation planning is still rare. In addition, in conservation planning there is a prevalence of single case studies relying on one or very few parameter combinations, which provide little guidance for conservation decisions outside the parameter space tested (Langford et al. 2009). I propose the use of scenarios to investigate the role of conservation assumptions in chapter 2 and put it in practice in chapters 3,4 and 5 to answer specific research question relevant to my thesis.

1.4.4 Incorporating conservation planning into future global change scenarios

Anthropogenic biodiversity loss is ultimately caused by human consumption, which determines all the main threats to biodiversity, including habitat loss, direct killing and harvesting, spread of invasive species and climate change (Brook et al. 2008; Diamond 1984). Thus, to effectively abate threats to biodiversity, conservation planning scenarios need to include future development pathways, thereby taking into account the broader context in which conservation planning takes place. Even the most advanced methods and the best data to schedule conservation actions over time may not be sufficient to ensure biodiversity persistence if the main effect of these actions is to displace destruction elsewhere. This leakage of habitat destruction can have negative effects if the new areas destroyed are also important for biodiversity (Ewers & Rodrigues 2008).

The advent of global and regional scenarios of socio-economic development with spatially explicit projections of land use and climate change, such as those created for the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005b) and the Global Environmental Outlook (UNEP 2007), provide unprecedented opportunities for conservation planning. They allow identification of conservation priorities based on information that goes beyond the spatial pattern of biodiversity, costs and local threats, but address also the opportunities and threats coming from improved technology, population growth, consumption, trade and other broad-scale considerations. I take advantage of these opportunities in chapter 5 by using scenarios from the Millennium Ecosystem Assessment to identify future hotspots of terrestrial mammal loss with different human development trajectories. .

1.5 Thesis objectives

The goal of my thesis is to advance the theory and practice of dynamic conservation planning by filling key knowledge and methodological gaps. These gaps are highlighted in the previous paragraphs. To achieve this goal, I identified the following research objectives:

1. Provide a framework to identify influential assumptions in dynamic conservation planning and test their effects on the spatial pattern of conservation priorities and on the effectiveness of a proposed plan.
2. Explicitly incorporate biodiversity processes (habitat connectivity) nd variable site costs in dynamic conservation planning.
3. Identify the conditions in which habitat vulnerability needs to be accounted for in dynamic conservation planning.
4. Consider the utility of future global change scenarios, involving models of biodiversity loss, for conservation planning by applying these to predict the future conservation status of terrestrial mammals.

1.6 Thesis outline

This thesis consists of six chapters (see Figure 1 for the links between thesis objectives and chapters). The present introductory chapter provides the context and objectives of the thesis. The second chapter (first research chapter) sets the scene by investigating the influence of assumptions on conservation-decision making with a focus on proactive and reactive approaches to priority setting. In this second chapter I propose that the process of making assumptions explicit and testing them with scenarios and sensitivity analyses can help in reconciling contrasting approaches to prioritization, and find an informed and more effective balance between proactive and reactive conservation. In the third chapter I test the influence of two assumptions when scheduling conservation actions: 1) that populations are viable in small fragments; and 2) that costs are homogeneous in the study area. In the fourth chapter I identify the conditions in which it is useful to incorporate habitat vulnerability in prioritization algorithms. I use computer simulations to investigate the role of various parameters in determining the best choice between three options: 1) using existing vulnerability values when setting priorities; 2) investing in data collection to improve the accuracy of vulnerability estimates before selecting priority areas; or 3) discarding vulnerability altogether and selecting priority areas based only on biodiversity value and cost. In the fifth chapter I explore the implications for the conservation of terrestrial mammals of four global scenarios of human development from the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005b) and identify the future hotspots of global mammal conservation. In the sixth and concluding chapter I summarize the findings of my thesis, discuss the broader implications of my research, outline the lessons learnt, and suggest future research directions.

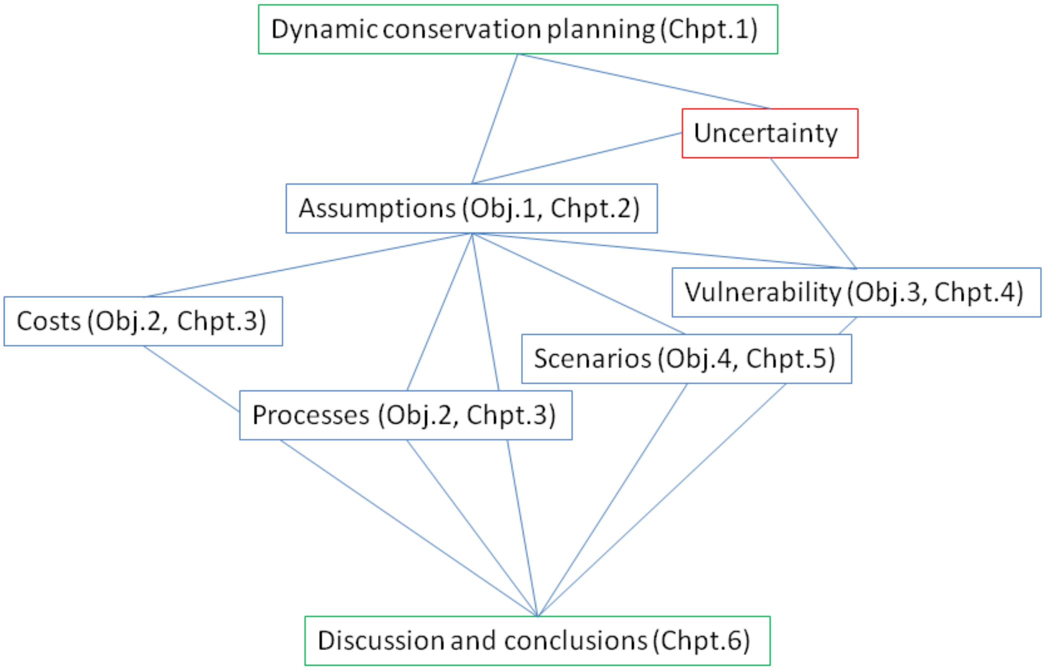

Figure 1.1 Thesis structure. Blue boxes represent data chapters, the red box is a context element, and green boxes depict the general introduction and discussion.

Chapter 2. Balancing proactive and reactive conservation approaches: the role of assumptions

Abstract

Even though there is one fundamental goal for biodiversity conservation – to minimize biodiversity loss – different, and occasionally contradictory, approaches to conservation prioritization exist. For example, some approaches avoid vulnerable areas to invest in areas of comparative wilderness (proactive approaches), whilst others actively prioritize investments in threatened areas (reactive approaches). Assumptions about the relevance and quality of ecological and socio-economic data underpin contrasting approaches to conservation prioritization, although these assumptions are rarely made explicit. Here I demonstrate how different approaches to identifying conservation priorities, and their associated assumptions, can be evaluated with a simulation study that uses scenarios to evaluate the outcomes of changes to particular decision-making parameters. I selected three assumptions that I believe are both common and influential in conservation decision-making, and are applied at different spatial scales. I show how the relative benefits of proactive versus reactive approaches to conservation can change in response to a strengthening or relaxing of each of these assumptions. I found that assumptions about species overlap between wilderness and threatened areas and the viability of species in habitat fragments significantly affect the balance between proactive and reactive priority setting. All three assumptions potentially have severe negative consequences for conservation outcomes when they prove invalid. My analyses demonstrate that scenarios can be usefully applied to test assumptions and proposed conservation approaches in a "risk-safe" environment before applying them in the real world where every action and decision count.

2.1 Introduction

Continuing biodiversity declines and limited resources mean that priority areas must be identified for conservation investment. Even though there is one fundamental goal for biodiversity conservation – to minimize biodiversity loss – different approaches to conservation prioritization exist, some of which are apparently in direct opposition. The diversity of approaches reflects the multiplicity of conservation objectives (Bottrill et al. 2006; Redford et al. 2003), different circumstances under which such objectives are to be achieved, and different assumptions about ecological and socio-economic variables and their interactions that are used to guide choices (e.g. Brooks et al. 2004). Any assumption, "that which is assumed or taken for granted" (The Oxford English Dictionary 1989) could shape approaches to conservation prioritization and their effectiveness in minimizing biodiversity loss. I test this assertion in this chapter focusing on the choice between proactive and reactive conservation.

Proactive and reactive conservation

Approaches to prioritization lie on a continuum between proactive and reactive conservation, depending on how they address vulnerability (i.e., the likelihood of an area losing some or all of its biodiversity in the absence of further intervention). Some conservation approaches avoid vulnerable areas through proactive conservation (i.e., focused on protecting wilderness areas), while other approaches focus investments towards vulnerable areas through reactive conservation (i.e., focused on protection in the “threat frontiers”, my term here for places where development is imminent, Brooks et al. 2006).

Proactive conservation aims to protect important areas and species long before they become threatened and while opportunities exist to develop effective protected area systems that safeguard large-scale ecosystem processes (Laurance 2005; Peres 2005). Global-scale examples include the Amazon and Congo basins, the North American deserts, and the Siberian tundra (Mittermeier et al. 2003; Sanderson et al. 2002). Landscape-scale proactive approaches prioritize, for example, less accessible and fertile mountainous hinterlands ((a.k.a. "rock and ice", Joppa & Pfaff 2009) or areas suitable for development but presently remote from infrastructure (Pressey et al. 2000). In contrast, reactive approaches aim to save important species or areas that are imminently threatened. Examples at the global scale are biodiversity hotspots (Myers *et al.* 2000) or crisis ecoregions (Hoekstra et al. 2005). At the landscape scale, examples are areas adjacent to expanding towns and agricultural land (Visconti et al. 2010b). Consequently, the two approaches differ in the attributes of areas that are given priority - wilderness versus the threat frontier - and therefore differ in the spatial allocation of priorities and conservation resources (Brooks et al. 2006).

Recognizing trade-offs

Existing global conservation priorities encompass both wilderness and threatened areas (Brooks et al. 2006). Similarly, regional conservation plans typically include both extensive, remote areas and highly threatened fragments (Cowling et al. 2003). However, identification of a broad suite of priorities is one thing, and their effective protection is another. Ongoing attrition of biodiversity combined with incremental progress towards mitigating threats mean that choices about what to protect at any one time are also choices about what will be lost at that time or subsequently. These trade-offs can be spatial (e.g., focus on wilderness or threatened areas) and/or temporal (e.g., protect an area now, in the future, or never). Scheduling (i.e., prioritizing conservation actions in space and time) can be used to explicitly address the trade-offs, but it is rarely used (Meir et al. 2004). Instead, trade-offs are often resolved implicitly, without any assessment of the conservation outcomes of alternative scheduling approaches (Leader Williams et al. 2010; Wilson et al. 2010).

Belief systems or conservation science?

Much of the decision making process in conservation is strongly influenced by implicit assumptions and hidden choices (Leader Williams et al. 2010; Sutherland et al. 2004). Because implicit assumptions are undisclosed and therefore untested, decisions made on their premises are not scrutinized. Assumptions are unavoidable because information is always limited, but assumptions are problematic when not made explicit. Conservation practitioners might not realize that they are making assumptions, though, when they work without questioning their mental models. Mental models are the cognitive frameworks that people use to interpret and understand the world. They influence all choices, including those surrounding conservation investments (Biggs et al. 2011; Gelderblom et al. 2003; Knight et al. 2006). Different mental models of how best to approach conservation can arise from the experiences of people that make up a conservation planning team. For example, a person or organization with interests in large carnivores or large-scale ecosystem processes would be more inclined to protect large intact areas than maintain small habitat fragments. By contrast, a person or organization with a background in local conservation projects in a region of ongoing development would lean more towards the protection and restoration of habitat fragments representing the last vestiges of once widespread ecosystems.

Assumptions can also be made deliberately and explicitly when, for example, data are sparse or of low quality and there is an imperative to proceed with actions using the information available (often limited to personal experience or expert judgement); however these assumptions are rarely tested (Sutherland et al. 2004). Different kinds of experiences can suggest different strategies and yield different biodiversity outcomes (Leader Williams et al. 2010). Given the inevitability of assumptions, their critical evaluation is essential for effective conservation investments.

The uncritical use of assumptions underpinning conservation decisions prevents a constructive discussion about the relative costs and benefits of proactive versus reactive conservation strategies and how they might be balanced. Decisions shaped by untested assumptions preclude the evaluation of opportunity costs of poorly informed actions in the face of ongoing loss of biodiversity. Given that every investment, by definition, uses resources that could be applied in another place at another time, assessing the opportunity costs of decisions is central to understanding whether a particular approach does, in fact, minimize the loss of biodiversity (Bottrill et al. 2008).

Reconciling different approaches to prioritization

Using decision theory to formulate a quantitative conservation problem comprised of objectives, benefits, costs, actions, and constraints is an intuitive platform to assess some of the necessary trade-offs between different conservation decisions and identify priorities for conservation (Wilson et al. 2010). Relatively few key parameters are involved in formulating and solving conservation prioritization problems (Box 1). Varying these parameters according to different assumptions can alter projected outcomes and change the balance of investment between proactive versus reactive conservation approaches. It is this variation in key parameters that I suggest underlies much of the implicit choices between proactive and reactive approaches.

Here I demonstrate that alternative conservation approaches, i.e. the methods used to identify conservation priorities and their associated assumptions, can be usefully evaluated through a simulation exercise that explores alternative assumptions with scenarios. Simulation has several benefits. First, it tests the validity of assumptions in the context in which conservation has to take place (e.g. are all target species viable in the small fragments present in the region?). Second, this method can anticipate the conservation outcomes of a given conservation approach both when the assumption is valid and when it is not (e.g. by measuring the viability of target species in the network of candidate conservation areas). Third, illustrates how the portfolio of conservation choices differs depending on the use of different assumptions and the broader impact thereof (e.g. what are the regional conservation outcomes when assuming that species are viable in small fragments?). Fourth, simulations can make explicit the mental models of planners and managers. Their subsequent testing can produce shared mental models and resolve debates that would otherwise proceed in a data-free environment (Biggs et al. 2011). Here I use simulation of conservation outcomes for terrestrial mammals in South America to test three assumptions that I believe are common and influential in conservation decision-making generally.

Box 1. A general model of conservation priority setting

Conservation planning, when couched in a decision theory framework, can be turned into a mathematical formulation that uses costs, actions, and constraints to evaluate objectives and set priorities for conservation (Figure 2.1). The aim is typically to achieve a set of objectives for biodiversity (habitat, species, populations), and increasingly also ecosystem services, with one or more conservation actions, while minimizing the total cost. Each candidate area for action is described by a set of attributes or state variables for which objectives are to be achieved (biodiversity features and ecosystem services, Figure 2.1, in green). The conservation value of an area depends on the extent to which the biodiversity and ecosystem service features of that area are needed to meet the conservation objectives (grey). Other state variables are the probability of success (determined by the set of opportunities for and constraints on the successful implementation of conservation actions) and the vulnerability of candidate areas and species to future loss. Vulnerability – an estimate of the consequences of not taking conservation action - increases the expected benefits from conservation actions (blue) relative to doing nothing. Expected benefits also increase with higher contribution of the proposed conservation actions to the achievement of objectives. The choice of implementing a conservation action in a given place is a binary control variable, that is, the variable to be chosen in the decision-making problem. Switching control variables changes the total costs (red) and benefits (blue) of the set of conservation actions proposed and can be used to set conservation priorities (violet).

The conservation prioritization problem is often framed as a minimum set problem whereby the goal is to achieve all conservation objectives at the minimum cost, or as a maximum coverage problem whereby the goal is to maximize the extent to which objectives are met under a budgetary constraint (Possingham et al. 2000). This problem formulation assumes that all proposed actions in all selected areas can be implemented before threatening processes adversely affect the features occurring in those areas. This planning situation (Fernandes et al. 2009; Pressey et al. 2009) is probably much less common than situations where protracted implementation of actions is accompanied by ongoing attrition of biodiversity (Pressey et al. 2004). The dynamic allocation of conservation actions often follows the identification of a set of priority areas for conservation (Margules & Pressey 2000; Pressey & Bottrill 2009; The Nature Conservancy and World Wildlife Fund 2006). Therefore, a more sophisticated method to evaluate conservation decisions is to measure the net benefit achieved by applying sequential conservation actions subject to budgetary constraints and with priorities progressively updated during expansion of threatening processes (Conservation Scheduling Problem, Costello & Polasky 2004; Pressey & Taffs 2001; Pressey et al. 2004; Spring et al. 2007; chapters 3,4). These dynamic simulations require data on possible future spatial patterns of major threats to biodiversity and the human and ecological responses to these threats and to conservation actions. With a dynamic simulation, the final conservation outcome of a given conservation approach is measured as the expected persistence of biodiversity, which can be compared against the counterfactual outcomes of no action taking place or alternative conservation approaches (Andam et al. 2008; Langford et al. 2009; Pressey et al. 2004; chapters 3,4). Both static and dynamic analyses can identify the opportunity costs of decisions and the trade-offs between taking action based on different approaches (Bottrill et al. 2008). More importantly, they can be used to explore different scenarios based on different parameter settings. Dynamic simulations provide some additional insights in terms of future persistence of conservation values. For example they can be used to assess the extent to which species conservation objectives will be compromised by future loss of habitat within and outside conservation areas. However, I was primarily interested in the influence of assumptions on the spatial pattern of conservation priorities which is determined before considerations of scheduling. I therefore chose to use static analyses, which require less data and modelling skills, to demonstrate how an easily implementable empirical framework can help to evaluate the implications of assumptions in spatial priority setting and to find the approach to prioritization that is most robust to uncertainty.

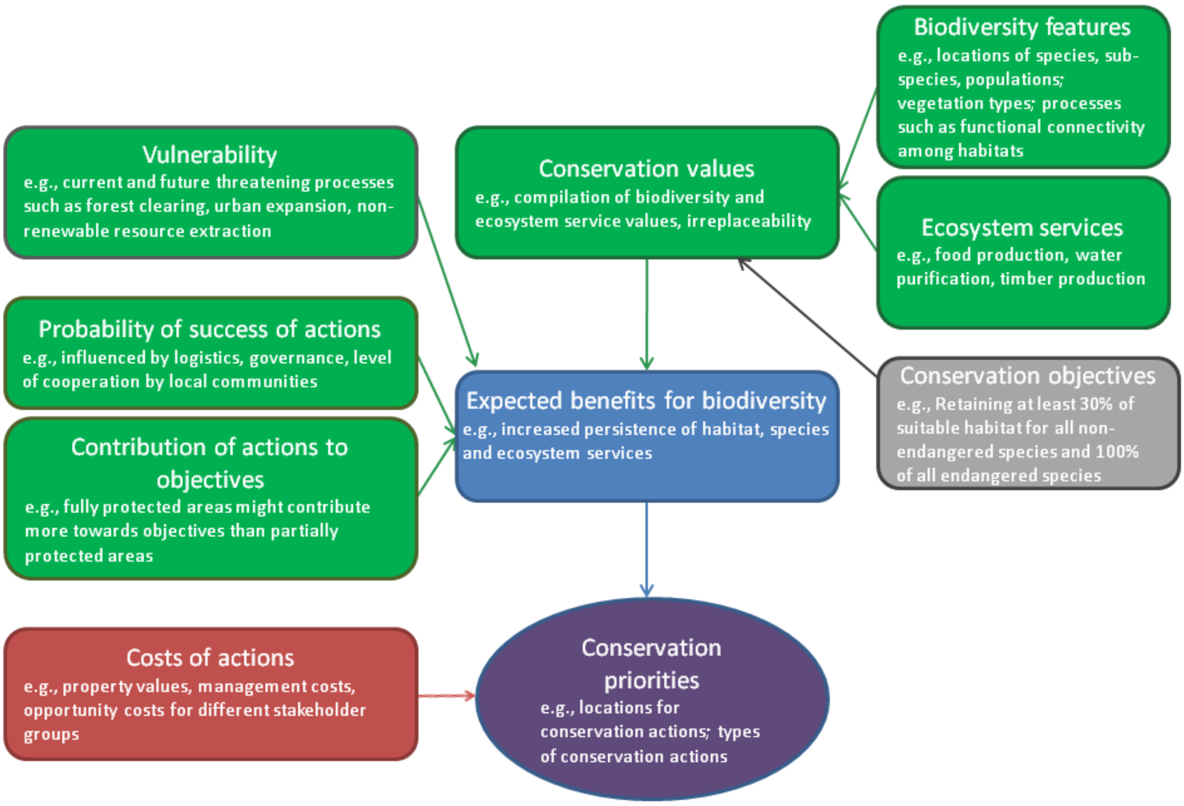

Figure 2.1. Key parameters involved in formulating and solving conservation planning problems.

2.2 Methods

2.2.1 Identification of assumptions

In selecting and reviewing assumptions, it was not possible to cover all the aspects of conservation decision making described in Figure 2.1. I focused on assumptions that are common in the conservation planning literature and practice, that apply to different realms and parts of the world, and that operate at different spatial scales. I reviewed the literature and used the collective experience of myself and my collaborators in conservation planning theory and practice to select three assumptions to investigate (others worthy of further attention are in Appendix 7.1.1). The assumptions I examined were: (1) there is compositional overlap in biodiversity features between wilderness and threatened areas; (2) species of conservation concern will survive in small habitat fragments; and (3) cost-effectiveness of protection is higher in wilderness than in the threat frontier. To demonstrate the pervasiveness of the three assumptions, their validity, and potential effects on conservation outcomes, I referred to published studies in different regions of the world and for different taxa. To demonstrate the influence of these assumptions in determining the balance of priorities between wilderness and the threat frontier, I generated spatially explicit conservation priorities based on varying parameters for these assumptions, using the conservation of South American mammals as a case study.

2.2.2 Data and models

Depending on values for the key parameters (below), I created different portfolios of priority areas for conservation in South America to represent all terrestrial mammals for which fine-scale habitat suitability maps were available (1158 species, Rondinini et al. 2011). The suitability maps were based on the altitudinal range and habitat types where the species was commonly found, as well as their tolerance to human disturbance. For each assumption tested, I created multiple scenarios, each reflecting a different value assigned to the key ecological or socio-economic parameter in question. I varied one assumption at a time to assess the consequent shift (if any) between proactive and reactive conservation. I assessed this balance by measuring the extent to which new priority areas fell within the wilderness or the threat frontier. I defined the threat frontier as any area less than 15 km from cropland or built-up areas (Bartholomé & Belward 2005).This distance threshold, although likely conservative, follows one of the criteria for determining the human footprint index (Sanderson et al. 2002). Everything outside of the threat frontier was considered wilderness (Figure 2.2).

I kept planning units, objectives, and some constraints consistent for all analyses. Priority areas were selected among 10 km by 10 km planning units with the software Marxan (Ball & Possingham 2000). The priority areas for protection were identified as the solution to a maximum coverage problem (Possingham et al. 2000), i.e. the areas that, if protected, would maximize the extent to which conservation objectives were met subject to a budget constraint. I used an arbitrary objective to represent 10% of the suitable habitat for all terrestrial mammals. For the first two assumptions, I set an arbitrary constraint on protected area expansion of 5% of South America (87,650 km^2) and therefore I used planning unit area as a surrogate for cost in all scenarios. I used a different cost measure for the third assumption (see below). I included existing protected areas (IUCN categories I-IV) in all solutions by identifying planning units with more than 50% protection. I considered these planning units as already contributing to conservation objectives and excluded them from calculations of cost in my scenarios. I ran Marxan 10 times (10 problem solutions) for each scenario to account for the variability in solutions between repeat runs of the selection algorithm.

For each solution, I measured the percentage of the total extent of new selected planning units (excluding existing protected areas) lying in wilderness and the threat frontier. I reported the average value of these percentages, across 10 repeat runs, as the result for each scenario.

2.2.3 Analyses of assumptions

1. *Biodiversity pattern: There is compositional overlap in biodiversity features between wilderness and threatened areas*

Purely proactive approaches (those that ignore the threat frontier) implicitly assume that wilderness and threatened areas are inhabited by the same set of species or contain the same habitats. To test whether the assumption holds for South American mammals, I measured the number of terrestrial mammals endemic and near-endemic to the threat frontier (with more than 90% of their distributions there). To test the implication of this assumption for conservation prioritization I compared the portfolio of priority areas in three scenarios. The first scenario was the baseline, i.e. had the observed number of species (158) endemic to the threat frontier. The second scenario was created by artificially doubling the number of endemics in the threat frontier, and the third scenario had no endemics in the threat frontier (Appendix 7.1.2).

2. *Biodiversity persistence: Species of conservation concern will survive in habitat fragments*

Conservation areas in production landscapes are often small and embedded in a matrix of agriculture or other developed landscapes. Prioritizing these fragments rests on the assumption that the biodiversity values they contain can be maintained (Carroll et al. 2004; Kuussaari et al. 2009; Tilman et al. 1994). To test the influence of this assumption in determining conservation priorities for South American mammals, I created two scenarios using the area requirements of different umbrella species to identify habitat fragments too small to ensure their viability. All planning units in these fragments were excluded from the analyses. This has been a common approach in conservation planning theory and practice (Shafer 1995). I compared the portfolio of areas selected for protection in these scenarios with those of a baseline scenario in which no fragments were excluded and all species were assumed to be able to persist, regardless of fragment size. For the two scenarios with excluded fragments, I chose as umbrella species the Jaguar *Panthera onca* and Golden-headed Lion Tamarin *Leontopithecus chrysomelas* and chose 100 years as a viability goal (Appendix 7.1.3). Although Jaguars can also survive in disturbed landscapes, I chose this species because it has the largest area requirements (minimum fragment size 2,154 km^2) based on its natural density and the estimated minimum viable population size. I choose the Golden-headed Lion Tamarin (minimum fragment size 37.3 km^2) to represent species with small area requirements.

3. Costs: Cost-effectiveness of protection is higher in wilderness than in the threat frontier

An argument for proactive conservation is that conservation costs (e.g. property values) increase towards the threat frontier, reflecting, for example, higher opportunity and management costs. However, the benefits from conservation can still be higher when investing in the threat frontier if costs are offset by higher risk of loss in the absence of action (Visconti et al. 2010b). To test how much cheaper wilderness is than the threat frontier and how the presumed pattern of conservation costs affects conservation priorities, I created three scenarios. For the first, baseline scenario I used area as a surrogate for cost with a budget equal to the amount of land protected in the second scenario in which I used opportunity costs. This gave me comparability between these scenarios, although I expected them to differ in the patterns of selected areas, with the first scenario not distinguishing between more expensive areas in the threat frontier and cheaper ones in wilderness. In the second scenario, I assigned a cost to each planning unit equal to the potential forgone revenue from agricultural activities incurred from setting aside the land for conservation. I used a global database on gross return from land (USD/hectare) from all major crop and livestock types based on their distributions, market prices, and local estimated productivities (Naidoo & Iwamura 2007). This was the opportunity cost of conservation for agricultural activities (Naidoo & Adamowicz 2006). I multiplied the maximum opportunity cost between livestock and crop per hectare by the size of each planning unit (with marginal ones trimmed to the coastline) to give the total opportunity cost for that planning unit. I created a third scenario in which costs were uniform across the continent and equal to the average cost per hectare. In the second and third scenarios I chose an arbitrary budget constraint of 239 million US dollars, which is the annual spending on protected area management from national and international funding in South America (Bovarnick et al. 2010). The second and third scenarios reflect common assumptions about cost data in conservation planning practice (Carwardine et al. 2008). In all three scenarios, I used the same species distribution data used for the baseline scenarios in previous sections (no exclusion of fragments and the observed distribution of endemics in the threat frontier).

2.3 Results and Discussion

2.3.1 Assumptions

Most of the South American continent (59.4%) falls within the threat frontier. About 64% of the total extent of protected areas is in wilderness and 36% within the threat frontier (Figure 2.2), although the threat frontier contains most of the protected areas (63%; n = 696).

Assumption 1. There is a compositional overlap in biodiversity features between wilderness and threatened areas

Protecting species in remote regions is commonly justified because it would minimize conflicts with other human activities (Mittermeier et al. 2003). Such a strategy would work if – as is often implicitly assumed – wilderness areas contained the same suite of species as the threat frontier, because then no species or habitats would be endangered by abandoning the threat frontier to intensified development. However, this implicit assumption does not hold; about 35% of the world’s vertebrates are endemic to biodiversity hotspots, broad areas under past or imminent threat of development. This biogeographic pattern and the widespread bias of protected areas towards "rock and ice" (Joppa & Pfaff 2009; Runte 1979; Shands & Healy 1977) has resulted in species in the threat frontier becoming more threatened while *de facto* protected habitat and species gain protection (Rodrigues et al. 2004).

In the baseline scenario of my South American example, 158 mammals were found only in the threat frontier and would necessarily be left unprotected by an exclusively proactive approach to conservation. Some 332 species (28.7% of the total) would require some protection in the human-modified landscapes of the threat frontier to have 10% representation in protected areas (i.e. more than 90% of their suitable habitat was within the threat frontier). The proportions of newly selected areas did not vary substantially from the baseline scenario when eliminating or doubling the number of species endemic to the threat frontier (Figure

2.3a). This is because the 158 mammals endemic to the threat frontier were on average rarer than the rest of the species. In fact, their suitable habitat covered a median of only 0.023% of the continent, compared to 0.67% for the full set of South American mammals. Thus, little area was required to fully meet conservation objectives for these species.

In summary, while a strong compositional overlap in biodiversity features between wilderness areas and threatened areas would favour a proactive approach, both at the global level and in South America, the overlap is such that a substantial degree of reactive conservation is required to safeguard the full complement of biodiversity.

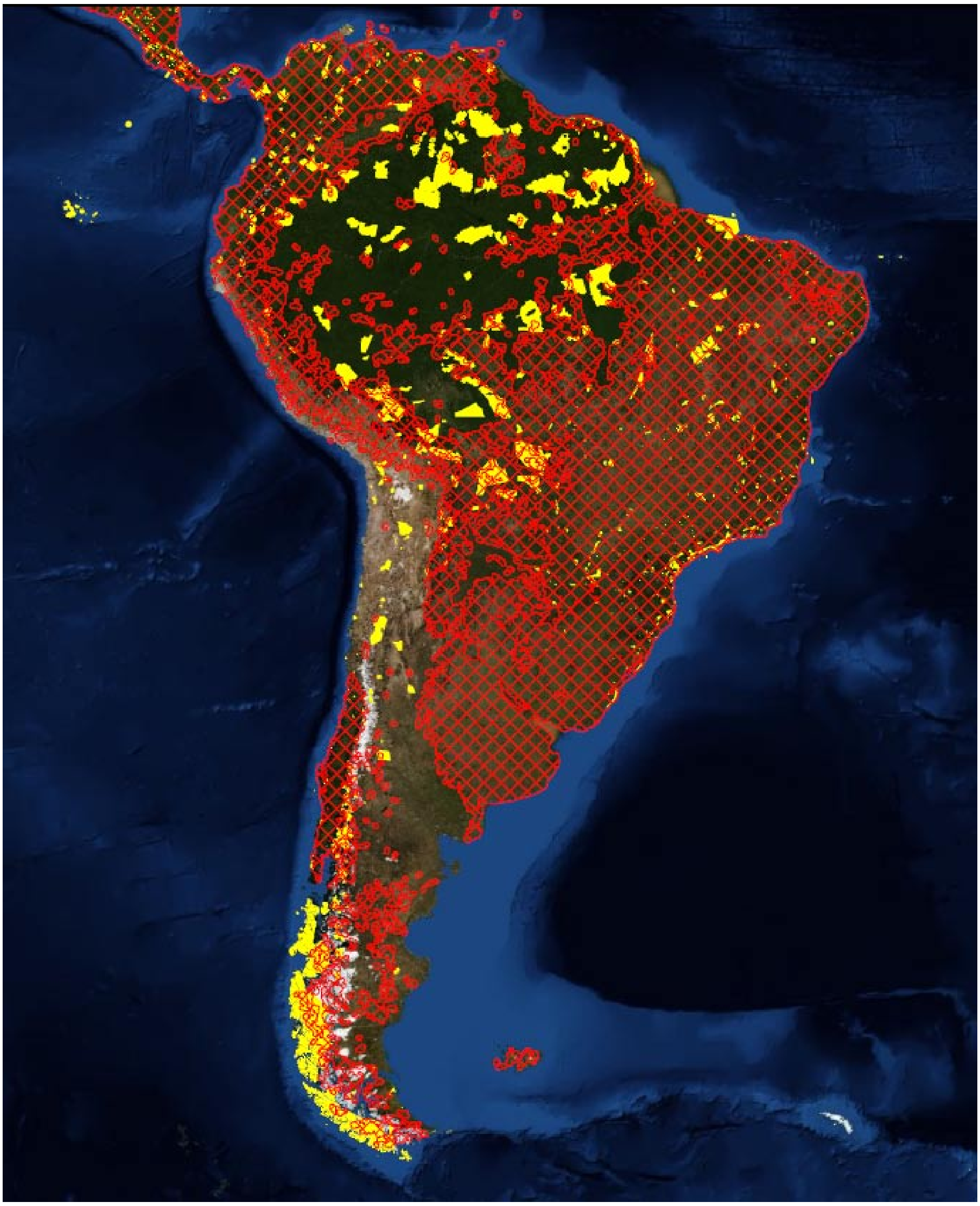

Figure 2.2 South America with the threat frontier in red (hatched) and IUCN category I-IV protected areas (UNEP-WCMC 2009) in yellow.

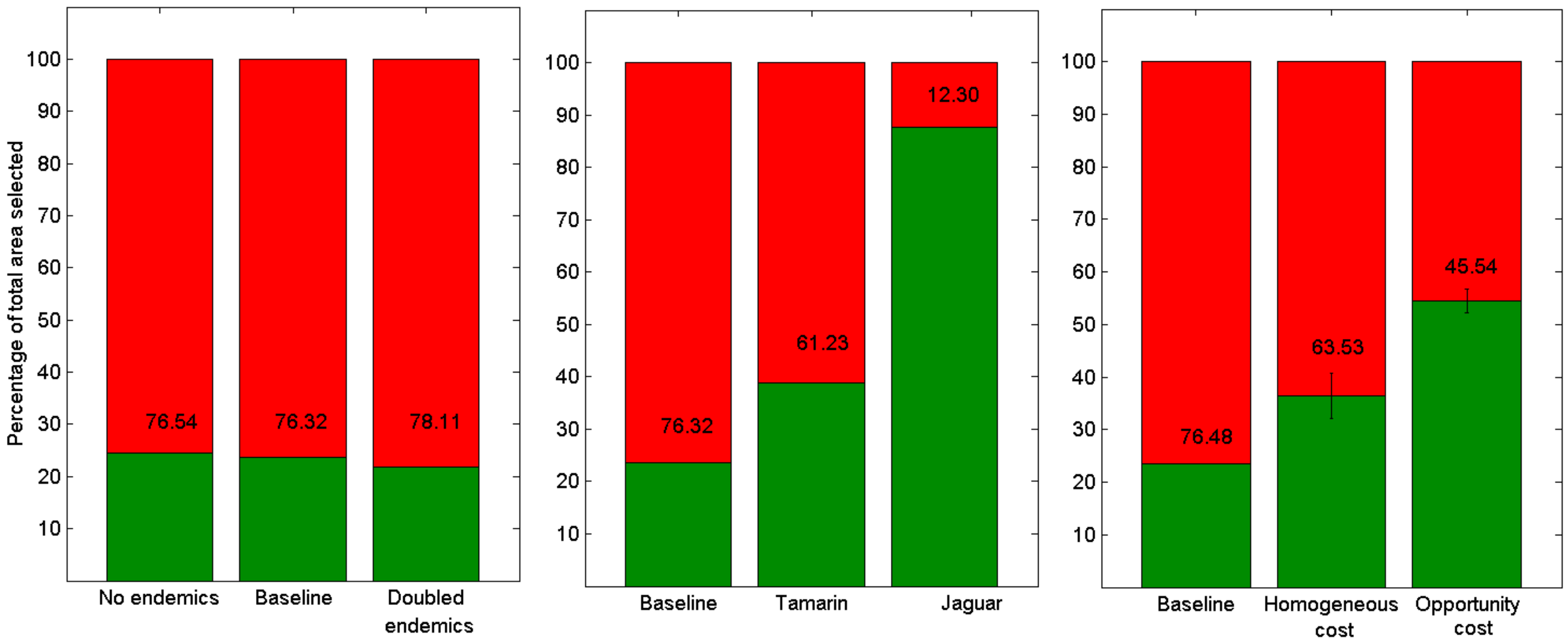

Figure 2.3. Variation in area allocated for conservation of South American terrestrial mammals across wilderness and threat frontier. Each bar express the percentage of the total extent of area selected, in relation to the three assumptions tested here; wilderness is the green portion of the bar and the threat frontier is the red portion. The vertical lines represent standard deviations (shown only if they exceeded 1%) around the mean proportions of wilderness and threat frontier across the 10 repeat runs of the prioritization algorithms. (a) Three scenarios of overlap in species composition between wilderness and threatened areas: *baseline* , observed number of endemics ; *no endemics*, endemics in the threat frontier artificially removed; *doubled endemics*, endemics in the threat frontier artificially doubled. (b) Three scenarios of minimum size of habitat patches required for the long-term persistence of terrestrial mammals in protected areas; *baseline*, no exclusion of habitat fragments; *Tamarin* and *Jaguar* respectively have minimum area requirements of the Golden-headed Lion Tamarin and the Jaguar as umbrella species to exclude insufficiently large fragments from candidate areas for protection. (c) Three scenarios of conservation costs; *baseline*, area used as a surrogate for cost; *homogeneous cost*, the opportunity cost of protection per hectare assumed to be the same across the continent; *opportunity cost*, the cost of protection was equal to the local opportunity cost for agriculture or meat production.

Assumption 2. Species of conservation concern will survive in habitat fragments
Protection of habitat fragments implicitly assumes that these areas are viable and species will survive therein. Globally, however, 50% of the terrestrial protected areas in IUCN categories I-IV are smaller than 1 km^2, an arbitrary threshold in size below which many animal species are unlikely to persist in isolated populations (Turner & T. Corlett 1996).

The validity of the assumption depends on both the fragment size and the biodiversity features of conservation interest. The assumption might often be valid for habitat generalists (Norris & Harper 2004) and species living at high densities and with small home ranges such as many small vertebrates (Fischer & Lindenmayer 2002) many plants (Cowling & Bond 1991; Laguna et al. 2004), and some invertebrates (Brook et al. 2002). Small fragments can also be important for the persistence of metapopulations if they contribute to the connectivity of the patch network and serve as nuclei for recolonization (Hanski & Ovaskainen 2003; Ovaskainen 2002). In addition, small fragments can maintain local-scale biodiversity processes such as crop pollination (Bodin et al. 2006) and mineralization of soil nutrients (Billings & Gaydess 2008).On the other hand, the assumption is invalid for many species. The negative effects of representing species in small, isolated fragments can take some time to manifest because of the delay in local extinctions. This is referred to as the extinction debt of a landscape (Tilman et al. 1994), which can also apply to the decline of biodiversity processes (e.g., cascade effects changing the trophic structure, Laurance et al. 2002; Terborgh et al. 2001). Extinction debts are widespread but, because of poor data on likelihood of persistence of species and processes, are often overlooked in conservation (Kuussaari et al. 2009). Extinctions debts are manifested in observed losses of species from undersized reserves (Rivard *et al.* 2000; Parks & Harcourt 2002) , continental islands isolated during the last major rise in sea level (Okie & Brown 2009), and freshwater islands created after inundations (Terborgh et al. 2001).

My baseline scenario for this assumption ignored viability of species in habitat patches and focused only on present occurrences, selecting 77% of the extent of new protected areas in the threat frontier (Figure 2.3b). When I excluded habitat patches too small to host viable populations of Jaguars, priority areas shifted substantially, with 87% allocation to wilderness (Figure 2.3b). In this scenario, 377 of the 1158 species could not be sufficiently represented, i.e. had less than 10% of their remaining suitable habitat in patches larger than the threshold patch size. In contrast, using the Golden-headed Lion Tamarin as an umbrella species to exclude small fragments resulted in an allocation across wilderness and the threat frontier similar to the baseline scenario (61% in the threat frontier), and there was no species for which targets were unachievable.

In summary, excluding areas from protection based on area-demanding species can come at the expense of the protection of habitats and species that cannot be protected elsewhere (see also Shafer 1995). Some of these species could well be viable in small fragments. One solution to account for species viability in conservation prioritization is to filter species databases according to species-specific area requirements, eliminating from each fragment only those species unlikely to persist there (e.g. Kerley et al. 2003). Another approach would be to evaluate the trade-offs between missed opportunities for protection and the potential extinction debt of proposed reserves.

Assumption 3. Cost-effectiveness of protection is higher in wilderness than in the threat frontier

A common argument for proactive conservation is that conservation costs increase towards threatened areas, but this relationship is sometimes assumed instead of empirically tested. The recent emphasis on cost minimization (Bode et al. 2008; Carwardine et al. 2008) coupled with evidence that costs are positively related with threats (Merenlender et al. 2009; Newburn et al. 2005), and the difficulties in obtaining accurate cost layers, have induced some NGOs and conservation practitioners to use threat as a surrogate for cost in conservation planning (Possingham et al. 2009). Furthermore, the diminishing management cost per hectare of larger protected areas (Armsworth et al. 2011; Bruner et al. 2004; Frazee et al. 2003) has resulted in calls for the protection of wilderness areas for their presumed cost-effectiveness (Balmford et al. 2003; Bode et al. 2008; Mittermeier et al. 2003; Pimm et al. 2001). Protected areas at the threat frontier might also have larger per-unit-area management costs because of the higher prevalence of threats such as poaching (Woodroffe 2000), invasive species, and fires (Frazee et al. 2003). In addition to management costs, opportunity costs are increasingly being considered. These can be used as approximations of acquisition costs where land markets are not developed and estimating acquisition costs directly is infeasible. Opportunity and acquisition costs tend to increase with proximity to the threat frontier because they depend on tenure, presence of infrastructure, local suitability for proposed uses, and profitability (Adams et al. 2010; Naidoo & Adamowicz 2006). These factors, for example infrastructure and proportion of land privately owned, tend to increase towards threatened areas, driving up opportunity costs. Conservation costs can vary globally more widely than biodiversity benefits, suggesting that costs could be at least as important as biodiversity values in determining cost-effective priorities (Balmford et al. 2003; Bode et al. 2008; Naidoo & Iwamura 2007).

In the baseline scenario which used area as a surrogate for cost and as a constraint for reserve network expansion, the total area selected for protection was 76% within the threat frontier and 29 species could not be sufficiently protected with the budget. In the scenario that used spatially variable opportunity costs and a monetary budget (239 million USD), priorities shifted strongly towards proactive conservation (54% of new protected area in wilderness, up from 24% in the baseline scenario, Figure 2.3c). This portfolio, however, failed to adequately represent 134 species because of budget limitations. Those species left under-represented were more abundant in the more costly parts of the threat frontier (Cerrado and Atlantic forest, Figure 7.1). This economic triage, however, might not be the most effective for species persistence because the area with the highest concentration of species left under-protected is predicted to incur extensive future loss of habitat (chapter 5).

The scenario that used homogeneous costs and a budget of 239 million USD selected 61% of new protected area in the threat frontier and 39% in wilderness. For this scenario, averaged across the 10 replicates, 356 species could not be adequately represented, almost three times the number of species under-represented in the scenario that used spatially variable opportunity costs. This difference arose from the potential in the second scenario to protect many species cost-effectively in areas with low opportunity for agriculture development; protecting these species became more expensive when assuming homogeneous opportunity cost.

My results support previous evidence that the relative variation of costs with respect to biodiversity value can be high enough to alter conservation priorities. However, caution should be exercised in assuming that lower cost per hectare (cost-efficiency) equals higher cost-effectiveness (Arponen et al. 2010). In fact, the amount of biodiversity loss avoided can still be higher when investing in areas that are relatively more expensive but at higher risk of loss (Merenlender et al. 2009; Newburn et al. 2006; chapter 3). Spring et al. (2007) found that the balance between proactive and reactive investment schedules when cost and threats were accounted for depended on how biodiversity benefits scale with area. If it is necessary to protect a large area to observe a gain in biodiversity benefit, then there is a premium in prioritizing currently inaccessible and cheaper sites (a more proactive strategy) to secure large areas before they become threatened and more expensive. If biodiversity benefits increase rapidly with area protected, even small and costly investments in threatened areas (a reactive approach) can yield substantial benefits and reduce the expected biodiversity loss at a lower cost than a more proactive approach (Spring et al. 2007).

2.3.2 Assumptions and proactive/reactive conservation

The only way to resolve arguments about the relative merits of proactive and reactive conservation investments is to test assumptions about threats, biodiversity values, and other factors that enter into conservation decision-making and how different assumptions can influence conservation outcomes (Pressey & Taffs 2001). Here I have used scenarios to demonstrate how assumptions can drive conservation priorities in different ways with important implications for conservation outcomes.

I found that two of the three assumptions reviewed had substantial effects on the balance between proactive and reactive approaches to conservation in South America. Weakening the assumption of species compositional overlap between wilderness and the threat frontier did not substantially shift the balance of selections towards reactive conservation with respect to the baseline level of endemism. A larger representation target for rare and endangered species would have shown a more marked shift of conservation priorities towards the threat frontier when doubling the number of endemics. I also found that fully proactive approach would fail to represent 10% of suitable habitat for 42% (n = 490) of the South American terrestrial mammals. Given the extent of my analyses and the large number of species accounted for, the implications of assuming a full overlap in species composition between wilderness and threat frontier are likely to be general and applicable to other areas and species. Weakening the assumption of species survival in small fragments by excluding fragments too small to support populations of an area-demanding species shifted conservation priorities towards the wilderness. However, this came at the expense of the adequate protection of 32.6% (n= 377) of the species considered in this study. These results could change depending on the study region and species considered. Different distributions of fragments in terms of size and spacing and consideration of species with smaller area requirements would alter the biases in selections observed here.

Strengthening the assumption of positive correlation between threats and cost in South America by using realistic estimates of opportunity costs shifted priorities strongly towards the wilderness. This revealed a trade-off for terrestrial mammal conservation involving areas and species, because it was not possible to protect sufficient area to represent all species with the budget tested. This trade-off was resolved at the expense of species prevalent in the threat frontier when using realistic conservation costs (Figure 7.1). This is potentially problematic for species with no other options for protection in the future if their habitat is not protected now. These results can be generalized to other continents since the higher opportunity costs from agricultural activities at the threat frontier are a global pattern.

2.3.3 Further improvements of the method

While easily replicable in other contexts, these analyses cannot address the temporal trade-offs in the protection of habitat and species that are manifested when scheduling conservation actions over time. The dynamic analyses suggested in Box 1 would be required to explore these trade-offs and compare proactive and reactive conservation in terms of their contributions to biodiversity persistence. These dynamic analyses would be useful to explore other assumptions related to the type and timing of conservation actions to be implemented in the areas identified as priorities for conservation (Appendix 7.1.1)

An additional improvement would involve accounting for parameters interaction. I varied the parameters independently, thus ignoring interactions between them. Some of these interactions might prove to be important in determining the balance between proactive and reactive conservation.

2.3.4 Beyond assumptions

Here I have considered the choice between reactive and proactive conservation as a decision about different means (locations of conservation actions) towards the same end (achieving a representation target for all terrestrial mammals). However, differences in conservation prioritization also arise because of different ends, i.e. different conservation goals (Redford et al. 2003). These reflect different values and beliefs about what aspects of the natural world are important and how they should be protected. Examples are the value of wilderness and vast expanses of natural habitat as sources of aesthetic enjoyment and spiritual renewal (Noss 1991) as opposed to the value of endangerment, often in heavily modified habitats (Hunter & Gibbs 2007). Reconciling these values is not straightforward, even, according to some, impossible (Justus et al. 2009). Therefore, different conservation priorities ultimately result from the combination of different conservation goals and different assumptions about the means to achieve these goals. Following my first premise that the ultimate goal of conservation biology is to minimize biodiversity loss, I argue that, regardless of the distinctions between goals and specific objectives of different conservation organizations, the implications of their conservation choices should be always assessed in terms of avoided biodiversity loss.

Another element that has promoted the differentiation of conservation approaches is the strong marketing behind them which is used to attract donors and to increase the public profile of their sponsoring organizations (Smith et al. 2010).While increasing conservation budgets is potentially beneficial, the expected increase in funding opportunities from the protection of a charismatic region or species should be assessed against the marginal benefits for all biodiversity, e.g. what are the benefits for biodiversity in general from fundraising and protection of pandas compared to investing all available resources on other species? In the same way as I tested different assumptions about biodiversity pattern, costs and species viability, different conservation budgets scenarios can also be evaluated, each resulting from a different conservation campaign and donations, which in turn influence and are influenced by prioritization approaches.

2.3.5 Conclusions

While evidence-based conservation is the ideal practice, assumptions are pervasive and the empirical evidence is often missing. Approximations in data and models are ubiquitous in conservation planning (Moilanen 2008). Worryingly, conservation outcomes can be extremely sensitive to the accuracy of information about costs (Bode et al. 2008), threats (chapter 4), socio-economic opportunities (McBride et al. 2007), and biodiversity values (Moilanen & Cabeza 2005; Moilanen et al. 2006).The *apparent* performance of a conservation approach (based on estimates involving high level of uncertainty) can be quite different from the *true* performance (based on accurate data, Langford et al. 2009). There is nothing like exact data in ecology and conservation, so the sensitivity of conservation prioritization approaches to uncertainty in the accuracy of data and models need to be tested. Additionally, in a dynamic and uncertain world, the assumptions valid today when making decisions for the future might not be valid tomorrow when these decisions are realized. Given these uncertainties in underlying data and models, can conservation planners have confidence in the outcomes of their conservation approaches without having tested their assumptions and verified the robustness of their choices? I believe that the answer is no, and I argue that acknowledging and testing assumptions should be an explicit part of any prioritization exercise. The imperative of testing assumptions with realistic scenarios is underlined by the large amounts of money invested in conservation (6 billion USD in the last 20 years from the World Bank only, Whitten 2010) and the consequences of investing in the wrong places at the wrong time in the wrong ways.

Scientific debate is the fuel of scientific progress and conservation planning is no different from other disciplines in this respect. However, to further our understanding of the merits and demerits of different prioritization approaches in different planning situations, debate needs to be based on repeatable tests, scientific evidence, and consistent metrics of performance. I believe that my framework combining decision-theory and scenario planning can be used to cut across the debate about different approaches to priority setting and find an informed and more effective balance between the two.

The very process of thinking about alternative plausible futures can actually bring to the surface unspoken assumptions (Schwartz 1998). Scenarios can therefore provide insight into drivers of change, reveal the implications of current trajectories of ecological and socio-economic variables, and illuminate options for action (Peterson et al. 2003). As the authors of the Millennium Ecosystem Assessment put it: *“The process of building scenarios is about asking questions as well as providing answers and guidance for action”*. In a dynamic and uncertain world, scenario-based conservation plans are more likely to deal with emerging threats and opportunities because many of these would have been anticipated.

Chapter 3: Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence[2]

Abstract

Conservation actions frequently need to be scheduled because both funding and implementation capacity are limited. Two approaches to scheduling are possible. Maximizing gain (MaxGain) which attempts to maximize representation with protected areas, or minimizing loss (MinLoss) which attempts to minimize total loss both inside and outside protected areas. Conservation planners also choose between setting priorities based solely on biodiversity pattern and considering surrogates for biodiversity processes such as connectivity. I address both biodiversity processes and habitat loss in a scheduling framework by comparing four different prioritization strategies defined by MaxGain and MinLoss applied to biodiversity patterns and processes to solve the dynamic area selection problem with variable area cost. I compared each strategy by estimating predicted species' occurrences within a landscape after 20 years of incremental reservation and loss of habitat. I found that the performance of conservation strategies could be improved by incorporating species-specific responses to fragmentation. MinLoss was the best approach for conserving both biodiversity pattern and process. However, due to the spatial autocorrelation of habitat loss, reserves selected with this approach tended to become more isolated through time; losing up to 40% of occurrences of edge-sensitive species. Additionally, because of the positive correlation between threats and land cost, reserve networks designed with this approach contained smaller and fewer reserves compared with networks designed with a MaxGain approach. I suggest a possible way to account for the negative effect of fragmentation by considering both local and neighbourhood vulnerability to habitat loss.

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[2] Visconti, P., R. L. Pressey, D. B. Segan, and B. A. Wintle. 2010. Conservation planning with dynamic threats: The role of spatial design and priority setting for species' persistence. Biological Conservation **143**:756-767.

3.1. Introduction

It is usually unrealistic to assume that conservation actions can be implemented all at once or that there are no obstacles to implementation arising from limits on funds, availability, feasibility of interventions and so on (Meir et al. 2004). For this reason, managers are required to schedule conservation actions (Pressey & Taffs 2001). Scheduling is the coordination of actions over time and space depending on the urgency for intervention, the spatial options for protecting features, the availability of funds, and other factors. Scheduling calls for the formulation of the dynamic area selection problem in which protection and loss are incremental, parallel processes (Costello & Polasky 2004).

Comparisons of MaxGain and MinLoss in solving the dynamic area selection problem have shown that MinLoss loss generally outperforms MaxGain in retaining biodiversity features. One exception to this occurs when there is low spatial variability in vulnerability to threats, in this case the assumption made by MaxGain is valid, i.e. vulnerability is homogeneous and the two approaches effectively converge. A second exception occurs when there is considerable uncertainty in future conservation funding or implementation opportunity (Costello & Polasky 2004; McBride et al. 2007; Wilson et al. 2006).

Among the scientific and practical challenges to effective scheduling of limited conservation resources is the need to promote the persistence of biodiversity processes. Biodiversity processes, such as ecological and evolutionary dynamics are fundamental in maintaining and generating biodiversity (Balmford et al. 1998). Despite this, few studies have attempted to combine attention to biodiversity processes with dynamic threats (Pressey et al. 2007, but see also chapter 1). Cabeza and Moilanen (2003) assessed an indicative reserve system based only on biodiversity pattern and the assumption of static threats. By accounting for population dynamics and habitat loss outside the reserves, they predicted that some species would decline and disappear from the system. Cabeza (2003) and Van Teffelen et al. (2006) asserted that the impact of habitat loss and fragmentation on metapopulation dynamics might be reduced if reserve selection were based on species models that incorporated connectivity measures as predictor variables. Carroll et al. (2003) and Noss et al. (2002) integrated a spatially explicit population model and a reserve selection algorithm to identify priorities for mammalian carnivores in the Rocky Mountains. To measure priority for reservation, they expressed irreplaceability and vulnerability (sensu Margules & Pressey 2000) respectively as the population growth rate and its expected decrease without conservation intervention. Williams et al. (2005) developed an approach to selecting reserves that accounted for range adjustments in response to climate change by designing a set of reserves that would provide connectivity over space and time for species with different dispersal abilities. Although connectivity or spatial population dynamics are receiving increasing attention in reserve design (chapter 1), I am aware of only two studies, that have considered both connectivity and threat within a scheduling approach (Harrison et al. 2008; Sabbadin et al. 2007). This is probably due to the complexity of the problem.

The few systematic conservation planning exercises that have addressed scheduling with respect to biodiversity processes and dynamic threats have not considered an important issue, the variable cost of conservation action, assuming instead that costs were uniform. Conservation costs are rarely uniform across any region, and considering them can increase the cost-efficiency and feasibility of conservation (Naidoo et al. 2006). Moreover, land value is a major conservation cost and is often positively correlated with vulnerability to habitat loss because value is related to potential profits from extraction. Targeting vulnerable areas of low cost-efficiency can therefore preclude the protection of large, intact areas with higher cost-efficiency (Newburn et al. 2006; Spring et al. 2007). The implications of such choices only become obvious when variable costs are considered (chapter 2).

Here, I address both biodiversity processes and dynamic threats by testing four different strategies defined by maximizing gain and minimizing loss applied to both biodiversity patterns and processes (species-specific responses to habitat fragmentation) to solve the dynamic area selection problem with variable area cost. This application of MaxGain and MinLoss algorithms differs from previous ones because it is applied to the prioritization of forest patches based on the expected persistence of animal populations as opposed to minimizing extinctions of entire species (McBride et al. 2007; Murdoch et al. 2007; Wilson et al. 2006). I use models of predicted probability of occurrence to approximate persistence, on the assumption that the predicted probability of occurrence of a species at time *t* is equivalent to the probability of persistence from now until time *t*. Probability of occurrence has been used previously as a surrogate for probability of persistence because both are dependent on the same factors related to habitat quality (Araujo & Williams 2000). This surrogacy gains credibility when occupancy models incorporate neighbourhood covariates such as the proportion of suitable habitat in a defined radius. These models are also likely to relate to processes relevant to population viability such as edge avoidance, spatial population dynamics and lowered persistence of local populations in small habitat fragments (Araujo et al. 2002; Moilanen & Wintle 2007). Species' persistence depends, of course, on extrinsic factors such as habitat loss (Araujo & Williams 2000). account for this by using a land use change model to simulate loss of native vegetation. I use the results to answer the following questions:

1) Can information about species-specific fragmentation effects be used to schedule conservation actions and improve conservation outcomes?
2) Is minimizing loss better than maximizing gain when reservation cost and species-specific influences of fragmentation are incorporated into conservation planning?

3.2. Methods

3.2.1 Study region and species

The Lower Hunter Central Coast (LHCC) region in central-eastern New South Wales includes seven local government areas (Figure 3.1a). These local governments have established a Regional Environmental Management Strategy to integrate biodiversity information and coordinate approaches to nature conservation, producing detailed vegetation and fauna survey and mapping (LHCCREMS 2004; Wintle et al. 2004). For my analyses, I used a ~ 600-km^2 subregion of the LHCC (hereafter the planning region, Figure 3.1b). The planning region is representative of the larger region in terms of vulnerability to anthropogenic threats, habitat suitability for the target species, and land costs.

I selected three species of regional conservation concern with distribution models of high predictive power (see Wintle et al. 2005), differing responses to fragmentation (Moilanen & Wintle 2007), and differing associations with land suitable for development. The squirrel glider (*Petaurus norfolcensis*) is an arboreal marsupial that feeds mostly on flowering *Acacia* and *Banksia* (Menkhorst & Knight 2004). It occurs in vegetation types at risk from loss through urban and agricultural expansion in the lowlands of the study region. Its home range size is about 0.75-1.75 ha and its maximum juvenile dispersal is about 500 m (Quin 1995). The yellow-bellied glider (*Petaurus australis*) is another arboreal marsupial occurring mainly in undisturbed patches of eucalypts and sap trees. Its home range size in a region with similar ecological characteristics varies between 46 and 59 ha (Goldingay & Kavanagh 1993). In the study region, it is most abundant in higher-altitude forests that are less suitable for conversion to agriculture and urban development. The sooty owl (*Tyto tenebricosa*) tolerates some fragmentation and discontinuity in forest cover but relies on large tree hollows for nesting and preys on forest-dependent species, making it susceptible to declines in prey abundance after fragmentation (Kavanagh 2002). Its home range size (200-800 hectares) depends on habitat productivity (Kavanagh & Jackson 1997). Its estimated juvenile dispersal is 10-20 km (NSW Department of Environment and Conservation 2005). In the study region, it is most abundant on the south-eastern coastal uplands.

3.2.2 Planning units

I divided the region in 3698 planning units, which served as the primary units of assessment and comparison. Planning units ranged in size from 1 to 34 hectares (Figure 3.1b), and where possible, were matched to the boundaries of existing forest fragments (Appendix 7.2.1). This had several advantages: coupling ecological units with planning units; reducing spatial variance in cost and biodiversity benefit; and avoiding the costs of very large planning units exceeding annual constraints on budget.

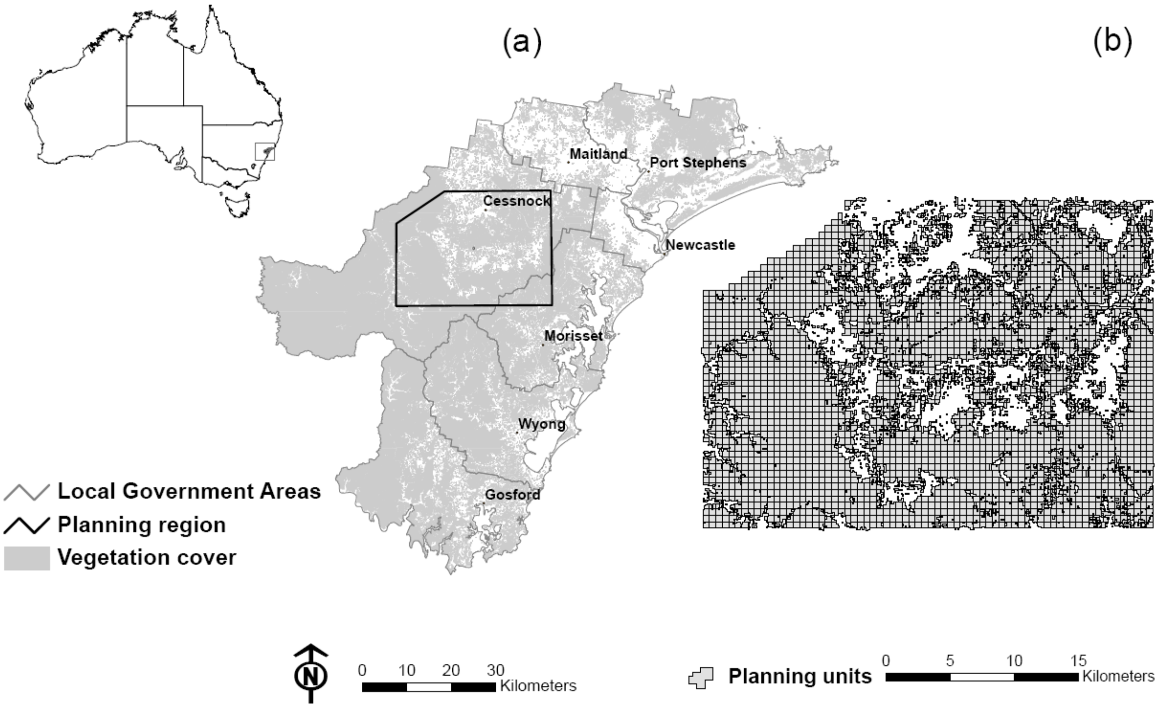

Figure 3.1 The study region. (a) Overview of the Lower Hunter and Central Coast region, showing the boundaries of the smaller planning region; (b) The planning region; white areas are deforested and small irregular polygons are fragments that represent their own planning

units.

3.2.3 Study design

Combining two approaches (maximizing gain and minimizing loss) with two types of species distribution models (local and neighbourhood, below), gave four reserve selection strategies (Figure 3.2a). I simulated each strategy under different scenarios defined by two rates of habitat loss and two rates of reservation (budgets available to managers for land acquisition), giving 16 simulations (Figure 3.2b).

I also simulated each strategy under the two extreme scenarios of loss and reservation (both high and both low) using planning unit area as a surrogate for cost to test the impact of using realistic cost data in dynamic conservation planning.

(a)

(b)

Loss rate		**low(l)**	**high(L)**
Reservation rate	**low (r)**	lr	Lr
	high (R)	lR	LR

Figure 3.2 Study design.(a) For each approach to priority setting (columns) and each approach to modelling species (rows) I defined a reserve selection strategy (cells). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey cells indicate maximum gain strategies and unshaded cells indicate minimum loss strategies. The MaxGain-local strategy maximizes the number of occurrences of species in reserves based on the predictions of the local model. The MinLoss-local strategy minimizes the loss of occurrences of species across the whole planning region as predicted by the local model. The MaxGain-neighbourhood strategy maximizes the number of occurrences of species in reserves as predicted by the neighbourhood model. The MinLoss-neighbourhood strategy minimizes the loss of occurrences of species across the whole planning region as predicted by the neighbourhood model. (b) I tested each strategy with four different scenarios defined by combinations of two rates of habitat loss and two rates of reservation.

3.2.4 Simulation of reserve scheduling

In each year, I simulated annual, parallel loss and reservation of forest in the study region. Each annual cycle of the simulations consisted of the following steps:

1. Predict species’ probability of occurrence.
2. Select planning units for protection. I allocated a fixed annual budget and selected planning units up to the limit of the budget with each reserve selection strategy.
3. Simulate habitat loss. At the beginning of the planning period, I assigned a vulnerability value to each planning unit V_p, which equalled its annual probability of being cleared,

depending on its tenure and suitability for agricultural and urban development. When planning units lost their forest, they were removed from the simulations.

4. Update environmental predictors. At the end of each annual cycle, I updated the vegetation map and the input for species models for the next cycle.

For each simulation, I repeated these steps 20 times to simulate a 20-year planning process. I then projected habitat loss, without further reservation, until year 40 or until there were no planning units available for reservation or development. While a 20-year planning period is more similar to the usual horizon of conservation decision-making, I wanted to observe how strategies diverged in performance over time and what would happen if habitat loss continued after the implementation of the reserve network. The performance of each conservation strategy was the proportion of the initial expected occurrences of each species given by the neighbourhood model that were still extant after 20-40 years.

3.2.5 Species models

Presence and absence point records of the three species and the environmental layers used for model fitting and model projection at 1 ha resolution were made available by the University of Melbourne and the Lower Hunter Central Coast Regional Environmental Management Strategy. I used two different sets of species distribution models to measure the biodiversity benefit of conserving each planning unit. “Neighbourhood” models are described in Wintle et al. (2005). I use the term “neighbourhood” models because their predictor variables (Table 7.2 in Appendix) included contextual measures of habitat value, such as the proportion of unmodified forest within 2 km of a 1 ha cell, reflecting the spatial arrangement of forest patches and the edge effects caused by loss of adjacent patches. During the simulations, these models could therefore predict reductions in expected occupancy of cells because of clearing of nearby forest. Strictly speaking, with the neighbourhood models I modelled patterns of occupancy influenced by spatial population processes. I derived the set of “local” models ex novo. These include only local covariates in model fitting: attributes of individual 1 ha cells that are independent of neighbouring cells. The predictors included predominant vegetation type, temperature and rainfall. The local models predicted loss of species occurrences only because of forest clearing in individual cells. Despite their shortcomings (e.g. Van Teffelen et al. 2006) I used local models for two reasons. First, models that ignore spatial configuration of habitat are still commonly used for conservation planning. Second, I wanted to explore the interaction between model choice and scheduling approach (maximizing gain or minimizing loss). I fitted generalized linear models (McCullough & Nelder 1989) and generalized additive models (Hastie & Tibshirani 1990) with a binomial response in R (R Development Core Team 2008). I reduced predictor variables with the Akaike Information Criterion (Akaike 1974). For each species I chose the model with the highest area under the Receiving Operating Characteristic (ROC) curve (Hanley & McNeil 1982). Formulae of best local and neighbourhood models and ROC values are in table 7.2

3.2.6 Land use change model

I assumed that agricultural and urban development were the only sources of habitat loss and that all forest within a planning unit was lost if the planning unit was selected for development. For vulnerability to agricultural development, I used a map of land capability (Emery 1988) that delineated four classes in my study region. Classes 4 to 2, (62.8% of the planning region), contained private land with decreasing capability for intensive agriculture (respectively 1.7%, 32.3% and 28.8% of the planning region for classes 4 to 2). Class 1, (26% of the planning region), comprised unreserved public land, including production forest. I also included a class 0, (11.1% of the planning region), which consisted of reserves existing in 2007. I modelled vulnerability to urban development as inversely proportional to the distance from existing urban settlements and directly proportional to rates of growth of these areas (Appendix 7.2.2). I reclassified the continuous urban vulnerability map into discrete classes to match those for agriculture. I then assigned each planning unit on private land the highest of either agricultural or urban vulnerability.

I modelled annual loss of forest as a series of independent probabilistic events. In each of the 20 annual cycles of the simulations, I removed all forest from a random sample of planning units in each vulnerability class. The size of the sample depended on the annual loss rate for the class. I simulated two rates of loss. The low rate involved annual loss of 2%, 1%, and 0.05% of the initial forest in classes 4, 3 and 2, respectively. These loss rates are consistent with recent land clearing rates in the study region (Pressey et al. 2004) and corresponded to annual losses of about 25, 250 and 115 ha, reflecting both different percentages and different initial areas of forest following more extensive historical deforestation in higher classes. The high rate of loss was five times higher in each class. When all vegetation in a vulnerability class had been lost or protected, I assumed that the loss rates in the other classes increased proportionally to maintain a constant rate of loss across the planning region.

3.2.7 Cost of reservation

I considered two different cost surfaces. The first one reflected some of the known spatial heterogeneity of land values in the region and consisted of the summed opportunity cost for agriculture and urbanization. I assumed that this was a surrogate of acquisition cost (see Naidoo & Adamowicz 2006 and Appendix 7.2.3 for details). I intended the resulting land values, at 1 ha resolution, not to be exact acquisition costs, but rather to capture the relative spatial variations in cost. The cost of each planning unit was the sum of the estimated acquisition costs across the 1 ha cells it contained. With the second cost surface, I attributed to each planning unit a cost equal to its area. The purpose of this cost layer was to explore the quantitative effects of ignoring spatial variation in land value in reserve design.

3.2.8 Reserve selection strategies

I tested four different strategies for reserve selection (Figure 3.2a), each with a different objective function to minimize subject to a budgetary constraint and each complementing the existing reserves in the study region. All variables and subscripts used in the following formulas are in table 3.1. The objective functions contained two arguments:

- the planning unit cost $\$_{x;}$
- the target penalty which was equal to the cost of raising a species up to its target representation/retention level.

Both arguments of the objective function are therefore expressed as costs. The first argument ensures that, everything else equal, the cheapest solution is preferred, the second argument ensures that, everything else equal, the solution that is closer to meeting a defined target for each species is preferred. I minimized each objective function with the Marxan software (Ball & Possingham 2000). I used two different budgets: \$1 million and \$5 million (Australian) per year. These corresponded to low and high rates of reservation, respectively. When using area as a surrogate for cost the budgets were 88 and 341 hectares per year. These measures were the average annual rate of protection across all scenarios and all replicates in the simulations using monetary budgets and cost.

I varied the calculation of the targets and the target penalty to produce a maximum gain and a minimum loss approach, each applied with both local and neighbourhood occupancy models. For MaxGain strategies, I set for all species a target T equal to 100% of the expected occurrences (EO_S) in the landscape expressed as $EO_s = \sum_u^N \sum_{i \in I_u} p_{is}$. p_{is} is the probability of occurrence of species *s* in cell *i* belonging to planning unit *u*. This probability was generated with the neighbourhood or the local model depending on the strategy applied. For MinLoss the target was 100% of the expected occurrences at risk (EOR_s) expressed as

$EOR_s = \sum_u^N v_u \sum_{i \in I_u} p_{is}$. v_u is the vulnerability (probability of loss) of planning unit *u*.

A generalization of the objective function to be minimized for all strategies is:

$$\sum_s^S SPF_s CR_s H(g_s) \left(\frac{g_s}{t_s} \right) + \sum_u^N \$_u x_u \qquad \text{(eq. 3.1)}$$

SPF_s is the species penalty factor, and is used in Marxan to weight the contribution of different species in the objective function. I applied a *SPF* of 1 for all species. CR_s is the cost of meeting the target for species *s* starting from no representation in the reserve network (details in Game & Grantham 2008). The shortfall or gap in protection g_s for MaxGain is the unmet representation target calculated as $g_s = EO_s - \sum_{u=1}^N x_u EO_{su}$ where e_u is the expected number of occurrences in planning unit *u* calculated as $EO_{su} = \sum_{i \in I_u} p_{is}$. For MinLoss the shortfall is $g_s = EOR_s - \sum_{u=1}^N v_u x_u EO_{su}$ and represents the difference between the expected number of occurrences at risk in the landscape and the potential loss of occurrences averted by the proposed reserve network. The Heaviside function, *H(g),* is a step function taking the value of zero when $g=0$ and 1 otherwise.

All else being equal, MinLoss gives higher priority to planning units in higher vulnerability classes. MaxGain strategies instead would base their priorities only on the return on investment in protecting a planning unit.

While the hypothetical MinLoss managers had no prior knowledge of which specific planning units would be lost in the next step, I assumed that they had perfect knowledge of the probability of conversion of each planning unit. It is possible that incorporating uncertainty in estimates of vulnerability could affect the results. I did not test this possibility here but will explore it in chapter 4.

Table 3.1. Explanation for symbols

Symbol	*Explanation*
CR_s	Cost of meeting the target for species *s* starting from the zero representation
EO_{su}	Expected number of occurrences of species *s* in planning unit *u*
EO_s	Total expected number of occurrences of species *s* in the landscape (only MaxGain)
EOR_s	Total expected number of occurrences at risk of species *s* in the landscape (only MinLoss)
g	is the gap between current representation and target (shortfall)
i	Cell index
I_u	Index set of cells within planning unit *u*
p_{is}	Probability of occurrence of species *s* in cell *i*
N	Number of planning units in the region
$s=1...S$	Species index
S	Number of species
SPF	Species penalty factor
T	Target: *EO* for MaxGain and *EOR* for MinLoss
$u=1...N$	Planning unit index
v_u	Vulnerability (probability of loss) of planning unit *u*.
x_u	1 if planning unit *u* is reserved, 0 otherwise
$\$_u$	Cost of planning unit *u*

3. 2.9 Evaluation of the performance of reserve selection strategies

I measured the performance of each selection strategy for each species as the total number of remaining occurrences predicted by the neighbourhood model across the study region at the end of the 20 years planning period. Each of the 16 simulations followed an independent trajectory of lost occurrences. Because my model of vegetation loss was probabilistic, different repetitions of the same simulation could result in different levels of species' persistence depending on which planning units were lost and reserved, obscuring the between-simulation variation that I wanted to measure. I therefore ran ten replicates for each simulation, which gave me a statistical power of 0.9 to detect a difference in mean performance of 2% between simulations for all species. For each combination of loss and reservation rates, I compared the distribution of persistence values among the four strategies. I calculated the relative improvement from a worse strategy to a better strategy as:

$$\Delta P = \frac{P_{better} - P_{worse}}{P_{worse}} \qquad \text{(eq. 3.2)}$$

Where P_{better} and P_{worse} are respectively the mean persistence achieved by the better and worse of the strategies in the pairwise comparison.

3.2.10 Measuring the effect of fragmentation

Habitat loss during the planning period had two components: direct loss (*d*), which occurred when vegetation was removed from the focal planning unit, and loss due to fragmentation (*f*), which occurred when neighbouring planning units lost their vegetation and reduced the expected occurrences of species in the focal planning unit. These two combined represent total loss of expected occurrences. I calculated the fraction of this total habitat loss resulting from each component for both loss rates. To do so, I first measured the absolute number of occurrences lost through fragmentation (*f*), which is the difference in expected number of occurrences given by the neighbourhood model between the beginning (prior to fragmentation) and end of the planning period for all planning units still vegetated. I then divided this amount by the total loss of occurrences, including those from planning units that were cleared during the planning period, to give the proportion of the total loss attributable to fragmentation $f/(f+d)$. For each species and each loss rate, I calculated this proportion for nine simulations. One simulation was without new reservation (potentially a worst-case scenario) and the remaining ones combined the four reservation strategies and the two budgets. I recorded the mean, minimum and maximum proportion across the nine simulations. For each simulation, the proportion was the average across the 10 replicates. I also measured the post-selection loss of occurrences in reserves due to their isolation by fragmentation during the planning period. This measure differed from the previous one in evaluating the impact of fragmentation on species only in actual and simulated reserves. I applied this second analysis for the strategies that used a neighbourhood model.

3.3 Results

3.3.1 Correlation between vulnerability, species abundance and cost

Across all planning units, the combined abundance of all three species was strongly negatively correlated with vulnerability ($\rho = -0.58$ for the neighbourhood model, $\rho=-0.48$ for the local model; both $p<0.001$). The neighbourhood model predicted that approximately 49% of the expected occurrences of yellow-bellied glider, 34% of those of the squirrel glider, and 76% of those of the sooty owl were in existing protected areas or on public land not vulnerable to clearing. Similar values came from the local model. These relationships meant that MaxGain and MinLoss strategies produced spatially different reserve networks. MaxGain strategies placed reserves mostly in unreserved public land where the highest number of occurrences could be sampled with minimum cost. In contrast, MinLoss strategies focused reservation on parts of the planning region that were more vulnerable but had fewer occurrences of each species.

The correlation between habitat suitability and land cost was species-specific. Squirrel glider occurrences tended to be in more expensive areas ($\rho = 0.19$, $p<0.001$) then either the sooty owl ($\rho = -0.04$, $p<0.05$) or yellow-bellied glider ($\rho = -0.06$, $p<0.001$).

Across all planning units, vulnerability and cost per hectare were slightly correlated ($\rho = 0.12$, $p<0.001$). Across private land, subject to habitat loss in my scenarios, the correlation was stronger ($\rho = 0.31$, $p<0.001$). Therefore, the emphasis of the MinLoss strategies on averting loss rather than maximizing protection meant that they tended to reserve more expensive planning units, exacerbating the budget stress already inherent in the conservation planning problem.

3.3.2 Reserve selection strategies

Can information about species-specific fragmentation effects be used to schedule conservation actions and improve conservation outcomes?

Fragmentation was a strong component of the total loss of expected occurrences for the sooty owl and the yellow-bellied glider (Figure 3.3a). In the low loss rate scenario, an average of 65% of the expected loss of yellow-bellied glider occurrences was attributable to fragmentation. This average percentage decreased to 46% with the high loss rate (minimum with MaxGain-local applied with high budget; maximum without reservation). For the sooty owl the averages for low and high loss rates were, respectively, 82% (minimum without reservation; maximum with MinLoss-neighbourhood applied with high budget) and 69% (minimum with MaxGain-neighbourhood applied with high budget; maximum with MinLoss-neighbourhood applied with high budget). The squirrel glider was barely affected by fragmentation given its small home range.

I found no significant advantage in performance when using a MaxGain approach with a neighbourhood model compared to the same approach with a local model (Figure 3.4).

When vulnerability was considered in the selection strategy (MinLoss), the choice of the appropriate model became more important. MinLoss-neighbourhood achieved better outcomes than MinLoss-local in scenarios with high loss and reservation rates. The relative improvement of the first strategy on the latter were 9.2% for the yellow-bellied glider (515 expected occurrences), 3.5% for the squirrel glider (553 expected occurrences) and 5.3% for the sooty owl (193 expected occurrences). A complete evaluation of all strategies including extended analyses to year 40 of the simulations is in appendix 7.2.4.

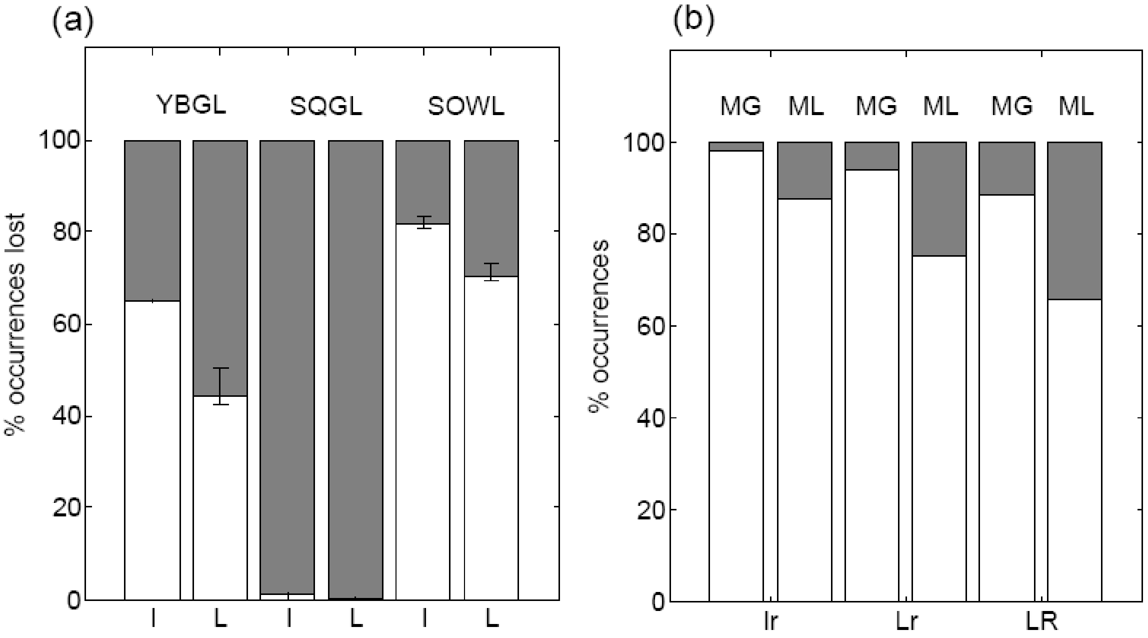

Figure 3.3 Effects of habitat fragmentation on study species.(a) Percentages of occurrences lost in the landscape trough the effects of fragmentation (unshaded portions of bars) and direct habitat loss (grey portions). l = low loss rate; L = high loss rate. YBGL = yellow-bellied glider; SQGL = squirrel glider; SOWL = sooty owl. Each bar shows the mean percentages across replicate simulations for combinations of reserve selection strategy and reservation and loss rate. Minimum and maximum proportions are shown with line-bar where extreme values differed by more than 2%. (b) Effect of habitat loss outside reserves on sooty owl occurrences inside the system of existing and simulated reserves. MG = MaxGain; ML = MinLoss; r = low reservation rate; R = high reservation rate. Both MaxGain and MinLoss were applied with the neighbourhood model. The grey portions of the bars are the percentages of the initial expected occurrences lost by isolation of reserves after their establishment. The unshaded portions of the bars are the percentages remaining in the reserves at the end of the planning period.

Is minimizing loss better than maximizing gain when reservation cost and the species-specific influence of fragmentation are incorporated into conservation planning?

For this comparison, I focused on the strategies that applied a neighbourhood model. There were strong differences between MinLoss and MaxGain when both rates of loss and reservation were high (Figure 3.4). In this comparison, the outcomes from MinLoss were 8.3 % higher for the yellow-bellied glider (471 expected occurrences), 12.4% higher for the squirrel glider (1804 expected occurrences), and 5.0 % higher for the sooty owl (183 expected occurrences). The difference between the performances of these two strategies increased with time for all three species, particularly after the end of the planning period when habitat loss was the only process operating in the region (Appendix 7.2.4).

While a MinLoss approach resulted in higher levels of extant occurrences across the planning region, this net advantage was smaller than it might have been. Areas selected by MinLoss experienced greater subsequent losses of occurrences due to habitat fragmentation than those selected with the MaxGain approach. Post-selection loss of expected occurrences of the sooty owl was more evident with both high loss and high reservation rates, when it reached almost 40% of initial expected occurrences (Figure 3.3b). Results were similar for the yellow-bellied glider but not for the squirrel glider which was insensitive to isolation of reserves.

When applying area as a surrogate for cost the improvement in performance of MinLoss over MaxGain increased, both when applying neighbourhood and local distribution models (Figure 3.5). In particular, with the neighbourhood model and high rates of loss and reservation the difference increased by 15.3% for the yellow-bellied glider, by 12.6% for the squirrel glider and by 20.2% for the sooty owl compared to using my estimates of acquisition costs.

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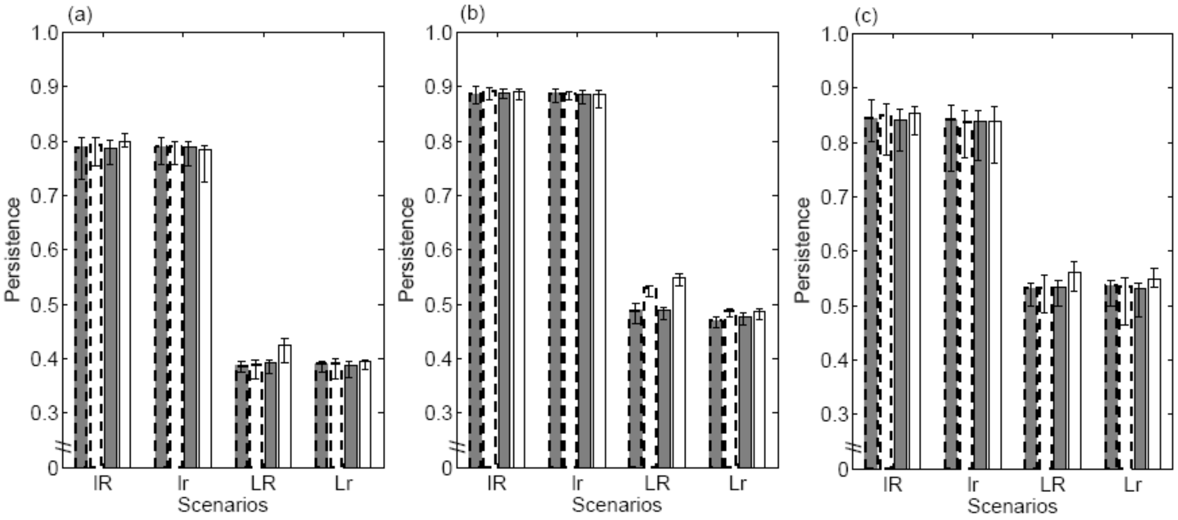

Figure 3.4 Pairwise comparisons of reserve selection strategies in the base scenarios.The y-axes show the proportion of occurrences persisting at the end of the planning period (year 20) as predicted by neighbourhood models (“persistence”). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey bars indicate maximum gain strategies. Unshaded bars indicate minimum loss strategies. (a) Yellow-bellied glider (b) Squirrel glider (c) Sooty owl. l = low loss rate; L = high loss rate; r = low reservation rate; R = high reservation rate. For each strategy, the 90% confidence intervals of the persistence values are also shown.

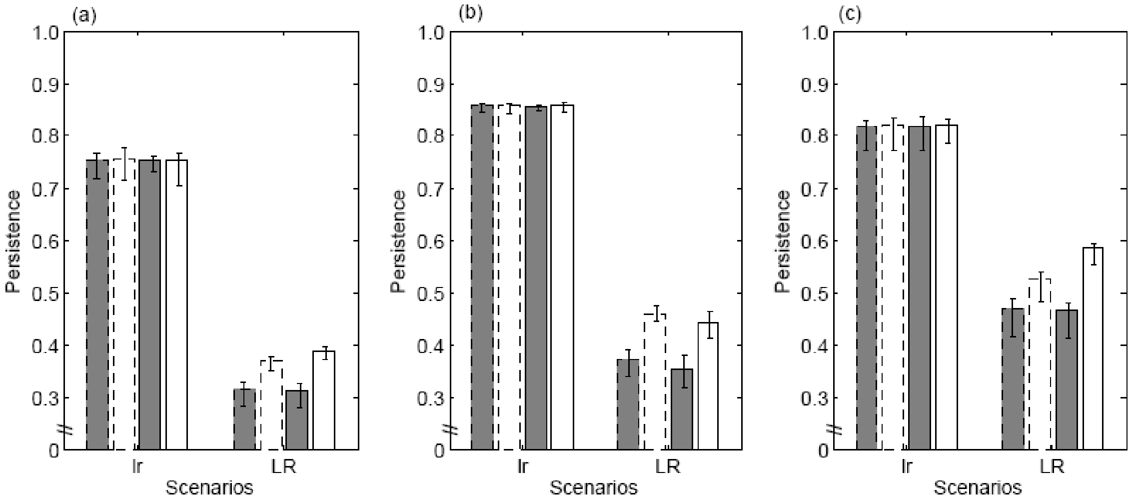

Figure 3.5 Pairwise comparisons of reserve selection strategies using area as a surrogate for cost.

Symbols and colour-coding are the same as in Figure 3.4. The y-axes show the proportion of occurrences persisting at the end of the planning period (year 20) as predicted by neighbourhood models ("persistence"). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey bars indicate maximum gain strategies. Unshaded bars indicate minimum loss strategies. (a) Yellow-bellied glider (b) Squirrel glider (c) Sooty owl. l = low loss rate; L = high loss rate; r = low reservation rate; R = high reservation rate. For each strategy, the 90% confidence intervals of the persistence values are also shown.

3.4. Discussion

I simulated the effect of incremental, interacting reservation and land conversion for 20 years for three species with a variety of reserve selection strategies and differing rates of reservation and loss of forest. I considered the effect of fragmentation on the predicted occurrence of the target species by including neighbourhood context measures as predictors in the species distribution models. I also considered realistic spatial variation in costs of reservation and compared my results with planning unit area as a surrogate for cost.

My findings indicate that fragmentation is important in explaining loss of occurrences of two species, the sooty owl and the yellow-bellied glider. The squirrel glider was barely affected by fragmentation (Figure 3.3a). Not surprisingly, the reserve selection strategy that minimized loss and considered the effects of fragmentation was better at promoting species persistence (Figure 3.4). However, the neighbourhood model generally gave no consistent improvement over the local model when the approach was maximizing gain (Figure 3.4). This counterintuitive result was due to the local model predicting occupancy values that were less negatively correlated to vulnerability than the neighbourhood model. The MaxGain-local strategy therefore, incidentally, tended to focus more reservation on vulnerable areas than MaxGain-neighbourhood. The greater ability of MaxGain-local to mitigate direct habitat loss generally counterbalanced the superiority of MaxGain-neighbourhood in maximizing expected occurrences in reserves. This result reflects the idiosyncratic nature of the species occupancy patterns. Its generality is difficult to judge and it does not necessarily justify the use of a simplistic model. Instead, the results overall reinforce the importance of incorporating data on vulnerability directly into priority setting and complementing these with the best available data on biodiversity.

Previous studies have argued that maximizing gain is less efficient than minimizing loss because it over-allocates budgets to secure areas and under-allocates them to areas more likely to be lost (Costello & Polasky 2004; Drechsler 2005; O'Hanley et al. 2007; Pressey et al. 2004; Strange et al. 2006; Wilson et al. 2006). My simulations support the same conclusion (Figure 3.4 and Appendix 7.2.4). While generally these previous studies did not observe a difference between the two approaches larger than 5%, in this case MinLoss outperformed MaxGain by up to about 12.4%. This is probably due to the larger size of my problem (~ 4000 planning units), and to a longer planning period. Large problems increase the number of possible solutions and therefore the potential difference between better and worse strategies. The differences in performance among reserve selection strategies tended to increase over time (Appendix 7.2.4). In fact, during the planning period, MaxGain accumulated ‘suboptimal’[3] decisions, progressively widening its inferiority to the MinLoss approach. This kind of trend was also noted by Pressey et al. (2004) and Moilanen and Cabeza (2007). With short planning periods the two approaches perform similarly. However minimizing loss could be a risky approach if the habitat loss continues without further investment in conservation. In these conditions, part of the high-value habitat left unprotected by MinLoss because of low vulnerability can be lost afterwards, thus making the approach less effective. MaxGain is a more precautionary approach in this instance, because it secures areas of high biodiversity value in the short time allowed for protection. An algorithm has been proposed that is almost as good as MinLoss in terms of retention but is better in ensuring high representation, thus making it more resilient to further loss beyond the planning period (Moilanen & Cabeza 2007).

Three factors might have prevented MinLoss to perform even better. First, vulnerability and cost were slightly correlated. Prioritizing vulnerable areas therefore translated into reserving smaller and fewer reserves than when vulnerability was ignored. My finding that the difference in performance between MinLoss and MaxGain increased when using planning unit area as a surrogate for cost supports this explanation. Previous studies that ignored variable costs might have failed to accurately identify this trade-off.

A second explanation is related to the species used in the study. The sooty owl and the yellow-bellied glider tended to occur in extensive, intact forest with low suitability for

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[3] Suboptimal is quoted because neither of the algorithms provides a guaranteed optimal solution to the problem.

development and were already largely protected. Therefore, expanding protected areas in the lowlands subject to habitat loss added only marginally to the persistence of these species.

The last explanation relates to the spatial autocorrelation of vulnerability. In my simulations, the pattern of vulnerability values tended to be clustered. Therefore, areas with high vulnerability values were likely to be surrounded by other areas with high vulnerability values. As a result, the neighbourhoods of areas reserved by the MinLoss approach tended to become more fragmented through time, reducing the 20-year outcomes of reserved areas for the yellow-bellied glider and the sooty owl (Figure 3.3b). The extinction of local populations inside reserves after their isolation is well documented elsewhere and can be caused by stochastic events affecting small populations, breakdown of ecological processes, edge effects, or interactions between these (Newmark 1996; Woodroffe & Ginsberg 1998). Overall, my results strengthen the case for MinLoss strategies that consider neighbourhood processes in scheduling, while also indicating the potential value of a more sophisticated approach than the one used in my study. This improved approach would also consider the vulnerability of areas in the neighbourhood of areas being considered for reservation (below).

My analyses can be improved in several ways. I accounted for a contagion effect in deriving the initial probability of conversion to urban areas but did not have similar information for agricultural suitability. I therefore assumed that successive losses of vegetation were spatially independent (see chapter 6 for further discussion).

I placed no spatial constraints on the displacement of land clearing by reservation, assuming only that it was moved elsewhere within vulnerability classes, whereas reservation can also attract or inhibit nearby development pressure. My intent here was to test different scheduling strategies in more realistic scenarios than in previous studies by accounting for species dynamics and heterogeneous land cost. This is a fundamental step towards forecasting the effect of conservation policies on biodiversity persistence and allowed me to observe novel and unexpected behaviours of two common reserve selection approaches. Building an accurate model of urban and agricultural development for the Hunter valley was beyond the scope of this research. Moreover, a more sophisticated model of land use change, incorporating the potential dynamic interactions between reservation and development pressure would not necessarily yield different results. The dynamics of costs (Armsworth et al. 2006), are also part of this more complex picture.

Prior to this study, the impact of ongoing habitat loss outside previously established reserves had not been explicitly identified in a scheduling framework. Because habitat loss is typically spatially auto-correlated (Overmars et al. 2003), strategies that consider habitat loss in priority setting are more likely to encounter the adverse impacts of fragmentation and isolation of reserves on species with large area requirements (see also chapter 2). These strategies are likely to benefit from considering the vulnerability of areas in the neighbourhoods of focal areas as well as that of the areas themselves. My findings here have directed my future work toward accounting for neighbourhoods of focal areas in two ways: first by considering habitat configuration at the time of selection (in this study) and, second, by also anticipating the isolation of areas after they have been selected for conservation investment.

Chapter 4. Habitat vulnerability in conservation planning - when it matters and how much[4]

Abstract

Addressing the vulnerability of areas to habitat loss remains a challenge for conservation planners. Different areas are often assumed equally vulnerable to habitat loss or, worse, conservation attention focuses on remote, unproductive areas contributing little to minimizing biodiversity loss. Understanding vulnerability is crucial to planning but gathering the required information can be time consuming and expensive; and any data on vulnerability will be uncertain. I investigated the circumstances in which including vulnerability data produces better conservation decisions. I found that it is best to use existing information on vulnerability only when uncertainty is less than 20-30%. With higher uncertainty and large spatial variance in vulnerability, it is best to improve vulnerability data before making conservation decisions. Otherwise, it is best to ignore vulnerability and consider only biodiversity value. Other important factors are whether reservation displaces or inhibits habitat loss and the correlation between biodiversity value and vulnerability.

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[4] Visconti, P., R. L. Pressey, M. Bode, and D. B. Segan. 2010. Habitat vulnerability in conservation planning—when it matters and how much. Conservation Letters **3**:404-414.

4.1 Introduction

Conservation actions must be scheduled when resources are limited, because it is often infeasable to simultaneously protect all features of conservation interest (Possingham *et al.* 2009).

Conservation priority-setting therefore occurs over two dimensions: space and time (Pressey & Taffs 2001). Many approaches to scheduling are possible but two iterative heuristics define its extremes: minimizing biodiversity loss (hereafter MinLoss) and maximizing biodiversity gain (hereafter MaxGain) (chapters 1,3 and Wilson et al. 2006).

Prior studies have found that MinLoss outperforms MaxGain in retaining biodiversity features when ongoing habitat loss is considered, except when there is low spatial variability in habitat vulnerability (Costello & Polasky 2004; Wilson *et al.* 2006). In these circumstances, the approaches converge to the same solution. They also converge when loss rates are much higher than reservation rates - circumstances that partially validate MaxGain's underlying assumption that everything will eventually be lost (Wilson *et al.* 2006). MaxGain outperforms MinLoss with uncertain funding or implementation opportunities, when areas with high biodiversity values and low short-term vulnerability cannot be scheduled for later protection (as assumed by MinLoss). Examples include abrupt funding cessation (McBride *et al.* 2007) or uncertain availability of areas for conservation (Meir *et al.* 2004). Each of these analyses, however, assumes that MinLoss uses accurate vulnerability estimates – but these are not always available. As Wilson et al. (2005) state: “If vulnerability is overestimated, scarce resources could be allocated to areas that do not, in fact, need protection. Conversely, if vulnerability is underestimated, areas that are, in fact, threatened could be overlooked and have their conservation values reduced or eliminated.” Using a badly informed MinLoss might therefore be worse than ignoring vulnerability altogether. Intuitively, such negative consequences would be worse if biodiversity value was positively correlated with vulnerability (Balmford and Long 1994), because areas of high biodiversity value would be consistently under-prioritized. The impacts of such correlations remain unexplored. Furthermore, the prediction of future habitat loss is typically based on two alternative assumptions. Either a constant number of areas are lost each time-step regardless of reservation ("threat displacement", e.g. Pressey *et al.* 2004; Spring *et al.* 2007), or the number of areas lost diminishes through time as reservation proceeds (“threat inhibition”, e.g. Costello & Polasky 2004; Wilson *et al.* 2006). With displacement, destructive activities locally prevented by reservation are displaced elsewhere within the region because the drivers of habitat loss are unaffected by the diminishing supply of land resulting from ongoing loss and reservation (Armsworth *et al.* 2006). Alternatively, inhibition would occur if the drivers of habitat loss require particular, non-substitutable areas, as when new reserves are buffered by development restrictions or reduced supply increases land prices and reduces demand (Armsworth *et al.* 2006).

Table 4.1 summarizes the main factors known or expected to influence the relative performance of MinLoss and MaxGain. These factors are likely to determine the most effective allocation of limited conservation resources, yet some are unexplored while the effects of others are understood from only one or a few studies.

Here I assess the relative performance of MinLoss and MaxGain in a suite of scenarios that reflect the range of ecological and socio-economic conditions encountered by conservation planners. To construct these scenarios, I vary the following factors from Table 4.1 in combination:

1) Spatial correlation between biodiversity value and vulnerability
2) Displacement or inhibition of biodiversity loss by new reserves
3) Spatial variance of vulnerability
4) Uncertainty in vulnerability estimates

I limited the factors to focus on those not already investigated plus vulnerability variance, which interacts directly with the remaining factors.

I measured the influence of these factors on the relative performance of MinLoss and MaxGain in terms of retention, i.e., the proportion of biodiversity value in the hypothetical study region still extant after 10-years of simulated, interacting habitat loss and reservation. I interpreted the results by providing rules of thumb for conservation practitioners to apply in deciding whether to: 1. take conservation actions based on the available information on vulnerability; 2. improve information on vulnerability; or 3. discard information on vulnerability and prioritize solely on biodiversity benefit.

Table 4.1. Factors known or expected to affect the relative performance of MaxGain and MinLoss.

Factor	Effects	References
Spatial variance in vulnerability	Increasing values favor MinLoss	(Wilson *et al.* 2006)
Vulnerability uncertainty	Increasing values could disfavor MinLoss	
Correlation between vulnerability and biodiversity value	Positive values might amplify the effects of vulnerability uncertainty. Wider difference between MinLoss and MaxGain with negative correlation.	Moilanen and Cabeza (2007)
Inhibition or displacement effects of reservation on habitat loss	Unknown	
Uncertainty about future conservation opportunities	Increasing values disfavor MinLoss	(McBride et al. 2007; Wilson et al. 2006)
Correlation between cost and vulnerability	Positive values disfavor MinLoss	(Newburn et al. 2006; Spring et al. 2007; Visconti et al. 2010*)
Spatial autocorrelation of habitat loss	Increasing values disfavor MinLoss for species sensitive to habitat fragmentation	(Visconti *et al.* 2010)
Rates of habitat loss and reservation	Increasing values amplify the differences determined by other factors	(Moilanen & Cabeza 2007; Pressey et al. 2004; Visconti et al. 2010);
Conservation targets	Larger targets amplify the differences determined by other factors	(Pressey *et al.* 2004)
Length of planning period	Increasing values amplify the differences determined by other factors	(Moilanen & Cabeza 2007; Pressey et al. 2004; Visconti et al. 2010);

* This reference contains the results presented in chapter 3.

4.2 Methods

4.2.1 Study design

My study design (Figure 4.1) involved simulated landscapes made of environmentally homogeneous habitat patches, which I considered as potential conservation areas. I chose a simulation study because this gave me complete control over the range of variation in key factors. I expect actual conservation regions to be located within this parameter space. Each landscape was characterized by a level of vulnerability variance among areas and populated by biodiversity features with specific levels of correlation between their abundances and the vulnerability values of areas. For the MinLoss approach, I tested different levels of uncertainty in the vulnerability estimate (MaxGain does not consider vulnerability). Finally, for each combination of uncertainty and variance in vulnerability, I simulated two effects of reservation on habitat loss: displacement and inhibition.

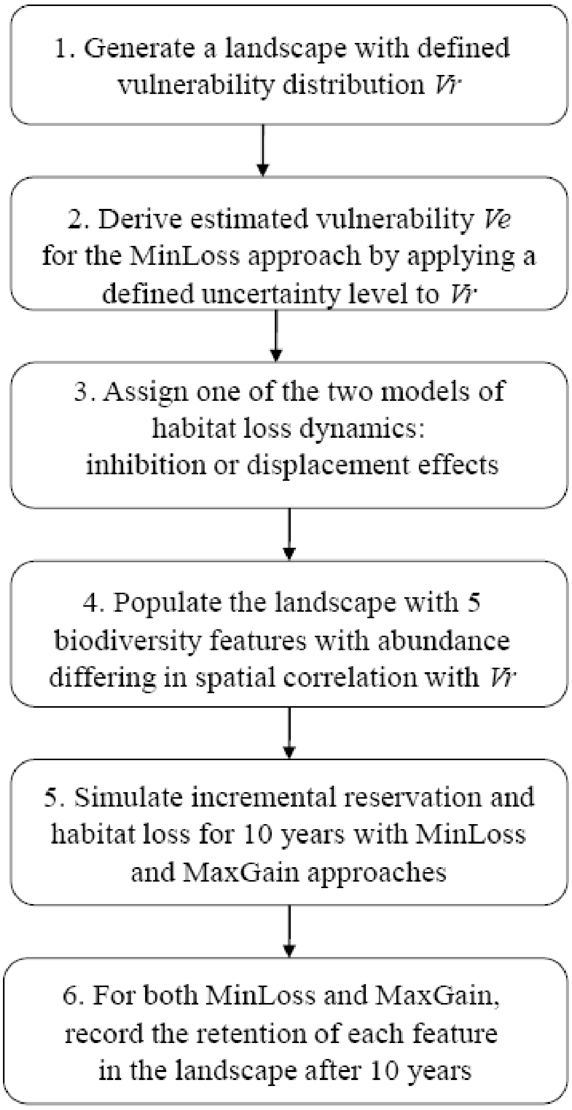


Figure 4.1. Study design. I varied four factors simultaneously: 1. Spatial variance in vulnerability across the landscape (21 levels); 2. Uncertainty in vulnerability estimates provided to managers for applying the MinLoss approach (11 levels); 3. Type of interaction between habitat loss and reservation (2 levels); and 4. Correlation between abundance of biodiversity features and vulnerability (5 levels). All 5 levels of correlation (the 5 features) were subject simultaneously to the variation of the other factors because the 5 features co-existed in the same landscape. I simulated each of the 462 combinations of the first three factors 100 times to account for the variation in performance of individual simulations related to their independent sequences of reservation and stochastic loss events.

4.2.2 Simulations

Model definition

The system consisted of a set of $N = 1000$ areas for conservation assessment. Each area n

contained five biodiversity features. The correlation between each feature's abundance and vulnerability varied independently, between -0.8 and +0.8 in intervals of 0.4. Total abundance and the variation in local abundance among areas were constant for each feature. Each area immediately lost all features if it was developed. If reserved, all features were preserved in perpetuity.

Reserve selection

Managers made decisions about the locations of new reserves using either MinLoss or MaxGain approaches. The objective functions and constraints applied to these heuristics are in Appendix 7.2.1. Managers could reserve a maximum of 20 areas per year.

Habitat loss models

The annual probability that an area would be lost P_{n0} was equal to its vulnerability, multiplied by the habitat loss rate LR (the proportion of habitat lost per year), reflecting the development pressure in the region. Areas with high inherent vulnerability have characteristics that make them amenable to development (e.g., high soil fertility) but even these would not be developed in the absence of a driving force such as human population growth. I applied an annual loss rate LR of 5% of the areas to all simulations. Such high habitat loss rates can amplify the differences between good and poor approaches to scheduling conservation action (Pressey *et al.* 2004; Visconti *et al.* 2010). They can also alter conclusions about best-performing algorithms for scheduling (Moilanen *et al.* 2009). Therefore, I also tested a lower loss rate (2%) to assess the sensitivity of the rules of thumb to this parameter.

I implemented the displacement model using a weighted random sample without replacement (Efraimidis & Spirakis 2006), with the sample equal to the (constant) number of areas lost annually: $N*LR$. The vulnerability of an area determined its relative probability of being part of the sample.

I implemented the inhibition model as follows:

1. Compare the probability of loss of each area against a random number U~[0,1].
2. Destroy areas with probability of loss higher than this number.

The expected proportion of areas lost in the first year with the inhibition model was $LR/2$ (mathematical explanation in Appendix 7.2.2). To ensure the same expected loss (in the first year only) as with the displacement model, I doubled the P values for the inhibition simulations. Subsequently, the proportion decreased because higher vulnerability areas were lost faster than lower vulnerability areas, reducing the mean vulnerability of extant areas. Reserving areas with high vulnerability values had the same effect, hence the inhibition.

Spatial variance in vulnerability

Across the 1000 areas, I generated 21 different spatial distributions of vulnerability (details in Appendix 7.2.3). All distributions were symmetric beta distributions, with a mean of 0.5, and with variances ranging from 0.004 (very little variation around the mean) to 0.083 (vulnerability values distributed uniformly between 0 and 1).

Vulnerability uncertainty

To simulate managers' uncertainty about vulnerability, I chose a random subset of the values from the "real" vulnerability distribution *Vr,* (used in the habitat loss model), and permuted them randomly. The result is a distribution of "estimated" vulnerability *Ve,* representing the knowledge of managers, used to set priorities with MinLoss. The size of the subset reflected the degree of uncertainty (e.g., 10% of the values were permuted for 10% uncertainty). This method ensured that *Ve* and *Vr* had the same variance.

To test the sensitivity of my results to the different effects of uncertainty, I tested an alternative method to derive *Ve* from *Vr*. For *x*% uncertainty I let *Ve* vary uniformly between $\left[\max\left(0, \mathrm{Vr} - \mathrm{x}/100\right), \min\left(1, \mathrm{Vr} + \mathrm{x}/100\right)\right]$ (details in Appendix 7.2.4).

4.2.3 Evaluation

The total number of scenarios was 462 (combinations of 21 levels of vulnerability variance, 11 levels of vulnerability uncertainty, and 2 habitat loss models). To account for the stochastic variation in loss events, I replicated each scenario 100 times. I recorded the retention of each feature for each replicate and for both MaxGain and MinLoss approaches.

I calculated the relative improvement of one approach over the other as the difference in retention of feature *f* between the approaches: $RPB_f = RetML_f - RetMG_f$. I also measured relative performance in terms of the minimum retention (the worst-case outcome of reduced abundance) across all five features: $RPminret = \min\left(RetML_1 \ldots RetML_f\right) - \min\left(RetMG_1 \ldots RetMG_f\right)$. I evaluated each scenario, across its 100 replicates, with mean *RPB* and *RPminret*.

To analyze the influence of each factor on the relative performance of MaxGain and MinLoss

I performed a 4-way ANOVA with RPB_f as the response variable and, as independent variables, the 4 factors investigated plus their second order interactions. I also performed a 3-way ANOVA with *RPminret* as the response variable and, as independent variables, all factors except the correlation between the features' abundance and vulnerability. I derived regression coefficients from a linear regression and the effect size (η squared) from the ANOVAs, representing respectively the direction and strength of each effect.

4.3 Results

4.3.1 Minimum retention

Measured by minimum retention across all features, MinLoss outperformed MaxGain for most of the parameter space (Figure 4.2). MinLoss performed better under threat inhibition than displacement. With both habitat loss models, the difference in performance decreased with increasing uncertainty in *Ve*. The difference increased with increasing variance but only for low uncertainty values. Applying a random deviation from real vulnerability, rather than a permutation, shifted the level of uncertainty at which MaxGain performed best to almost 100% (Figure 7.2 in Appendix). A loss rate of 2% produced identical gradients in relative performance but decreased the magnitude of the differences by ~50% for both methods of generating uncertainty (Figures 7.3 and 7.4 in Appendix).

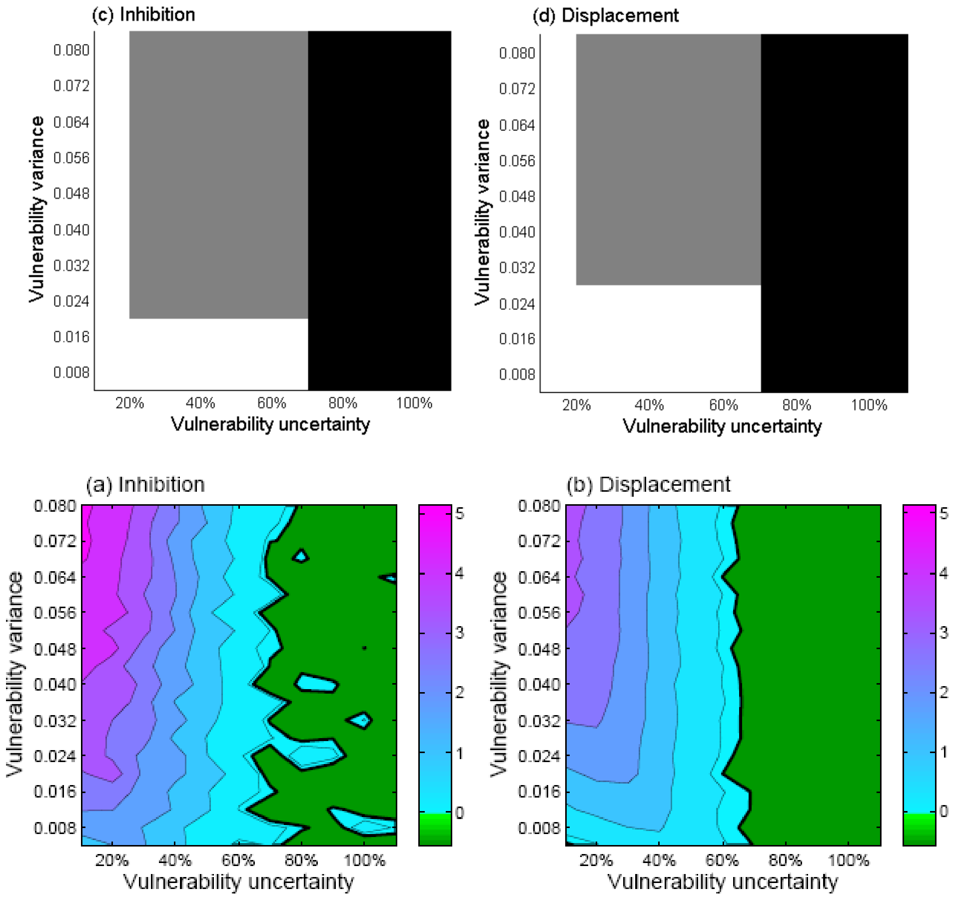


Figure 4.2. Difference in minimum retention across 5 biodiversity features between MinLoss and MaxGain and implications for managers. For (a) and (b), retention was measured as the percentage of initial abundance still extant at the end of the planning period. I calculated percentage difference as MinLoss retention (%) – MaxGain retention (%), so positive values indicate higher retention for MinLoss and negative values (green) indicate higher retention for MaxGain. Each contour line represents an increment of 0.8%. The thicker contour line represents zero difference. x-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). y-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape). Parts (c) and (d) represent the decision space for scheduling conservation actions based on the results in panels (a) and (b). White indicates that the manager should take a MinLoss approach with existing vulnerability data. Grey indicates that the manager should improve the vulnerability estimate before taking a MinLoss approach. Black indicates that the manager should take a MaxGain approach.

The differences in figure 4.2 manifest underlying patterns in the performance (*RPminret*) of MinLoss and MaxGain individually. MinLoss performed worse with higher variance combined with higher uncertainty in vulnerability (Figure 4.3). With higher variance, vulnerability is important in predicting biodiversity loss, so higher uncertainty can direct MinLoss towards lower priority areas. With lower variance, higher uncertainty has a smaller detrimental effect because there is reduced scope for mistakes. For MinLoss, inhibition produced best results with high variance and low uncertainty, and worst results with high variance and high uncertainty (Figure 4.3). Displacement produced a different interaction. MinLoss performed best with low variance and low uncertainty and worst with high variance and high uncertainty (Figure 4.3). For displacement and low uncertainty, MinLoss improved over MaxGain with increasing vulnerability variance (Figure 4.2b), despite the absolute performance of MinLoss remaining the same along this gradient (Figure 4.3). This is because MaxGain performed more poorly across the same parameter space (Figure 4.3). MaxGain ignored vulnerability, so was better when vulnerability was less variable and made less difference to conservation outcomes (Figure 4.3). For the same reason, vulnerability uncertainty did not affect MaxGain.

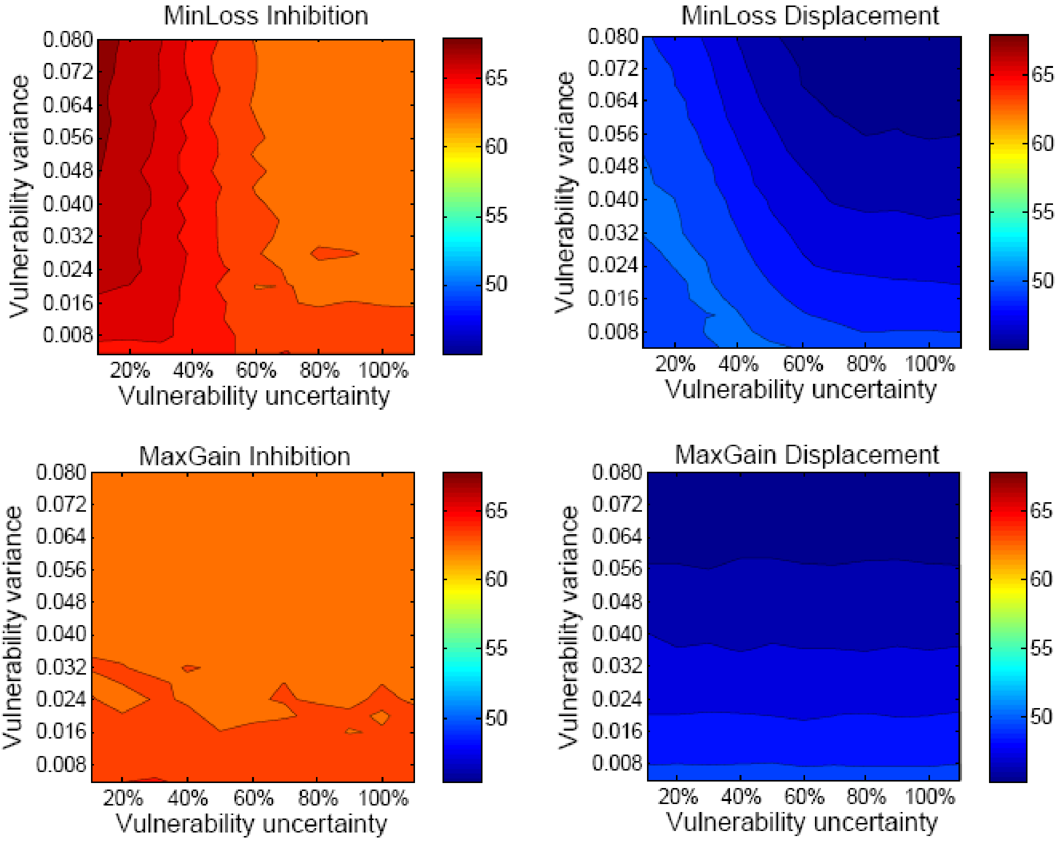


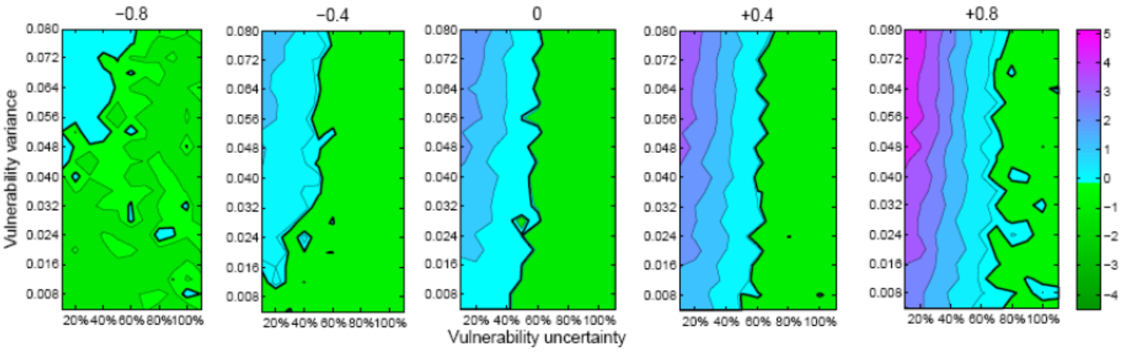
Figure 4.3. Distribution of values of minimum retention across 5 biodiversity features for MinLoss and MaxGain with inhibition and displacement effects.Values are the minimum percentages of initial abundances of features still extant at the end of the planning period. *x*-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). *y*-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape).

4.3.2 Features with different spatial correlation with vulnerability

MaxGain better protected features that were negatively correlated with vulnerability, whereas MinLoss better protected positively correlated features (Figure 4.4).

With inhibition, the relative performance of MinLoss decreased as uncertainty increased but, as I hypothesized, uncertainty had most effect on features that were positively correlated with vulnerability (Figure 4.4a). With displacement, uncertainty improved the relative performance of MinLoss for negatively correlated features, worsened it for positively correlated features, and was neutral for the feature with no correlation (Figure 4.4b). Like the results for minimum retention, vulnerability variance was influential only when uncertainty was low, especially with the displacement model.

(a Inhibition)



(b Displacement)

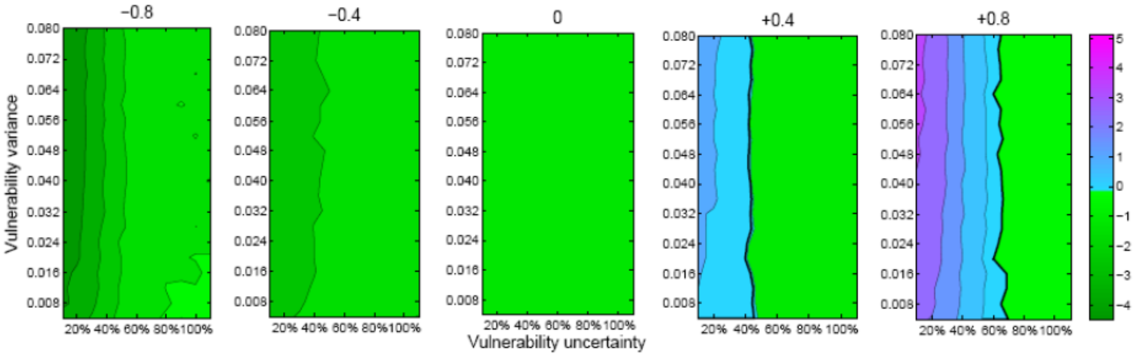


Figure 4.4. Differences in retention between MinLoss and MaxGain across 5 biodiversity features. Retention was measured for each feature as the percentage of initial abundance still extant at the end of the planning period. I calculated percentage difference as MinLoss retention (%) – MaxGain retention (%). The thicker contour line represents zero difference. Positive values indicate higher retention for MinLoss and negative values (green) indicate higher retention for MaxGain. x-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). y-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape). The correlation coefficient between each feature's abundance and the vulnerability of areas is above each graph.

4.3.3 Overall effects and interactions

Of all the factors tested, uncertainty in vulnerability had the greatest influence on *RPminret,* explaining about 38% of its variation (Table 4.2). The interaction term between vulnerability variance and uncertainty also had a moderate effect size. Overall, the three factors and their interactions explained about 48% of the variation in *RPminret*. For RPB_f values, the correlation between feature abundances and vulnerability was the strongest factor influencing variation, both in isolation and when interacting with vulnerability uncertainty (Table 4.3). In summary, vulnerability variance and the correlation between features’ abundances and vulnerability had positive effects on MinLoss, while vulnerability uncertainty had negative effects. Threat inhibition favored MinLoss more than threat displacement.

Table 4.2 ANOVA results with the response variable being the difference between MinLoss and MaxGain in minimum retention across all 5 features. The multi-linear regression coefficients (β) between minimum retention and each numerical factor are in the final column (no regression possible with the categorical variable loss model and its interactions terms). All coefficients are highly significant. The r^2 of the multiple linear regression is 0.407. η^2 is the effect size and represents the percentage variance in the response variable explained by each factor. η^2 values equal to 2, 6 and 14% represent respectively small, medium and strong effects of the factor on the response variable.

Source	**Sum Sq.**	**η^2 (*100)**	**d.f.**	**Mean Sq.**	**F**	**p**	**β**
variance (1)	0.48	2.28	20	0.02	99.34	0	0.2903
uncertainty (2)	8.00	37.86	10	0.80	3.30e+4	0	-0.0025
loss model (3)	0.30	1.40	1	0.30	1.22e+4	0	-
1*2	1.01	4.77	200	5.00e-3	20.80	0	-0.4475
1*3	0.01	0.07	20	7.66e-4	3.16	0	-
2*3	0.18	0.85	10	0.02	73.94	0	-
1*2*3	0.06	0.31	200	3.26e-4	1.34	<0.001	-
Error	11.09	52.46	45938	2.42e-4			
Total	21.15	100	46199				

Table 4.3. ANOVA results with the response variable being the difference between MinLoss and MaxGain in retention for each of the 5 features individually. The multi-linear regression coefficients (β) between feature retention and each numerical factor are in the final column (no regression possible with the categorical variable loss model and its interactions terms). All coefficients are highly significant. The r^2 of the multiple linear regression is 0.420. η^2 is the effect size and represents the percentage variance in the response variable explained by each factor. η^2 values equal to 2, 6 and 14% represent respectively small, medium and strong effects of the factor on the response variable.

Source	**Sum Sq.**	**η^2 (*100)**	**d.f.**	**Mean Sq.**	**F**	**p**	**β**
variance (1)	0.380	0.14	20	0.02	31.23	0	0.5689
uncertainty (2)	12.39	4.57	10	1.23	2.03e+3	0	0.0043
loss model (3)	18.62	6.88	1	18.62	3.05e+4	0	-
abundance-vulnerability correlation (4)	39.65	14.65	4	9.91	1.62e+4	0	0.0792
1*2	1.90	0.70	200	9.50e-3	15.56	0	0.1137
1*3	1.39	0.51	20	0.07	114.03	<0.01	-
1*4	0.42	0.16	80	5.40e-3	8.81	0	0.0754
2*3	6.47	2.39	10	0.65	1.06e+3	0	-
2*4	43.72	16.15	40	1.09	1.79e+3	0	0.0718
3*4	5.15	1.90	4	1.29	2.11e+3	0	-
Error	140.60	51.93	230610	6.1e-4			
Total	270.70	100	230999				

4.4 Discussion

4.4.1 Spatial correlation between biodiversity value and vulnerability of areas

I found that MinLoss better protected features that were positively correlated with vulnerability, while MaxGain was better for negatively correlated features. In contrast, Moilanen and Cabeza (2007) found that MinLoss was always superior to MaxGain but especially with negatively correlated biodiversity values. This implies a trade-off between biodiversity representation and retention overlooked by MaxGain, explaining the superiority of MinLoss in their study. The trade-off applies when the correlation with vulnerability involves the overall biodiversity value of an area. In this study, with different correlations for individual biodiversity features, the trade-off in protection was among features. The approaches resolved this trade-off differently. MinLoss favored features with worse retention (positively correlated with vulnerability) and MaxGain favored those with worse representation.

Although my results are not surprising, given the focus of MinLoss on vulnerable areas and features with the poorest outlook, it is important to consider their implications for ongoing decline of vulnerable species where opportunistic conservation takes place (Pressey 1994; Pressey *et al.* 2002; Turner *et al.* 2006). In principle, threatened features should have highest priority because delayed protection will likely result in their decline or extinction. My results indicate that managers should therefore take a MinLoss approach, although the choice depends also on other factors, below. However, given chronic funding shortages for conservation, when reversing the prognosis for critically endangered features is unlikely, a triage approach suggests protecting areas with lower threats, thereby maximizing conservation efficiency and effectiveness (Bottrill *et al.* 2008).

4.4.2 Displacement or inhibition of biodiversity loss by new reserves

The nature of threat dynamics determined the magnitude of the difference between approaches but did not qualitatively alter the best approach. When reservation only displaced habitat loss, the improvement of MinLoss over MaxGain in terms of minimum retention was modest and attributable to MinLoss identifying areas with highest contributions to retention. This was subject, of course, to the uncertainty of information on vulnerability (below). With inhibition, the relative performance of MinLoss was stronger. MinLoss quickly removed suitable areas from development by reserving very vulnerable areas. In doing so, it not only influenced which areas would persist, it also reduced the total area lost by reducing the mean vulnerability in the landscape. There are many evidences all over the world of displacement (or leakage) effects of habitat loss by protected areas (Ewers & Rodrigues 2008). These result in a limited net gain of natural habitat or in some cases even a net loss compared to a baseline of habitat loss (Wittemyer et al. 2008). My findings reinforce this empirical evidence, and suggest that implementing protected areas have reduced benefits if their only effect is to displace habitat conversion into other ecologically valuable areas. In such circumstances habitat protection needs to be followed by political and economical incentives to reduce the consumption of environmental resources.

4.4.3 Spatial variance in vulnerability

This factor had a small but significant effect both in isolation and in interaction with other factors (Tables 4.2, 4.3). With inhibition, variance in vulnerability determined the extent to which MinLoss could decrease the mean vulnerability of remaining habitat. If variance was high, preempting development by reserving vulnerable areas could decrease the mean vulnerability of remaining areas thereby reducing the extent of further loss of features. When variance was low, the mean vulnerability of the landscape was unaltered by reservation so MinLoss and MaxGain performed equally. The stronger reduction in loss rate with higher vulnerability variance did not apply with displacement because the rate of development was fixed.

With both inhibition and displacement, increasing vulnerability variance increased the scope for MaxGain to misallocate conservation effort to areas with little contribution to biodiversity retention, thus widening the gap with MinLoss. Vulnerability variances similar to the maximum value tested here have been reported for terrestrial (Pressey *et al.* 1996) and marine regions (Halpern *et al.* 2008).

4.4.4 Uncertainty in estimates of vulnerability

Uncertainty in estimates of vulnerability was the most important factor in this study, accounting for much of the variability in the difference between MinLoss and MaxGain in minimum retention across features. With both loss models and across all levels of vulnerability variance, the best approach switched to MaxGain when approximately 70% of the estimates were incorrect (but at larger values with the random deviation method). Uncertainty also determined the magnitude of the difference between approaches via its interaction with vulnerability variance which explained ~5% of variation relative performance between approaches (Table 4.2). When variance was high, any increase in uncertainty caused an important loss of information about expected biodiversity loss, and therefore reduced the relative performance of MinLoss. When variance was low, increasing uncertainty made little difference because vulnerability itself was less influential. Uncertainty was also involved in a three-way interaction with the habitat loss model and vulnerability variance. With inhibition effects, strong vulnerability variance benefited MinLoss only with low uncertainty. Only in these circumstances could MinLoss effectively identify and secure the most valuable and vulnerable areas before they were developed, while reducing overall habitat loss. I discuss a second three-way interaction in Appendix 7.2.5.

4.4.5 Rules of thumb for conservation decision-making

To minimize biodiversity loss, I suggest using a MinLoss approach with existing vulnerability estimates (white areas in Figure 4.2 c,d) if uncertainty is estimated at less than 20%, regardless of vulnerability variance. This remains the best choice up to 70% uncertainty with variance < 0.02 (inhibition) and variance < 0.03 (displacement). With uncertainty between 20 and 70% and larger variance values, improving the estimate of vulnerability is the best strategy, given that a small reduction in uncertainty under these circumstances gives a large improvement in the relative performance of MinLoss (grey areas). With any other combination of values for both loss models, MaxGain is the best approach (black areas, which reduce to the right if uncertainty is generated with the random deviation method, Appendix 7.2.4).

To use my rule of thumb, managers need to estimate uncertainty in vulnerability, requiring expert scrutiny of the vulnerability model or a validation dataset of actual land use transitions. Validation could involve applying the model to a past landscape and comparing with the present.

Improving *Ve* will often require money and time to collect more data and/or develop better loss models. Although these investments are not necessarily large, the benefit of improving

Ve needs to be evaluated against potential lost opportunities for timely protection (Grantham et al. 2009; McDonald-Madden et al. 2008). Methods are still needed to balance these considerations when selecting a prioritization strategy and to develop adaptive approaches that set initial priorities with available vulnerability estimates, and then refine the approach as new data become available.

4.4.6 Applying the rule of thumb to real-world case studies

I tested the predictive ability of my rules of thumb with two case studies that applied simulations and measured retention for datasets used in actual planning exercises (Table 4.4). While these studies are not perfectly comparable because of slight differences in habitat loss models and longer planning periods, the results agree with my findings here, especially regarding the effects of vulnerability variance.

Table 4.4. Two case studies investigating relative performance of MinLoss and MaxGain. These simulations studies have reported values of some of the factors investigated here, and the observed improvement in biodiversity retention from considering vulnerability (equivalent to the benefit of MinLoss over MaxGain).

References	**Habitat loss model**	**Planning period**	**Loss rate (LR, % landscape p.a.)**	**Reservation rate (RR, % landscape p.a.)**	**Assumed uncertainty**	**Vulnerability variance***	**Performance difference**	**Features abundance vs. vulnerability correlation**
(Visconti *et al.* 2010)[†]	Displacement	20 years	0.65 (low) 3.25 (high)	0.15 (low) 0.75 (high)	0	0.051 (59%)	[‡§] 0.32% (low LR & low RR) 8.87% (high LR & high RR)	0.3653
(Pressey *et al.* 2004)	Displacement	25 years[¶]	0.17	0.3	0	0.11 (100%)[¥]	5.97%[#]	-0.3305

* The value in parentheses next to the vulnerability variances expresses the proportion of vulnerability distribution tested in the present study which had variance lower than the variance observed in the case study.

† This case study tested both variable costs and homogeneous costs; I report here only the results from using homogeneous costs for comparability with the present study.

‡ Across the species tested in this study I report only the Squirrel glider *Petaurus norfolcensis*, which, like the virtual species in the present study, did not exhibit responses to habitat fragmentation.

§ This case study reported the relative difference in performance [(best retention – worst retention) /worst retention] which I have expressed here in absolute differences for comparability with the present study.

¶ A longer planning period was simulated in this case study but 25 years was the available time-slice closest to the planning period tested in the present study.

¥ The vulnerability distribution in this dataset was strongly right-skewed and had a variance outside the scale of values possible with symmetric distributions like the ones tested here.

This study tested retention resulting from many approaches to scheduling. I have selected approaches that were the most similar to those tested in the present study. The value shown is the average gain in minimum retention from incorporating vulnerability into these scheduling approaches.

4.4.7 Limitations

My results only apply to MinLoss and MaxGain which I chose because they are widely published and often used for their ability to solve large, complex and realistic problems involving non-linearities such as the effects of connectivity. Other approaches include integer linear programming (Snyder *et al.* 2004) and stochastic dynamic programming (Costello & Polasky 2004; Strange *et al.* 2006; Wilson *et al.* 2006) and its approximations (Drechsler 2005; Moilanen & Cabeza 2007). Most of these can only solve simple problems (Moilanen 2008). Future research should expand my analyses to other dynamic reserve selection algorithms.

A second limitation is that I assumed homogeneous costs, despite the potential for costs to vary more than biodiversity value (Bode et al. 2008; Naidoo et al. 2006). The potential positive correlation of acquisition and opportunity costs with habitat vulnerability can influence the relative performance of MinLoss and MaxGain (Newburn *et al.* 2005; Visconti *et al.* 2010) but considering costs here would have added another dimension to an already complex study design, so I leave for later work the investigation of interactions between costs with other factors influencing retention.

Chapter 5. Future hotspots of terrestrial mammal loss[5]

Abstract

Current levels of endangerment and historical trends of species and habitats are the main criteria used to direct conservation efforts globally. Estimates of future declines, which might indicate different priorities than past declines, have been limited by the lack of appropriate data and models. Given that much of conservation is about anticipating and responding to future threats, our inability to look forward at a global scale has been a major constraint on effective action. Here I assess the geography and extent of projected future changes in suitable habitat for terrestrial mammals within their present ranges. I used a global earth-system model, IMAGE, coupled with fine-scale habitat suitability models and parameterized according to four global scenarios of human development. I identified the most affected countries by 2050 for each scenario, assuming that no additional conservation actions other than those described in the scenarios take place. I found that, with some exceptions, most of the countries with the largest predicted losses of suitable habitat for mammals are in Africa and the Americas. African and North American countries were also predicted to host the most species with large proportional global declines. Most of the countries I identified as future hotspots of terrestrial mammal loss have little or no overlap with present global conservation priorities, thus confirming the need for forward-looking analyses in conservation priority setting. The expected growth in human populations and consumption in hotspots of future mammal loss means that local conservation actions such as protected areas might not be sufficient to mitigate losses. Other policies, directed towards the root causes of biodiversity loss, are required, both in Africa and other parts of the world.

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[5] Visconti, P., R. L. Pressey, D. Giorgini, L. Maiorano, M. Bakkenes, L. Boitani, R. Alkemade, A. Falcucci, F. Chiozza, and C. Rondinini. 2011. Future hotspots of terrestrial mammal loss. Philosophical Transactions of the Royal Society B **1578**.

5.1. Introduction

Since the 1500’s, 76 species and 7 subspecies of mammals have gone extinct and another 2 are only extant in captivity. The hotspots of extinctions during this period have been Australia (because of direct killing, invasive rats, foxes, cats, habitat loss), the Caribbean (invasive rats and mongoose, direct killing), and South-Pacific islands (direct killing, invasive rats and snakes) (IUCN 2010a). Despite some conservation successes (Hoffmann et al. 2010), most species are still declining, including a further 29 that may already be extinct such as the Christmas Island Pipistrelle *Pipistrellus murrayi* , the Kouprey *Bos sauveli* and the Baiji dolphin *Lipotes vexillifer* (Schipper et al. 2008).

Twenty-five percent (n = 1144) of all mammals for which there is sufficient information for an assessment of conservation status are threatened with extinction. The largest concentration of threatened terrestrial species is in South and Southeast Asia, the tropical Andes in South America, the Cameroonian Highlands and Albertine Rift in Africa, and the Western Ghats in India. All these regions combine high species richness, high numbers of range-restricted species (Schipper et al. 2008) and high human pressure (Sanderson et al. 2002). Threatened marine species are concentrated in the North Atlantic, the North Pacific, and Southeast Asia, and these are also areas of concentration of range-restricted species (Schipper et al. 2008) and high human impact (Halpern et al. 2008).

Worldwide, the main threats to mammals are habitat loss and degradation (affecting 40% of all mammals) and harvesting (hunting or gathering for food, medicine, and materials, affecting 19%). Among the drivers of habitat loss for mammals, agriculture and pastoralism are the most important, together affecting 40% of terrestrial mammals (n=5330) (IUCN 2010a).

Recently, agriculture and grazing have expanded almost exclusively in the tropics (Gibbs et al. 2010). Between 1980 and 2000, cattle pastureland increased by ~35 million ha in South America and ~7 million ha in Central America (Food and Agriculture Organization of the United Nations 2009). Cropland area increased by ~5 million ha in South America, further fragmenting and reducing the natural habitats of the Llanos of Venezuela, the Atlantic forest of Brazil, the Cerrado and the Amazon. In Southeast Asia, most agricultural expansion during the same period has been for tree plantations which increased from roughly 11 million ha to 17.4 million ha (Food and Agriculture Organization of the United Nations 2009). Oil palm *Elaeis guineensis* plantations increased tenfold from 0.2 million ha to 2.7 million ha in Borneo alone. These plantations pose a serious threat to many threatened species such as the Bornean Orangutan (*Pongo pygmaeus*) with remaining populations occurring mostly outside protected areas in lowland areas of highly suitability for oil palm (IUCN 2010a). In the period 1980-2000, cropland area increased by ~50% in East Africa and ~25% in West Africa.

Globally, between 1995 and 2007, agricultural land increased by 400 million hectares in developing countries but decreased by 412 million hectares in developed countries (Food and Agriculture Organization of the United Nations 2009). The vast majority of this new agricultural land has come at the expense of native vegetation, particularly primary forest where clearing gives the added benefit of timber products (Gibbs et al. 2010). Worryingly, this agricultural expansion is expected to continue in the future. Demand for agricultural products is predicted to increase by up to 50% by 2050 with most expansion in tropical countries (Food and Agriculture Organization of the United Nations 2009).

An assessment of the projected impacts of agricultural expansion on mammals is of utmost urgency to facilitate pre-emptive and effective conservation actions. Here I estimate the impact of future scenarios of expanding agricultural land on the world’s terrestrial mammals. I couple fine-scale, species-specific suitability models for terrestrial mammals with fine-scale projections of land use according to four global scenarios of socio-economic development. I highlight the countries in which the largest global losses of mammal distributions are predicted to occur between 2000 and 2050 and those countries predicted to host the species most in need of protection during this period. I define these countries as the future hotspot of global mammal loss (using loss of habitat as a proxy for species decline and potential extinction), recognising that these future losses are likely to add to (rather than replace) those in areas currently concentrating high numbers of threatened species (Schipper et al. 2008).

5.2. Methods

5.2.1 Habitat suitability and land use change models

I projected the habitat suitability models described by Rondinini et al. (2011) for 5086 species of terrestrial mammals onto four scenarios of human development from the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005b). Two of the scenarios, TechnoGarden and Adapting Mosaic, assume that countries generally take a proactive approach to environmental challenges, with environmental policies implemented to preserve ecosystem services and biodiversity. The other two scenarios, Order from Strength and Global Orchestration, assume that countries will generally react to environmental challenges, with policies implemented only when ecosystem degradation negatively affects human wellbeing. TechnoGarden and Global Orchestration envisage a world with global coordination of economic and environmental policies and sharing and advancement of ideas and technology. However, in the former, coordination emphasize the environment while, in the latter, it emphasizes the economy. In contrast, Order from Strength envisages countries acting in isolation, trade barriers increasing, and global institutions weakening or dissolving. Adapting Mosaic follows the same assumptions as Order from Strength initially, then converges towards TechnoGarden around the second half of the 21st century.

For each scenario, I obtained spatially explicit projections of agriculture and pasture land at 6’ resolution (approximately 10 km at the equator) globally at decadal intervals from 2000 to 2050 using the GLOBIO/HYDE land use change model (Alkemade et al. 2009; GLOBIO 3.0 2010). I used the year 2000 as a baseline because data for 2010 were provided as projections for the Millennium Ecosystem Assessment scenarios. The scenarios are derived from quantitative, spatially explicit models of patterns and trends in human population growth, consumption, production and productivity at 30’ resolution from the integrated assessment model IMAGE (Bouwman et al. 2007) used for the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005c). For each decade, the GLOBIO/HYDE model uses the distribution and extent of crop and pasture in 18 macro-regions estimated by IMAGE to calculate the fraction of different land cover types (GLC2000, Bartholomé & Belward 2005) within 6’ cells using the algorithm described in Klein Goldewijk et al. (Klein Goldewijk et al. 2007, see Appendix 7.4 for details on the models).

I adapted the habitat suitability scores for terrestrial mammals (Rondinini et al. 2011) based on the GLOBCOVER 2.1 classification (European Space Agency 2008) to the classification of the Global Land Cover 2000 model (Bartholomé & Belward 2005) used in the land use projections. Both legends are based on the Food and Agriculture Organization (FAO) Land Cover Classification System (di Greggio & Jansen 2000), which facilitated the building of a correspondence table (Appendix 7.5) based on descriptions of land cover classes. When one

GLC2000 class corresponded to multiple GLOBCOVER classes, I averaged the suitability scores and rounded the value to the closest integer (0,1,2). I considered only GLC2000 cover types of high suitability for species (primary habitat for the species). I excluded medium suitability habitat (suitability score of 1), where the species can be found but not live permanently (Rondinini et al. 2011), to avoid overestimating loss of habitat to expanding land uses. I estimated the amount of suitable area for each species in each 6' cell by multiplying the area occupied by land cover types suitable for the species (from Rondinini et al. this issue) by the proportion of the cell within the species' altitudinal range extracted from the IUCN database (IUCN 2010a). I used 1" Shuttle Radar Topography Mission (SRTM) elevation to measure this proportion (United States Geological Survey 2006). Suitable habitat and suitable elevation were spatially correlated so I might have underestimated the amount of suitable habitat by multiplying these factors. However, this was the only feasible method because I had no spatially explicit data on land cover types within 6' cells. For each species, at intervals of 10 years starting from 2000 (reference year) and ending in 2050, I calculated the total area of suitable habitat (in km^2) within its range. I assumed species ranges to remain fixed until 2050, so assessed losses and gains of suitable habitat only within present ranges (IUCN 2010b). This might have underestimated both losses of habitat (range contractions) and gains (range expansions).

5.2.2. Loss measures

For each scenario, I aggregated the measures of loss of species' habitat by country. I intersected my gridded projections of suitable habitat with the boundaries of 206 countries and overseas territories from the VMap0 data (National Imagery and Mapping Agency 1997). Countries and territories too small to overlay with my 6' grid are in table 7.6 in appendix. I then calculated three different measures of concern or priority for future mammal conservation: species richness weighted by global loss ; species richness weighted by national contribution to global loss; and richness of species with large global declines.

Species richness weighted by global loss

I measured for each species the fraction of the global range in 2000 predicted to be lost by 2050 (relative global loss). I used this as a species weighting and summed these weightings for all species predicted to lose habitat by 2050, and excluded species that gained habitat, to obtain a weighted richness of declining species for each country.

Countries have high values for this weighted richness if they are rich in species incurring large proportional losses of habitat within their global ranges, even if predicted to lose little or no habitat within the countries' borders. Because the measure involves species richness, it is sensitive to country size. I also calculated a variant of this weighted richness which accounts for the proportion of a species range within one country. This proportion is a surrogate for the responsibility of this country for the conservation of the species. The weights applied were $w_s = glob\ loss_s\ p_{sc}$. Where p_{sc} was the proportion of the range of species *s* in country *c*.

Species richness weighted by national contribution to global loss

I measured for each species and each country the fraction of the global loss of suitable habitat by 2050 occurring within the country's borders. I multiplied this fraction by the percentage global loss of the species to emphasize species predicted to be of future global concern. The resulting weighting for species *s*, w_s was therefore

$$w_s = glob\ loss_s\ (\%)\,\frac{nat\ loss_s\ (km^2)}{glob\ loss_s (km^2)}$$

The final measure of weighted species richness indicated which countries contributed most to the global loss of suitable habitat for the species they host. In addition to species richness being correlated with size of country, the weighting itself is sensitive to country size because larger countries encompass larger proportions of the global ranges of many species (the fraction of national and global losses can approach or reach 1). Also for this measure I excluded species predicted to gain habitat, as these are not of conservation concern.

Richness of species with large global declines

For each scenario, I also mapped the number of species in each country with large projected global declines (>30%). This threshold of loss followed criterion A3 of the IUCN Red List for declaring a species as Vulnerable (IUCN 2001). However, according to this IUCN criterion, the projected future loss of habitat for a species must be expected to occur within 10 years or three generations from the time of listing, whichever is the longer. The timeline of 50 years will therefore classify as vulnerable more species than the IUCN criterion, especially among short-lived mammals.

5.2.3 Analyses

For each of the two measures of weighted species richness at the country level, I initially obtained four values, one for each scenario of global change. To assess the extent to which national or global losses varied across human development scenarios, I calculated for each country the variance across scenarios of each weighted richness measure. I report the top 10 countries with the largest variance values for both measures of weighted richness.

I also calculated a single value of each weighted richness measure for each country by averaging the country values across the four scenarios. This is mathematically equivalent to averaging the weights (species global and national losses) across scenarios and summing the mean weights within countries.

For my third measure, I aggregated the number of species with large projected global declines across the four scenarios in two ways. First, I created a worst-case outcome in which a species was accounted for if it was predicted to lose at least 30% of its suitable habitat globally in any of the four scenarios. This involved the unrealistic assumption that the outcome for each species in each country will arise from the combination of all and only the negative attributes of each of the four scenarios. This would require habitat losses within single countries to result from land-use changes predicted in different scenarios that are mutually inconsistent, such as extensive pressure for both meat and vegetable production. This provided an upper bound on the number of species with large projected declines. For my second method of aggregation, I created a best-case outcome in which a species was accounted for only if it lost at least 30% of its suitable habitat globally in all four scenarios. This provided a lower bound to the number of species with large projected declines. It carried the unrealistic assumption that the outcome for each species in each country will arise from the combination of all and only the positive attributes of each of the four scenarios. This is unrealistic because some factors positively affecting species persistence in one scenario can conflict with positive factors in other scenarios. For example, the increase in productivity predicted for some countries by TechnoGarden and Global Orchestration, arising from improved technology, is unlikely to be accompanied by low per capita consumption driven by the extreme poverty envisaged in the same countries by Order from Strength. To reiterate, while both the worst-case and the best-case outcomes are based on unrealistic assumptions, the rationale for them is to provide bounds around the number of species with large projected global declines rather than accurate predictions.

5.3. Results

5.3.1 Richness weighted by global loss

The country with the highest richness weighted by projected range-wide losses is Mexico, followed by Democratic Republic of Congo, Tanzania, Kenya, South Africa, several other Sub-Saharan countries, Brazil and USA. These countries are not necessarily predicted to incur large losses of habitat for mammals because these losses could occur anywhere within the ranges of species they host. In fact, although most of the top 15 countries ranked by these measures are very large, in average across species predicted to have large global declines (more than 30% decline; n=351), 69% of the loss of habitat is predicted to occur outside the borders of each individual country.

Some African species with very large relative global losses across different scenarios are the Pardine Genet *Genetta pardina* (minimum and maximum losses between Millennium Ecosystem Assessment scenarios of 45-63%), Maxwell's Duiker *Philantomba maxwelli* (58-62%), Malawi Galago *Galagoides nyasae* (63-74% of its very restricted range lost), Southern Talapoin Monkey *Miopithecus talapoin* (49-60%), Pouched Gerbil *Desmodilliscus braueri* (89-97%) and Matthey's Mouse *Mus matthei*, (82-90%). In North America, examples of species projected to have significant losses of habitat are the Mexican Spiny Pocket Mouse *Liomys irroratus* (in Mexico and USA, 41-87%), the San Cristobal Shrew *Sorex stizodon* (in Mexico only, 77-84%), and the Swift Fox *Vulpes velox* (in USA only, 37-53%).
Brazil does not have any species with notably high global losses, but this country hosts ~550 species that would lose some habitat globally (average projected change in habitat across the four scenarios) - more than any other country (Figure 7.6. in Appendix).
The ten countries with the largest variance in weighted richness among scenarios are Democratic Republic of Congo, Cameroon, Mexico, Congo, Cote d'Ivoire, Guinea, Nigeria and Ghana.

For African countries, Order from Strength predicts far worse habitat losses than the other three scenarios. Adapting Mosaic is the most favourable or perhaps more appropriately, the least worst scenario for African mammals, having lower but still significant losses of suitable habitat for most species. For Mexico, the best scenarios are TechnoGarden and Global Orchestration with very similar predicted losses, while the worst is Order from Strength.

5.3.2 Richness weighted by national contribution to global loss

The countries with the largest richness weighted by national contribution to projected global loss are Mexico, Brazil, USA, Democratic Republic of Congo, Tanzania, Ethiopia, India and Angola. These are all large countries with high levels of endemism. These countries were also flagged when using global loss weighted by the proportion of species range within one country (Figure 7.8 in appendix).

Examples of species with large national and global losses are the Tumbalà Climbing Rat *Tylomys tumbalensis* (24-53% of its global decline in Mexico), the Red-nosed Tree Rat *Phyllomys brasiliensis* (31-47% of global decline in Brazil), and the Angolan Long-Eared Bat (11-83% of global decline in Congo). In USA, large losses are predicted for two endemic canids, the Red Wolf *Canis rufus* (global decline of 10-51%) and the Swift Fox *Vulpes velox* (global decline of 42-53%), while in Tanzania the Mountain Dwarf Galago, *Galagoides orinus* is predicted to lose 14-41% of suitable habitat. An example for India is the Kashmir Muskdeer, *Moschus cupreus*; losses in India contributed 31% of the global decline of this endangered species, with overall global decline varying between scenarios from 37% to 56%. Finally, the projected 42-46% global decline of habitat for the Mountain Nyala *Tragelaphus buxtoni* is predicted to occur completely within Ethiopia’s borders.

The ten countries with largest variance among scenarios of richness weighted by national contribution to global loss are Democratic Republic of Congo, Mexico, Cameroon, Brazil, United States, Nigeria, Liberia, Congo, Tanzania and Russia.

The best scenario for the USA is Global Orchestration and the worst is Order from Strength. For Brazil, the best is Adapting Mosaic and the worst is Order from Strength. For Russia, the best is Global Orchestration and the worst TechnoGarden.

5.3.3 Richness of species with large global declines

In the worst-case outcome for species with large global declines (at least 30% of suitable habitat lost between 2000 and 2050 in at least one scenario), Democratic Republic of Congo takes the first place with 132 such species (Figure 5.1a). Mexico is second with 103 species followed by Angola, Cameroon and Nigeria each with 100 species. In the best-case outcome for species with large global declines (at least 30% lost in all four scenarios, Figure 1b), South Africa takes first place with 18 species, followed by USA with 11 and Namibia with

10. For the worst-case outcome, 28 countries have at least 50 species with large global declines and 63 have at least 10 species. For the best-case outcome, only 3 countries (USA, South Africa and Namibia) have at least 10 species with large global declines.

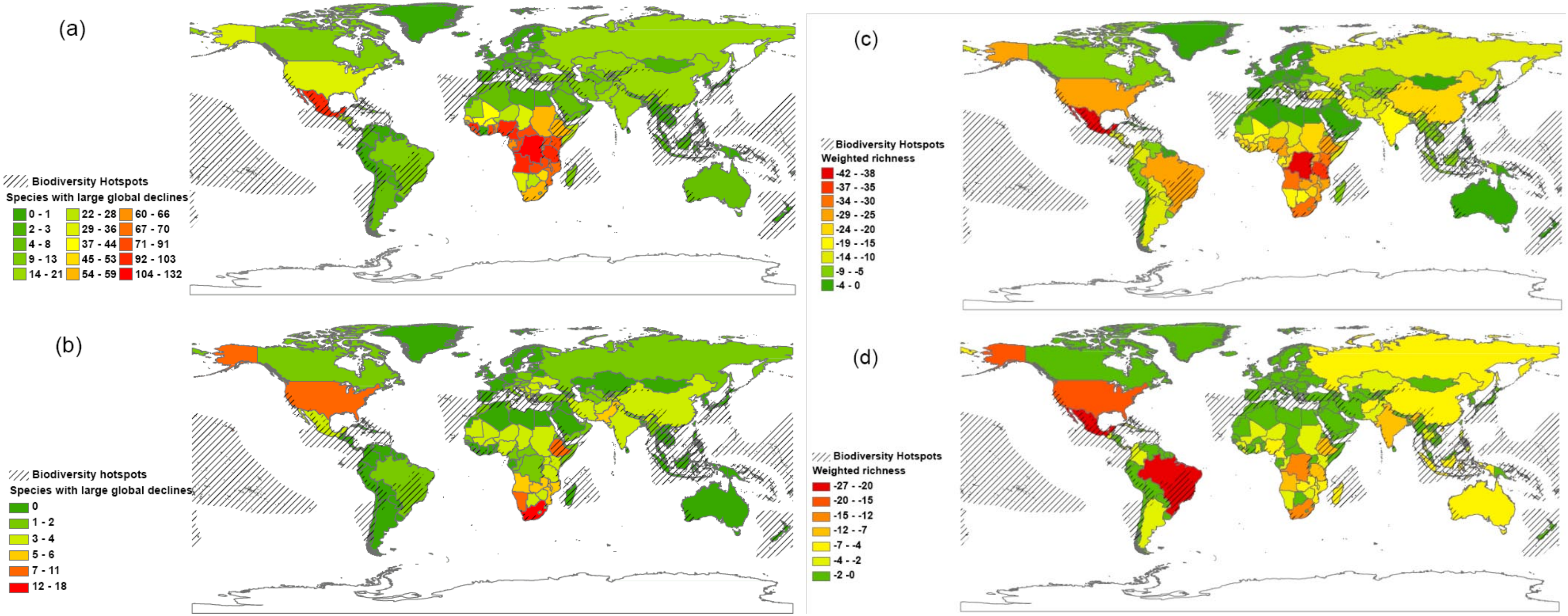

Figure 5.1 Global patterns of projected mammal loss in relation to global Biodiversity Hotspots (Myers et al. 2000) (hatched). (a) Worst-case outcome for number of mammal species in each country with large projected global declines (losing at least 30% of suitable habitat globally by 2050 in any Millennium Ecosystem Assessment scenario). (b) Best case outcome for number of mammal species in each country with large projected global declines (losing at least 30% of suitable habitat globally by 2050 in all four Millennium Ecosystem Assessment scenarios). (c) Mammal richness weighted by average global loss (GL) across the four scenarios. (d) Mammal richness weighted by average national contribution to global loss (NCGL) across the four scenarios. Legend categories use natural breaks adjusted to the closest integer with ArcGis 10 (ESRI (Environmental Systems Research Institute) 2008).

5.3.4 Overlap between current global priorities and future hotspots of loss for mammals

There is little overlap between the regions predicted, according to any criteria, to be future hotspots for terrestrial mammal loss and the current global conservation priorities exemplified by the Biodiversity Hotspots (Mittermeier et al. 1998) (Figure 5.1 a,b,c,d). Overlaps are confined to the Eastern Afromontane hotspot, the Brazilian Cerrado, the Madrean Pine-Oak woodlands in Mexico, the Cape Floristic Region in South Africa, and the Western Ghats in India.

5.4. Discussion

5.4.1 Patterns of global and national losses in relation to scenarios of the Millennium Ecosystem Assessment

My models show that Mexico is the country with the highest weighted richness of future declines, accounting for both global and national loss weightings. Mexico is also among the countries with the most species suffering large habitat declines by 2050. Large increases in food production and consumption are predicted in Mexico, especially from 2040, driven by accelerated growth of population and consumption. This is expected to require less land conversion in globalized scenarios than in regionalized ones because of the improved productivity in globalized scenarios from innovative agricultural practices and technological improvements (Millennium Ecosystem Assessment 2005a).

My models predict many African countries to rank among the top 10 in terms of national and global losses. Under Order from Strength, the African continent is expected to triple its 1995 population by 2050 (Millennium Ecosystem Assessment 2005a). Africa is also the only continent predicted by all scenarios to have a monotonic increase in human population until 2100 (Millennium Ecosystem Assessment 2005a). All scenarios predict economic improvement in Africa with steady increase in average income and household consumption. However, in Order from Strength, the increased consumption is predicted to outstrip productivity improvement and adoption of sustainable agricultural practices which will be hampered by low technology uptake, insufficient financial capital, and limited attention to environmental issues (Millennium Ecosystem Assessment 2005b). These combined effects result in a predicted increase in grazing and cropping land of 71% and 56%, respectively, across Africa in the Order from Strength scenario between 2000-50, with consequent severe declines of mammals.

Brazil is the only South American country among the top ten for any of my measures of mammal decline. Large expansions of cattle grazing, food crops and biofuel plantations in Brazil are predicted by the IMAGE set of models for all scenarios (Millennium Ecosystem Assessment 2005a). This agricultural expansion is predicted mainly in the Cerrado and the Atlantic forest, two ecoregions already severely impacted (Myers et al. 2000).
The USA is also among the countries with large global and national declines. In this country, regionalized scenarios predict increase in food crops and grazing areas to offset the reduced import of agricultural products. TechnoGarden, in contrast, predicts increases in biofuel plantations to become a key driver of habitat loss for mammals in the USA. The USA ranks seventh globally for number of endemic mammals, which explains its high values of richness weighted by national contribution to global loss.

Remarkably, Asian countries are absent from those highlighted here except for China and India. For these countries however, projected losses of habitat are modest compared to African and American countries. Their species richness brings them to conservation attention instead of the future conversion of natural habitat. Asian countries have suffered high level of habitat conversion in the past (Bradshaw et al. 2010) which have resulted in significant loss of habitat for mammals (Catullo et al. 2008; Schipper et al. 2008). Therefore, when using the year 2000 as a baseline to compare future loss of habitat, these countries show low relative losses. However, because Asian countries are expected to suffer high deforestation rates driven by timber harvesting, the importance of their future conservation should not be discounted (see paragraph limitations, below).

Some countries show large variations in predicted habitat declines among scenarios, reflecting idiosyncratic effects in particular regions. TechnoGarden, for example, gives the worst projections of loss for Russia and other countries in central Asia. This scenario involves smaller reductions than others in food crop production in this region because of smaller population reductions in ex-USSR countries (Millennium Ecosystem Assessment 2005a). In addition, land use models for TechnoGarden show meat consumption being replaced by vegetables and grazing land being replaced by cropland. This reduces the overall impact on mammals in areas with intensive man-made pastures or industrial livestock production, such as western Europe and the USA. However, TechnoGarden increases the pressure on mammals in central Asia where low-impact pastoralism on natural grasslands is expected to be replaced by cropland. Large losses of habitat under TechnoGarden are also driven by the projected expansion of biofuel plantations, in particular in the USA, central and Southeast Asia and South America.

Order from Strength has the most severe impacts on mammals in most countries. Mammals in developing countries are affected in this scenario by unchecked population growth and consumption, and by the dominance of economic security over biodiversity and ecosystem services (Millennium Ecosystem Assessment 2005a). In developed countries, the market fragmentation of Order from Strength expands food crops and pasture in regions, such as the USA and western Europe, where farmland would otherwise be abandoned (Millennium Ecosystem Assessment 2005a).

5.4.2 My results relative to other global assessments

Previous studies have estimated the biodiversity impacts of human development scenarios. Jetz et al. (2007) used the predictions of land use and land cover change (with climate change) for the Millennium Ecosystem Assessment scenarios at 30’ resolution to predict impacts on birds. With coarser resolution there is higher potential for overestimates in changes of suitable habitat. This can artificially increase proportional losses for small-ranged species. Therefore, the coarser resolution of their study, their accounting for climate change (see limitations, below) and their earlier baseline (1985 as opposed to 2000 in this study) all contribute to explaining their higher average estimates of loss per species by 2050 compared to my simulations (21–26% in Jetz et al. and 2.3-5.8% here). However, the spatial pattern of highest proportional losses is very similar, which is to be expected given the similar underlying data. In their study, however, the Himalayan region follows central Africa in terms of numbers of species losing large proportions of suitable habitat. In my study, Bhutan and Nepal do not rank among the countries with the most species having at least 30% loss (Figure 5.1). This is because the Himalaya is richer in range-restricted birds (Grenyer et al. 2006) than range-restricted mammals (Schipper et al. 2008).

In another study, Giam et al. (2010) ranked countries first by number of endemic plant species corrected by country area and then by the expected proportion of natural vegetation subject to land use or land cover change. They combined these rankings to measure future endangerment of plant species based on the assumption that endemics will be more threatened by future changes. Not surprisingly, countries with high plant endemism, such as Papua New Guinea, New Caledonia, Indonesia and Madagascar, figure prominently in their study but not in mine. Beyond differences in taxa, which are marginal given the high number of endemic mammals in these countries, the different results depend also on my more direct measure of threat, based on spatially explicit and species-specific impacts instead of the intersection of country-level endemism and habitat loss. This spatial explicitness is important because many endemic species might not be affected by loss of habitat and many non-endemic species might lose large amounts of habitat nationally and globally.

5.4.3 Current and future international conservation priorities

Some existing conservation priorities such as Biodiversity Hotspots (Myers et al. 2000) and Crisis Ecoregions (Hoekstra et al. 2005) have been based on rates of past conversion of natural habitat. However, consistent with other recent studies on other taxa (Lee & Jetz 2008), I show that predicted future hotspots of biodiversity loss according to the Millennium Ecosystem Assessment scenarios have only a partial alignment with present hotspots (Figure 5.1). This result persists when using a map of total net change in suitable habitat acrosss all species at 6' resolution instead of country-level aggregate (Figure 7.7). This may be partially due to the use of different taxa (i.e., plants rather than mammals, in the case of Biodiversity Hotspots), but it is also caused by a poor overlap between present and future projected patterns of habitat loss. This is reflected on the scarce concordance of areas rich in mammal species threatened by habitat loss now (Schipper et al. 2008 figure 2b) and in the future (this study). Therefore, reactive approaches to conservation - those focusing on regions with high past and present biodiversity loss - while fundamental to prevent imminent extinctions, are unlikely to mitigate these projected losses. Additionally, many countries identified here as priorities for terrestrial mammals are poorly protected and poorly represented in other global conservation priority schemes (cfr. Brooks et al. 2006), including the Global 200 Ecoregions (Olson & Dinerstein 1998), High-Biodiversity Wilderness Areas (Mittermeier et al. 1998), the Last of the Wild (Sanderson et al. 2002) and Endemic Bird Areas (Stattersfield et al. 1998). I do not suggest that my rankings and maps should directly guide future conservation investments. Instead, I join Lee and Jetz (Lee & Jetz 2008) in recommending that projected future threats to biodiversity should be accounted for in conservation priorities.

Future threats can be accounted for in different ways. A risk-averse (proactive) strategy would protect globally imperilled species in countries with lower pressure on mammal habitat, thereby maximizing the likelihood of success (Figure 5.2, top-left sector). A more risk-prone strategy would mitigate future losses in countries with high predicted losses of habitat and harbouring species with large expected global losses (Figure 5.2, top-right sector). No single prioritization strategy will work well in all circumstances, and different contexts require different strategies (chapter 2). A mix of approaches is necessary because countries with many endemic species are toward the right-hand side of the graph and will not benefit from a risk-averse strategy. When options are available to protect species in countries with different levels of predicted loss, the choice between proactive or reactive intervention will depend also on socio-political factors (some reviewed in chapter 2), including existing conservation initiatives (Bode et al. 2010), costs of protection (Naidoo et al. 2006) investment opportunities (McBride et al. 2007), governance (Smith et al. 2003), and the kinds of threats faced by species (see last paragraph).

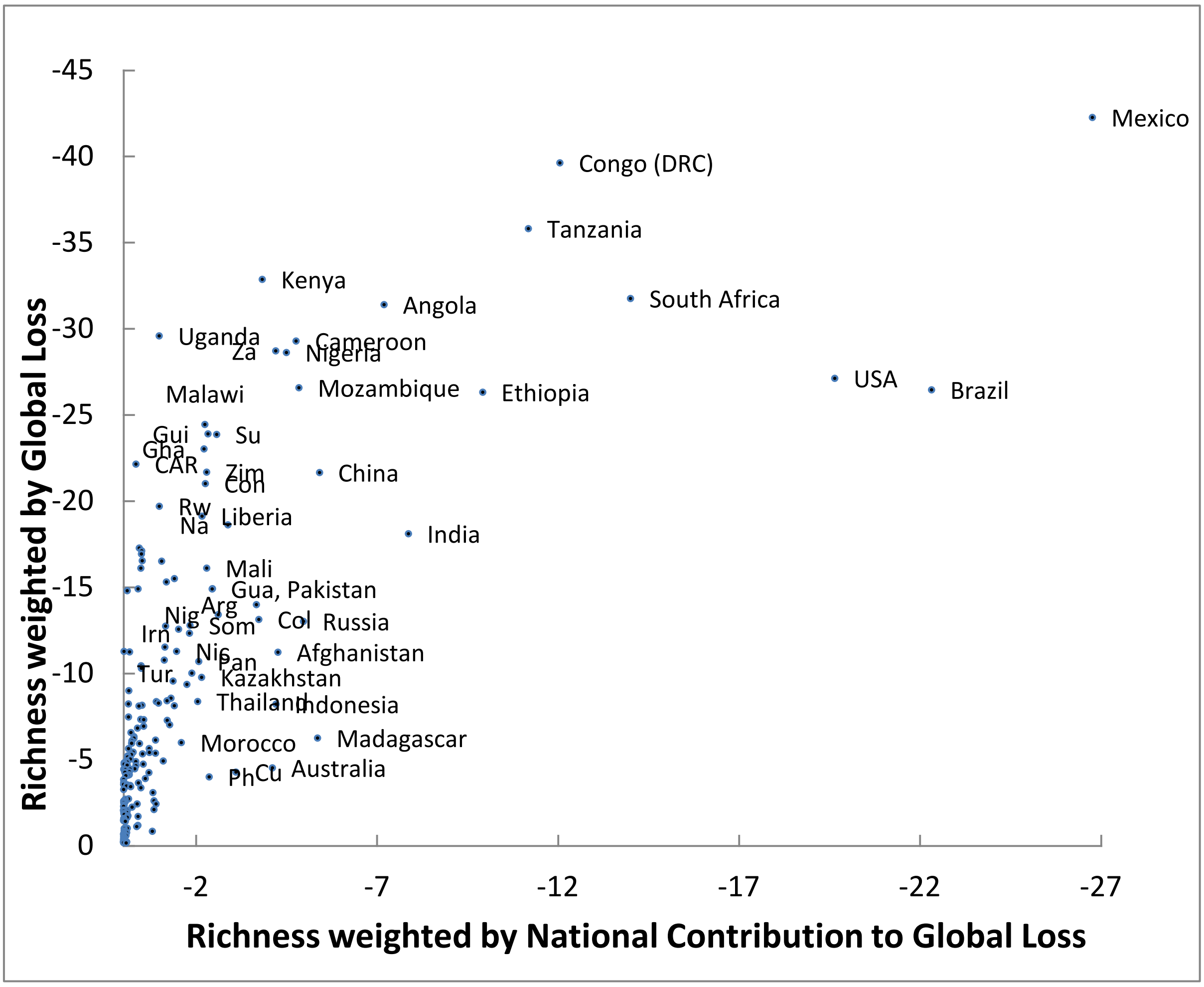

Figure **5.**2 Scatter plot of countries in relation to the two weighted richness measures. The *x*-

axis shows richness weighted by national contribution to global loss from 2000 to 2050, averaged across the four scenarios. The *y*-axis shows richness weighted by global loss from 2000 to 2050, averaged across the four scenarios. Country labels and names are in table 7.7 (Appendix).

5.4.4 National conservation priorities and reporting

My measures have some affinity with the Red List Index (RLI) that has been proposed for monitoring trends of taxonomic groups globally or nationally (Butchart et al. 2004; Butchart et al. 2007) and adopted by the Convention on Biological Diversity as one measure to assess progress towards the 2010 targets, which are also one of the Millennium Development Goals (UNEP 2006). The Red List Index is a compound measure synthesising the genuine changes (those not resulting from improved knowledge or taxonomic changes) in Red List status of all species in a taxon. A disadvantage of RLI is that it can track only changes in species status large enough to trigger down-listing or up-listing. My measures are instead continuous and can be complementary to RLI. Being based on the global status of each species, the RLI is also geographically coarse. Finer-scale monitoring is possible through national RLIs, but these are only possible for the very few countries having red lists available at two points in time. The African continent, which figures prominently in my study, has the lowest number of national red lists in the world. Only 10 countries out of 53 have compiled red lists within the last 10 years for at least one taxon. Only 3 countries have a mammal red list (Zamin et al. 2010).

I suggest that, by exploring a country's national loss measure and identifying which species most contribute to its score, it is possible to identify priority species and areas for conservation, monitoring and assessment. While I have summarized my results at the country level, the underlying analyses have a resolution of about 10 km^2 and can be further improved by incorporating more ecological and socio-economic information (see below) to derive spatially explicit prioritization maps within countries.

5.4.5 Limitations

Although my approach has merits, my study also faced data limitations that call for refinements. My study would have benefited from incorporating other threats to mammals such as direct killing and invasive species that are important in Asia (Sodhi et al. 2004), Australia and the Pacific (Hoffmann et al. 2011). Accounting for these factors might have changed the results proposed here, but I am not aware of any extensive projections of future patterns of these drivers of mammal decline. Moreover, countries in the Amazon and the Congo Basin, which I have highlighted here, have very high hunting pressures, second only to South-East Asia (Fa et al. 2002). They are likely to retain this primacy, given their increasing population densities in rural areas and their reliance on bush meat.

There are many uncertainties involved in projecting future global agricultural land cover, the major ones related to the assumptions about socio-political, economic, demographic and technological changes which are addressed by exploring multiple development scenarios. These scenarios are not meant to be accurate predictions of the future but rather explorations of the consequences of different development pathways. There are further uncertainties in the downscaling of the 30' land use change model. This process necessitated simplifications so that the criteria used to allocate regional conversion to crops and pasture locally were general enough to be valid globally. The model has been validated against the current global distribution of cropland and pasture, showing a good concordance (Klein Goldewijk et al. 2007) but its ability to predict land use change has not been explored.

My estimates of habitat loss are likely to be too small in some countries, because I did not incorporate projections of logging and other forestry activities for the four development scenarios. In IMAGE and GLOBIO the changes in forestry are not spatially explicit, being more or less randomly applied within macro-regions, and were therefore not suitable for my analyses. This exclusion of forestry activities explains why countries like Indonesia, Malaysia and Papua New Guinea are among the top priorities for mammals in other studies (Wilson et al. 2011) but are not highlighted here.

The mammal suitability models accurately predicted ~80% ± 16.8% of known species occurrences for a sample of species (n=263), and reduced false presences compared to using the species range for 92% of these species (Rondinini et al. 2011). However, the model accuracy is unknown for most species, suggesting that my results need to be taken cautiously. In addition, because of the many-to-one relationship between GLOBCOVER classes and the GLC2000 classes used by GLOBIO, the original scores by Rondinini et al. were averaged in some instances. In 5% of cases, the averaging involved different scores (e.g. suitable and unsuitable habitat). This happened mainly in the category "pasture and rangelands" which is not present in GLOBCOVER or in GLC2000 but was introduced in the GLOBIO land use change model. Future versions of these models will have to assign a specific suitability score to this land use category.

I did not incorporate climate change effects on species distributions except for the modest indirect effects of climate on suitability for agriculture, which were modelled in IMAGE and reflected in the land use change model used here (Appendix 7.4.1). At the time of writing I did not have species-specific models of climate change impacts on mammals. The relative contribution and the synergistic effects of climate and land use change on mammal distributions are of key importance in devising future conservation (Maiorano et al. 2011)..

Finally, I did not account for isolation and fragmentation effects on mammals. Different spatial patterns of habitat loss and different histories of landscape conversion will have different impacts on biodiversity (Crooks et al. 2011, chapters 2-3) and could potentially alter the ranking of countries presented here. However these effects are landscape- and species-specific and cannot presently be incorporated into my analyses.

5.4.6 Challenges in avoiding predicted losses

Technological improvements to increase productivity will be important but might not be sufficient to offset the increasing demand for agricultural products (Millennium Ecosystem Assessment 2005c). Estimates of future increases in productivity were part of the IMAGE scenarios. TechnoGarden involved optimistic assumptions about development and transfer of advanced agricultural technologies to developing countries. Yet, even in this scenario, African mammals pay a high cost for increased pastureland and cropland. Alternatively, in the fragmented world of Order from Strength, technological improvements are slow and technology transfer is limited, resulting in less land spared from production and worse outcomes for mammals. International trade and resource extraction will also determine outcomes for mammals. A global economy with little environmental responsibility, like the one assumed in Global Orchestration, envisages developing countries providing the labour and natural resources to shore up the prosperity of developed countries. This shift in agricultural land from developed to developing countries might come at a high environmental cost for developing regions, especially in the tropics (this study and McKinney et al. 2010). A policy of expanding protected areas will not be sufficient to avert the pressures on mammals from the growing demand for agricultural products, because protected areas often displace land use change to unprotected areas (Ewers & Rodrigues 2008). Relief from pressures on natural habitat and species will rely mainly on structural changes in production and consumption (Alkemade et al. 2010; Millennium Ecosystem Assessment 2005a). Regional and global studies have demonstrated that protected areas are necessary but insufficient to prevent future loss of biodiversity in developing landscapes and regions (Alkemade et al. 2010; Soares-Filho et al. 2006). Additionally, protected areas and other local conservation actions are at risk of failure in unstable and corrupt countries (Laurance 2004; McBride et al. 2007; Smith & Walpole 2005, and see also chapter 2). While socio-economic stability and corruption need to be taken into account for effective conservation of mammals (Eklund et al. 2011; Wilson et al. 2011) this does not imply that organisations should abandon these countries. On the contrary, conservation efforts need to be expanded in countries with the highest needs and the lowest means to undertake effective conservation (Lee & Jetz 2008). Integrating future scenarios of socio-political and economic development in conservation strategies (see chapter 2) could help identifying where the highest future needs and opportunities might be and prevent future biodiversity losses.

At a more fundamental level conservation efforts should be integrated with development strategies. For this to happen, conservation strategies need to be applied with the support of local communities by promoting activities that address both development and biodiversity conservation goals such as certified community timber enterprises and nature-based tourism (reviewed in Secretariat of the Convention on Biological Diversity 2010). Conservation will succeed in the future battlegrounds of biodiversity loss only if there is a serious global effort to enforce compliance with environmental rules, promote the use of technological improvements to increase productivity, stabilize human populations, encourage responsible consumption patterns, reduce losses of agricultural products before consumption, improve forest management, and limit the impacts of climate change.

Chapter 6: General discussion and conclusions

The common thread of my thesis is the need to expand dynamic conservation planning techniques to include methods for predicting outcomes of today's conservation decisions among multiple alternative futures. This requires planners to model sequential implementation of conservation actions as well as their interactions with destructive forces in different plausible future scenarios. Each scenario makes different assumptions about future ecological and socio-economic dynamics. This allows planners to identify the best approach to priority setting through space and time in a variety of possible futures, while also identifying potential winner and losers (among species, habitat and other biodiversity features, and stakeholders), the necessary budget to tackle conservation challenges, and the main threats that will be faced in the future. A limited number of scenarios can capture the extreme values of the likely distribution of parameters. Identifying the most robust strategy across these scenarios can thus identify a good approach to conservation across intermediate scenarios which were not tested.

A key contribution of my thesis lies in the potential of my methods and findings to inform more complex and realistic conservation planning problems than those addressed in the past. This contribution comes from addressing some important gaps in dynamic conservation planning. These gaps are: limited ability to deal with uncertainty in biodiversity data, costs and threats; reliance on untested and perhaps tenuous assumptions; testing methods with only single combinations of parameters and models; lack of incorporation into models of important factors such as local- scale connectivity and variable site cost; and failure to consider the broader context of socio-economic dynamics when setting conservation priorities. My findings show that addressing these limitations of past research improves outcomes for biodiversity of conservation efforts.

I identified 4 main objectives related to these research gaps, and below I summarize how my thesis achieved these objectives. I then discuss the limitations of my thesis and put my main findings in the context of ongoing research in the discipline. I conclude by providing my personal perspective on future directions in research on dynamic conservation planning research and conservation planning in general.

6.1 Thesis outcomes

I addressed the four main objectives of my thesis, identified in the introduction. Below I summarize how each objective was achieved.

1. **A new framework to identify assumptions in dynamic conservation planning and test their effects on the spatial pattern of conservation priorities and on the effectiveness of a proposed plan.**

In chapter 2, I investigated some of the factors that influence conservation decisions and highlighted the role of assumptions in the process of setting priorities for conservation. In that chapter I proposed that framing a conservation planning problem under the tenets of decision-theory (Possingham 2001) allows planners to identify the different parameters and processes that comprise the problem, such as spatial distribution of species, biodiversity processes and threats to their persistence. Trying to optimize conservation decisions to achieve the best possible outcome in the future requires planners to think about how the future might unfold and how they can anticipate opportunities and threats to the successful implementation of a conservation plan. This calls for the use of conservation scenarios, which I argue can be usefully applied to explore the implications of different assumptions about parameters and processes on the spatial pattern of conservation priorities, and their effectiveness in ensuring biodiversity persistence. In chapter 2, using this proposed framework, I demonstrated how implicit and explicit conservation assumptions can make a big difference in the spatial allocation of conservation resources using as a case study the conservation of South American terrestrial mammals. This study suggested that incorporating decision-theory and scenario planning constitutes a powerful tool to explore the implications of conservation assumptions and to assess the consequences of today's decisions on tomorrow's biodiversity outcomes. Blending the structured approach of decision-theory with the flexibility and foresight of scenario-planning (Peterson et al. 2003) constitutes an innovative line of research with great prospects for the future.

2. **Explicit incorporation of biodiversity processes (habitat connectivity) and variable site cost in dynamic conservation planning.**

In the introduction (chapter 1), I illustrated how little research has been carried out to incorporate species-specific isolation and fragmentation effects and variable site cost in dynamic conservation planning. In chapter 2 I addressed this knowledge gap by exploring how different assumptions about the role of small fragments for species viability influence the spatial allocation of conservation priorities for South American terrestrial mammals. In the same chapter, I also showed how different assumptions about the spatial variation in costs relative to the deforestation frontier can influence the spatial pattern of conservation priorities. In chapter 3, I relaxed these assumptions and measured their implications for conservation effectiveness (persistence of three forest-dwelling vertebrates) in a developing landscape. I did this by testing conservation strategies that differed in their accounting for fragmentation effects in species distribution modeling and their level of reactivity (incorporation of threats). I assessed these strategies against the protection of species with different area requirements, in different conservation scenarios, including one in which costs were assumed uniform and one in which realistic acquisition costs were estimated using published methods.

I discovered that accounting for fragmentation effects and realistic site cost can reduce the expected performance of a reactive strategy relative to a proactive one. Pressey et al. (2007) argued that, to better pursue the ultimate goal of biodiversity conservation (species and habitat persistence), conservation planning could benefit from incorporating biodiversity processes in the context of dynamic threats. Chapter 3 is a step further in this direction in that it simulates the dynamic interaction between species distribution, habitat loss and habitat fragmentation. In fact, previous studies have only performed retrospective analyses on indicative reserve systems to show that some species would decline and disappear from the system because isolation and small size of protected areas undermine the viability of metapopulations at least for wide-ranging species (Cabeza & Moilanen 2003). My findings suggest that new research might usefully develop conservation planning algorithms able to solve problems requiring the simultaneous minimization of the loss of habitat and fragmentation of the landscape when scheduling conservation actions.

3. Identification of the conditions in which habitat vulnerability needs to be accounted for in dynamic conservation planning.

The importance of accounting for species and habitat vulnerability to future threats in conservation planning has been highlighted in previous studies (Merenlender et al. 2009; Wilson et al. 2005a), but here I provided rules of thumb to identify the conditions in which incorporating habitat vulnerability improves conservation outcomes. In chapter 4 I compared two approaches to landscape and seascape conservation prioritization, MaxGain and MinLoss, and showed that, in most circumstances, MinLoss is more effective in ensuring biodiversity retention. The key difference between the two approaches is the use of vulnerability estimates. It is therefore intuitive to believe that with increasing uncertainty in vulnerability estimates, there will be a point in which using vulnerability can do more harm than good and a MaxGain approach is to be favoured. In chapter 4 I estimated where this critical level of uncertainty lies depending on a number of factors. I also identified the level of uncertainty for which, if possible, resources and time should be spent on improving estimates of vulnerability before prioritizing conservation actions. This critical level of uncertainty depended on the estimated spatial variance in vulnerability and the effect of conservation actions on threatening processes. The effect of conservation can be either inhibition (the threat is reduced throughout the planning region) or displacement (the threat is shifted elsewhere within the planning region). Understanding the circumstances in which protected areas displace or inhibit threats to biodiversity, and the effect this has on biodiversity conservation has been highlighted as one the most important conservation questions that need answering (Sutherland et al. 2009).

Pressey et al. (2007) anticipated that uncertainty in estimates of threats could be so large as to make them useless and suggested that planners dedicate more attention to uncertainties in the parameters and models for conservation prioritization. Chapter 4 confirmed Pressey's intuitions and suggested that estimates of uncertainty in threat data are fundamental to making informed conservation decisions and choosing the best policies for data acquisition and conservation prioritization.

4. Consider the utility of future global change scenarios for conservation planning by applying these to predict the future conservation status of terrestrial mammals.

In the introduction and in chapter 2 I argued that scenarios can be a valuable tool to place conservation decisions in context. This in turn facilitates the assessment of opportunities and constraints to conservation in different possible futures shaped by different assumptions about ecological and socio-economic parameters and dynamics. In chapter 5 I used existing global-scale scenarios of human development from the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005b) to identify the possible future hotspots of loss of habitat for terrestrial mammals. I combined the land use change component of these scenarios with species-specific habitat suitability models (Rondinini et al. In press). While the study did not try to optimize a specific conservation planning problem, it showed the geographic areas in which regional scale conservation plans should focus and identified the ultimate drivers of projected losses in different scenarios and different regions of the world (e.g. human population growth, per-capita consumption, global trade). This information is useful to place conservation plans (typically focused on addressing direct drivers of biodiversity loss such as forest clearing and logging) into a broader context in which the ultimate drivers of biodiversity loss are understood and mapped. I found that future hotspots of loss of terrestrial mammals will be in Sub-Saharan Africa, South America, the USA, Mexico and India, some of these countries are considered of relatively low priority for conservation based on the low current level of land conversion, however I found that the future predicted habitat loss in these countries poses as serious threat for the persistence of terrestrial mammals. Habitat conversion will expand in all scenarios because of many concomitant factors; population growth will be the main factor in Africa, while increased per-capita consumption and production of biofuels will be important drivers of habitat conversion in all regions.

6.2 Limitation of this study and future research directions

A number of feasible improvements to the theory and practice of dynamic conservation planning were not included in this study. Here I discuss some important knowledge gaps that my thesis did not address and some questions stemming from my research that could be potential future extensions of my work.

6.2.1 Conservation actions in addition to protected areas

Conservation planning has traditionally focused on protected areas despite the fact that the conservation toolkit includes several other types of conservation actions such as habitat restoration, weed and pest removal, and sustainable forest practices. In my thesis I highlighted some assumptions that relate to multiple conservation actions in chapter 2 but I only considered one type of conservation action (habitat protection) in chapter 3 and 4. This allowed me to keep the number of factors explored simultaneously within tractable bounds and still address my research objectives. This is, however, a limitation because the expansion of conservation area networks to reduce fragmentation and isolation effects could benefit from off-reserve conservation. For example, stewardship programs aimed at promoting sustainable practices within private properties surrounding reserves could be explored. This might have the advantage of guaranteeing a certain level of landscape connectivity but at lower economic cost than the implementation and ongoing management of protected areas.

As well as considering multiple actions and costs, in reality conservation practitioners have to deal with multiple threats to biodiversity. These threats can also interact with each other, creating new emergent properties of networks of conservation areas/actions (Evans et al. 2011). Modelling the cumulative effects of multiple threats presents conservation planners with difficult challenges unless, as in a few cases only, for each threat it is know its expected impact on species and habitats both in isolation and combination with other threats (e.g. Didier et al. 2009). These information were not available for my case studies.

6.2.2 Algorithms to minimize habitat loss and fragmentation when scheduling conservation actions

In chapter 3 I concluded that, when scheduling incremental expansion of a reserve network, one should consider future loss of habitat as well as future fragmentation and isolation of habitat. I suggested that future research should provide an algorithmic solution to this problem to resolve the trade-off that emerged with a MinLoss approach, i.e. minimizing loss of habitat versus minimizing fragmentation. This research should answer two questions: 1) what would an objective function for such problem look like? 2) What kind of solver would efficiently optimize a scheduling problem with this objective function? Algorithms developed to build connected reserve networks over time can be adapted to address these questions (see section 6.3.1).

6.2.3 Accuracy of land-use change models

In chapter 3 I used a simplistic model of agricultural and urban expansion focusing attention on comparing different reserve selection strategies rather than providing an accurate estimate of future habitat loss in the Hunter Valley region. This simplification in habitat loss modelling is reflected in much of the dynamic conservation planning literature, including papers that use real datasets. However, new satellite imagery and fine-scale land use maps of global extent (European Space Agency 2008), in combination with new modelling techniques (see section 6.3.3), make it possible to derive more realistic land use change scenarios to plug into dynamic conservation planning exercises. Even these improved models will not eliminate uncertainty, whose impacts on vulnerability estimates will need further examination (next paragraph).

6.2.4 Further examination of uncertainty in vulnerability estimates

In chapter 4 I discovered that uncertainty in vulnerability estimates is by far the most important parameter among those investigated in determining the relative performance of a proactive or reactive approach to prioritization of local conservation actions. However, I only considered two out of many possible ways in which uncertainty can enter into vulnerability estimates. One was a uniform distribution of the deviation of the real values of vulnerability from the estimated values within the bounds of the horizon of uncertainty tested (10%, 20% … 100%). The other was the random swapping of vulnerability values in the vulnerability map used to make conservation decisions. I chose to test only two distributions in vulnerability uncertainty to keep the problem to a level of complexity that was still manageable, and at the same time meet my objective of identifying the multidimensional space within which habitat vulnerability is worth considering. However, in reality the deviation of estimated values from real values can take many possible distributions and these uncertainty values can also vary spatially. Given the importance of estimating uncertainty in vulnerability before setting conservation priorities, there are several important and unresolved questions that need to be addressed: 1) How does uncertainty enter into habitat loss models and threat models in general? 2) How does uncertainty increase with the time of the prediction? 3) What form of statistical distributions do these uncertainty values take? When are these distributions uniform as assumed in chapter 4? When are they normal (i.e. most estimated values similar to the real values and increasing deviation from the true values having lower frequency)? Or, when are they multimodal (i.e. with some spatial dependency that clusters uncertainty values)? There are probably two complementary ways forward: first, estimating actual uncertainties in real landscapes by using older data to predict current, observable conditions; and, second, systematically exploring the effects of observed uncertainties by constructing artificial data sets within which the parameters of actual landscapes can be located.

6.2.5 Incorporating conservation opportunities

In my thesis I did not attempt to incorporate conservation opportunities in dynamic investment schedules (e.g., willingness to sell, land-owner management practices, etc.). This is a limitation because conservation opportunities could affect the spatial pattern of priorities and are fundamental to ensure that plans are implementable (Knight et al. 2010). In prioritizing my own research, I chose to focus on other aspects of dynamic conservation planning with which I was more familiar and left the issue of opportunities to others. Conservation opportunities are important because off-reserve conservation actions in private land requires the willingness to participate of landholders, and the acquisition of private land for conservation purposes is subject to willingness to sell. These are just two examples of the importance of mapping opportunities in conservation planning. As Knight et al. wrote "Mapping conservation opportunity provides an understanding of the factors that contribute directly to effective actions (i.e., a complementary suite of integrated instruments, incentives, and institutions) and improves identification of candidate areas where conservation action can be implemented feasibly" (Knight et al. 2010).

Some aspects of conservation opportunities are the exact opposite of threats e.g. landowner willingness to develop their land. An opportunistic approach to conservation would prioritize the engagement of the landowner in a conservation program if he is not likely to develop his land, whereas a minimum loss approach to scheduling would give his property low priority as it is not presently under threat to biodiversity. Thus there remains a need to integrate conservation opportunities as well as threats in systematic approaches to schedule conservation actions (Pressey & Bottrill 2008).

6.2.6 Effectiveness of expanding protected area networks in the context of future human development scenarios

In chapter 5 I did not simulate protected area expansion contextually with other dynamics. This left several questions unaddressed: 1) To what extent can protected area expansion mitigate the projected decline in habitat for mammals predicted for the four socio-economic scenarios in chapter 4? Would, for example, a 5 or 10-fold increase in budget for conservation be sufficient? Would conservation areas alone be able to solve the biodiversity crisis? 2) How much land can be realistically set aside for conservation given the projected expansion of agricultural and built-up areas? 3) What would be the benefit for terrestrial mammals if future conservation areas are expanded solely within existing global priority areas for conservation such as the Global 200 ecoregions of the world (Olson & Dinerstein 1998) or the Biodiversity Hotspots (Myers et al. 2000), or areas of high concentration of carbon which are suitable for protection under Reduced Emission from Deforestation and forest Degradation (REDD) schemes? All these questions are relevant for conservation planning research and need to be answered to develop effective global conservation planning strategies.

6.3 Cutting edge dynamic conservation planning science

Much of the required knowledge, data and methods to address the research gaps highlighted in the previous sections are available now are under development. The following paragraphs summarize cutting-edge research in dynamic conservation planning and in other fields that inform conservation decision-making. In each section I discuss how these improved techniques and knowledge can be applied to address the gaps of my own research and the future directions outlined above.

6.3.1 Improved prioritization algorithms

Recently proposed algorithms could be used to solve scheduling problems that incorporate biodiversity processes, including the problem posed in chapter 3 that simulates habitat fragmentation effects. For example, Spring et al. (2010) and Harrison et al. (2008) used graph theory in combination with the union-find algorithm (Sedgewick 1990), to create a reserve network over time with "reliable corridors" that were not likely to be interrupted during the projected ongoing deforestation in Costa Rica.

New conservation planning algorithms also include the option to plan for multiple actions at the same time (Klein et al. 2009; Watts et al. 2009), and for scheduling conservation actions (Wilson et al. 2010). These algorithms open up new frontiers for dynamic conservation planning by allowing planners to prioritize reserve and off-reserve management (see section 6.2.1).

Evans et al. (2011) proposed an algorithm that incorporates multiple interacting threats in conservation planning. This algorithm could be used to investigate the influence of uncertainty in the direction and intensity of these interactions on the spatial pattern of conservation investments (section 6.2.4). This research would expand on my findings in chapter 4 about the importance of measuring the accuracy of threat models before making conservation decisions.

Recent and improved objective functions (what is optimized by an algorithm) could be also adapted to address future research challenges. For example, assessing areas in terms of replacement cost could be useful in demonstrating the cost of misallocating conservation actions as a result of false assumptions.(Cabeza & Moilanen 2006; Moilanen et al. 2009). Replacement cost is the biological or economic cost that might be incurred if an area is included or excluded from a proposed solution.

6.3.2 Biodiversity distribution and dynamics

Minimizing future threats to biodiversity, such as habitat loss and fragmentation (section 6.2.2), requires appropriate ecological models to measure their impacts on species distribution and persistence. Therefore, improved predictive models of species and habitat distribution in future environmental condition would be a key advancement for dynamic conservation planning. This kind of distribution modelling is particularly challenging because it violates the assumption of equilibrium between species/habitats and the environment. Several approaches have been developed to use distribution models when extrapolating to new environmental conditions: species data can be weighted to represent the invasion process or the sample bias of records (Phillips et al. 2009), dispersal can be incorporated using estimates of dispersal rates (Midgley et al. 2006) or models of dispersal (Schurr et al. 2007) in combination with other life history traits (Willis et al. 2009). Other frontiers of species distribution modelling include the use of physiological models representing processes of change (Kearney & Porter 2009) and the accounting for species interactions (Araújo & Luoto 2007). These advances could be usefully incorporated in the derivation of a dynamic investment schedule that accounts for biodiversity processes.

New techniques have also recently emerged that incorporate uncertainty in future predictions. The uncertainties addressed are those of environmental variables, the variation in species distributions arising from multiple modeling techniques, and multiple model parameterization to create ensembles of species distributions (Araújo & New 2007; Thuiller et al. 2009). However, these techniques have not yet been incorporated into dynamic conservation planning. This is surprising given the importance of generating investment schedules that will be robust to uncertainty in model predictions.

6.3.3 Land use change modelling

I discussed land use change modelling as an example of mapping current threats and predicting future ones because land use change affects the most species and with the highest intensity (www.iucnredlist.org). However, conservation planning researchers will need to keep an eye on advances in modelling the distribution of other threats such as climate change, invasive species, diseases and direct persecution. Improved predictive models of threats to biodiversity will be key to improve conservation outcomes (chapter 4 and section 6.2.3). Models with good accuracy could be also used as reference to explore the different ways in which uncertainty enters in vulnerability estimates (section 6.2.4)

Some recent work in land use change modelling is focusing on creating models for separate typologies of landscape (characterized by different land use patterns and drivers of change) in order to capture the different land use change trajectories in different parts of study regions, driven by different processes (McDonald & Urban 2006; Verburg et al. 2010; Wassenaar et al. 2007). These models have not yet permeated into dynamic conservation planning, perhaps because the planning regions of dynamic conservation planning studies are often small enough to be characterized by one pattern of transformation to agriculture or urban use, driven by common anthropogenic processes across the region. Assuming that the same land use dynamics take place in different parts of large regions, however, may be inappropriate, and multiple local land-use change models might better capture the local variability in drivers and spatial pattern of land use change.

The effect of competing land uses (Lubowski et al. 2008; Wassenaar et al. 2007), spatial contagion of land use change (Overmars et al. 2003) and the incorporation of the likelihood of subdivision of cadastral parcels (Zhou & Kockelman 2008) are useful attributes of modern land use change modelling techniques that might also improve the land use change component of dynamic conservation planning simulations. For example, accounting for contagion effects may influence dynamic investment schedules by promoting the creation of protected areas at a distance from development nodes small enough to create local inhibition effects that provide natural buffers to edge effects from anthropogenic land uses. Explicitly accounting for the interaction of competing land uses may enhance the understanding of other feedbacks between reservation and other land uses, and between land cover change and land use change (Verburg 2006). Modelling the likelihood of subdivision has important implications for the modelling of acquisition costs and likelihood of success. The emergence and comparison of different statistical modelling techniques are also important elements of innovation to monitor (Lin et al. 2011).

6.3.4. Conservation costs

Accounting for multiple costs is an obvious byproduct of incorporating multiple conservation actions (sections 6.2.1 and 6.3.1). Costs elicited from conservation practitioners can be extrapolated beyond the areas that are currently managed with statistical methods and used to prioritize multiple management actions simultaneously (Januchowski-Hartley et al. 2011). Techniques to infer overall management costs of proposed protected areas from observed management costs and environmental and socio-economic variables also exist (Armsworth et al. 2011; Ban et al. 2011).

Accounting for multiple opportunity costs has been advocated to make conservation planning more equitable across all stakeholders (Adams et al. 2010b) and possibly more acceptable and therefore implementable (Adams et al. 2010a). While algorithms that can account for multiple costs already exist (Watts et al. 2009), and different costs can result in different spatial patterns and cost-effectiveness of conservation priorities (Adams et al. 2010b), their use is still in its infancy, but subject to ongoing research.

6.3.5 Conservation opportunities

It has been suggested that, to promote the implementation of conservation plans, more attention should be paid to the opportunities for implementation that can arise from social, economic and political factors (Knight & Cowling 2007). This has stimulated more research on these factors, (Pressey & Bottrill 2008; Pressey & Bottrill 2009) but this is by far the least explored aspect of conservation planning.

Cutting-edge research on the subject involves methods to estimate willingness to sell private properties for conservation purposes (Guerrero et al. 2010), willingness to participate in voluntary land conservation (Knight et al. 2010; Moon & Cocklin In press), and existence of local champions (Knight et al. 2010). Another approach that has been usefully explored is to lock in "wish lists" of conservation areas in conservation plans before running conservation prioritization algorithms (Ban et al. 2009). While this approach might not be the most efficient spatially, it allows local community to express their choices resulting in a higher "buy-in" of conservation.

All these models could be plugged into dynamic conservation planning algorithms to address the limitations highlighted in section 6.2.5 towards a more "informed opportunism" when scheduling conservation actions (Knight & Cowling 2007; Knight et al. 2010).

6.4 Concluding remarks: integrating dynamic conservation planning with land use planning and socio-economic scenario modelling

Above I have illustrated a specific research agenda that is linked with the limitations of my thesis and to further enquiries that emerged from my study. However, there are larger challenges and opportunities ahead for dynamic conservation planning specifically and conservation planning in general. I believe that, as well as expanding the conservation toolkit, conservation planning research and practice need to meet other disciplines to influence conservation decision at the local and the global scales.

At the local scale, conservation planning should seek a better integration with land use planning in order to influence local land use policies. Land use planners and conservation planners sometimes work in the same landscapes with no or little interaction. This makes conservation planning a strategy game in which conservation planners try to anticipate and mitigate the effect of the opposing forces rather than directly informing land use decisions. As a result, conservation planning can also instigate unwanted land use changes when triggering land market feedbacks (Armsworth et al. 2006) or displacing habitat destruction in high biodiversity areas (Polasky 2006). On the contrary, the development of zoning plans that integrate conservation objectives with development objectives, would turn dynamic land use and conservation planning into a concerted decision-making process in which trade-offs between anthropogenic land uses and biodiversity conservation are considered explicitly and resolved more effectively. There are several barriers that need to be addressed before an integration of conservation planning and land use planning can occur. First and foremost, there is widespread anecdotal evidence that land use planning teams often lack experts in ecology and conservation, and therefore such teams are unaware of the importance of planning for biodiversity persistence or have different objectives. Therefore the development of conservation goals (if any) is left to people that lack the appropriate training. Second, there are still many misplaced perceived limitations of systematic conservation planning that reduce its uptake by conservation professionals (Smith et al. 2006). The perceived limitations include the difficulty of using conservation planning software, their potential improvements over expert opinions, and data limitations (Smith et al. 2006). Third, conservation planning products are not designed to be interpreted and used by land use planners (Pierce et al. 2005; Theobald et al. 2000). The different terminology and layout of priority maps from those used by local government officials affects the likelihood of implementation (Theobald et al. 2000).

While many have pleaded for the integration of conservation planning and land use planning (Marzluff 2002; Pressey 1999; Theobald et al. 2000) and frameworks for this integration have been proposed (Knight et al. 2006; Pierce et al. 2005; Theobald et al. 2000; Theobald et al.

2005), their application remains limited. Future work, including my own, will need to review the theoretical principles underpinning integrated land use and conservation planning, understand the constraints, and revise existing frameworks to improve systematic conservation planning uptake from land use planners.

At the global, continental and regional level conservation planning needs to meet global Integrated Assessment Models (IAMs). These are meta-models used to transform scenario storylines into quantitative estimates of human population, GDP, per-capita consumption, patterns of land use, greenhouse emissions, climate change and many other socio-economic and physical parameters. IAMs are made of several interacting model components to simulate dynamics in demographic, economic, physical and ecological factors. They have been used by IPCC to predict climate change impacts on human and ecological communities but also in studies that investigate the links between socio-economic, cultural and technological changes and the dynamics of biodiversity and ecosystem services (Millennium Ecosystem Assessment 2005b; UNEP 2007). The last components of IAMs consist of ecological models that assess the biodiversity impacts of different trajectories in many ultimate drivers of biodiversity loss. These are often based on species-area curves (SARs) (Millennium Ecosystem Assessment 2005a; Pereira et al. 2010; Van Vuuren et al. 2006). SARs, however, do not indicate which species will be impacted, lack any mechanistic bases (Lewis, 2006) and have other fundamental ecological problems (He & Hubbell 2011). I argue that these studies can be improved by using more detailed ecological models such as habitat suitability models to allow for the projection of fine-scale and species-specific impacts of policy decisions that can be aggregated to understand impacts at higher levels of ecological organization (i.e., communities, ecosystems, ecoregions and biomes). These, in turn, can be related to ecosystem services and human wellbeing. IAMs, combined with fine-scale state of the art ecological models, constitute an ideal assessment platform to test the implications of regional and global policy decisions. These assessment platforms could investigate and help in resolving more fundamental trade-offs between human development and biodiversity conservation than the ones investigated through integrating conservation and land use planning.

A step further to develop comprehensive strategies aimed at ensuring the persistence of biodiversity and ecosystem services is to use spatial conservation prioritization tools to identify priority areas for conservation actions. Integrating systematic conservation planning into improved IAMs blends together the macroscopic and often non-spatial level of conservation shaped by national and international legislations, cultural changes and technological improvements, with the finer-scale and spatially explicit level of regional conservation plans. The spatial and non-spatial levels of conservation interact with each other because socio-economic scenarios determine the context in which conservation decisions at the local scale are made, but in turn, implementing conservation actions at the local scale brings about societal changes that can influence the future socio-economic development of local communities and nations. Integrated assessment modeling of future societal and environmental changes provides many opportunities to explore different solutions to the global biodiversity crisis. One of these is the design of regional and national conservation plans that are cognizant of emerging and future opportunities and threats to conservation in the form of future social norms, land uses, technology and climate change.

We have only started scraping the surface of the potential use of scenarios in biodiversity conservation and my study is a first step forward for the integration of scenario modeling and dynamic conservation planning. Future research in the field should aim at providing decision support tools for policy makers that would estimate conservation outcomes of different non-spatial policies as well as spatial land use and conservation plans. The goal of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service (IPBES) (Larigauderie & Mooney 2010) is to "build capacity for and strengthen the use of science in policy making" (www.ipbes.net). IPBES, also dubbed the "IPCC for biodiversity", will be tasked with providing world leaders with the most accurate and up-to-date scientific advice on the status of biodiversity and ecosystem services (BES) and projected impact of future development scenarios on BES. One of the ways in which IPBES will inform policy will be to produce new versions of the Millennium Ecosystem Assessments. My hope is that the future work of IPBES will include my proposed integration of systematic conservation planning principles into global biodiversity assessment to provide policy makers not only with scenarios of impacts but also with proposed solutions.

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Appendices

7.1 Appendices chapter 2

7.1.1 Description of other assumptions identified as worthy of further attention but not analyzed in this study

Probability of success: "Conservation actions in unstable or corrupt countries are successful"
By prioritizing areas for biodiversity conservation, international conservation organizations must often act in politically unstable regions because they host biodiversity that cannot be protected elsewhere (Smith *et al.* 2003). Despite the evidence for the negative impacts on conservation effectiveness of weak governance, armed conflict, and a lack of social empowerment among civil society (Barrett et al. 2001; Geist & Lambin 2002; Laurance 2004; McNeely 2003; Peh & Drori 2010; Wright et al. 2007), few conservation organisations take explicit account of governance factors in conservation priority setting (Smith et al. 2003; Smith & Walpole 2005). Those that do not account for governance risk conservation failure (BBC 2010; DeFries et al. 2005)

Probability of success: "Species reintroduction programs will have sufficient public support to be successful"
A common reactive response to biodiversity loss is the reintroduction or restocking of species in their natural habitats. However, the success rate of reintroduction programs varies between 11 and 44% across a variety of taxa (Fischer & Lindenmayer 2000; Griffith et al. 1989) and poor local support from landholders is an important cause of project failure (Reading et al. 1997). Yet, only 4% of publications on reintroductions discuss social factors influencing success (Seddon *et al.* 2007). Reintroduction programs are increasing at an exponential rate (Seddon et al. 2007), and the trend is likely to continue given the expanding number of critically endangered species. Additionally, translocations of animals and plants threatened by climate change to areas with future favourable climatic conditions have recently gained considerable attention (Hoegh-Guldberg et al. 2008; Hunter 2007; McLachlan et al. 2007). Therefore, assumptions about the socio-economic factors related to success of reintroduction programs will likely play an

important role in determining the success of future conservation efforts.

Probability of success: "Protected areas at the threat frontier can be maintained in the long-term despite development pressures".

Protected areas are often assumed to be permanent, despite widespread cases of downgrading, downsizing and degazettement (PADDD, Mascia & Pailler 2011). The most common causes for PADDD are oil and gas extraction (Terborgh 1999 p. 73), agricultural expansion (Adams 2004 p. 8), mining, timber harvesting and grazing (Runte 1979 p. 63). Access to natural resources for profit or subsistence is therefore the main direct driver of PADDD events (Mascia & Pailler 2011). Thus, the possibility of protected area failure needs to be taken into account and estimated before setting conservation priorities, especially in developing landscapes.

Contribution of actions to objectives: "Restored vegetation through plant reintroduction or natural recolonization will evolve towards the climax successional stage".

Restoring vegetation communities through passive or assisted plant recolonization is a form of reactive conservation. However, reported success rates of plant reintroductions (plant survival and reproduction) are very low (Godefroid et al. 2010) and plant recolonization, whether natural or assisted, often takes different trajectories from the one desired (Matthews & Spyreas 2010). This might be especially true as the effects of climate change become more apparent (Seastedt et al. 2008; Williams & Jackson 2007). Biodiversity and ecological indicators such as species richness, diversity, plant biomass, and carbon storage can be much lower than the reference values, even after several decades (Brown & Lugo 1990).

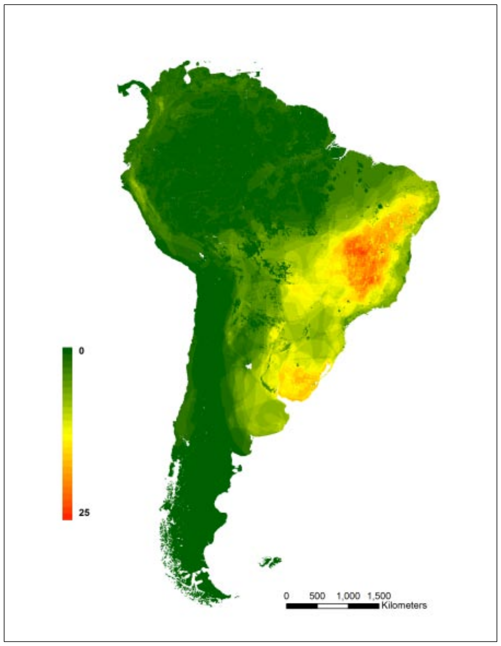
7.1.2 Creation of scenarios with different proportions of species endemic to the threat frontier

The observed number of species endemic to the threat frontier was 158. I artificially doubled the number of endemics in the threat frontier by selecting a sample of species and moving all their occurrences into randomly selected planning units within the threat frontier. These additional 158 species were selected according to their prevalence (extent of their suitable habitat in South America divided by the area of the continent), to reflect the same distribution of prevalence values of the existing 158 endemics in the threat frontier. I also created a scenario with no endemics in the threat frontier. I did this by randomly swapping occurrences of species endemic to the threat frontier with randomly selected planning units in South America to distribute them between the threat frontier and wilderness. I did this 1000 times for each species,

7.1.3 Calculation of minimum fragment size for two umbrella species

I used the minimum dynamic areas (MDAs) calculated from published population viability analyses to select minimum fragment sizes to be considered for my analyses. I calculated the average density of Jaguars (*Panthera onca*) using observed densities across biomes in Brazil (Sollmann et al. 2008), obtaining a value of 2.74 individuals per 100 km^2. Multiplying this value by the minimum viable population size (MVP) required to survive 100 years (59 animals) I estimated an MDA of 2154 km^2. For the Golden-headed Lion Tamarin, I used data from Zeigler (2010) who found an MVP for 100 years of 250 individuals which, assuming average estimates of density, yields an MDA of 37.3 km^2 (Zeigler 2010).

Figure 7.1 Richness of under-represented species when opportunity costs for agricultural activities were spatially variable. Numbers of species that did not achieve their representation target when selection of planning units was constrained by a monetary budget (239 USD) and opportunity costs for agricultural activities were spatially variable.



7.2 Appendices chapter 3

7.2.1 Planning unit design

I attempted to match, as far as possible, the boundaries of planning units with those of discrete patches of forest to couple management and ecological units. I also tried to limit the variance in size of the planning units so that very large planning units would not dominate investments in terms of high biodiversity benefit and very small planning units would not dominate investments in terms of low cost. I also wanted to avoid having planning units that were too expensive to purchase with an annual budget. I first excluded all areas without forest because all three of species were restricted to forest. Second, I transformed all vegetation fragments smaller than 25 ha into individual planning units. Third, I overlaid a 25 ha (500 m x 500 m) square grid layer on the larger polygons of forest to set the maximum size of planning units initially at 25 ha. I then clipped the 25 ha square grids to the external boundaries of the study region and to the external boundaries of fragments so that the configurations of fragments were retained. This clipping procedure created a large number of very small sliver polygons around the external edges of fragments and around the internal edges of the planning region. To reduce this number, I merged all planning units smaller than 3 ha with the neighbouring planning unit having the largest shared boundary if they had one. The largest of the final planning units (34 ha) constituted a 25 grid combined with three adjacent units slightly smaller than 3 ha.

Table 7.1. Abbreviated names and definitions of the final predictor variables in the “local” and “neighbourhood” habitat models.

Predictor	Description	Local	Neighbourhood
Rugg500	Topographic ruggedness: standard deviation in elevation within a 500 m radius		✓
Ter1000	Relative terrain position within a 1000 m radius		✓
Rain	Mean annual rainfall derived from ANUCLIM	✓	✓
Temp	Mean annual temperature derived from ANUCLIM	✓	✓
Dry2000	The percentage of cells in a 2000 m radius containing dry forest		✓
Percnonfor2k	The percentage of cells in a 2000 m radius classified as cleared of native vegetation		✓
Unmod	Factorial variable: 1 if the vegetation is unmodified, 0 otherwise	✓	
Unmod500	The percentage of cells in a 500 m radius containing unmodified forest		✓
Unmod2000	The percentage of cells in a 2000 m radius containing unmodified forest		✓
Ybglexp	Factorial variable: 1 if the cell is suitable for the yellow-bellied glider, 0 otherwise	✓	
Ybglexp2000	The percentage of cells in a 2000 m radius containing suitable yellow-bellied glider habitat		✓
Sowlexp	Factorial variable: 1 if the cell is suitable for the sooty owl, 0 otherwise	✓	
Sowlexp2000	The percentage of cells in a 2000 m radius containing suitable sooty owl habitat		✓
Sqglexp	Factorial variable: 1 if the cell is suitable for the squirrel glider, 0 otherwise	✓	
Sqglexp500	The percentage of cells in a 500 m radius containing suitable squirrel glider habitat		✓

Table 7.2. Final Local and Neighbourhood models and bootstrapped estimates of predictive discrimination given by the area under the Receiving Operating Characteristic Curve

Species	Model type	Preferred model	Model type	ROC area
Yellow-bellied glider	Local	sp ~ s(temp,2) + s(rain,2) + unmod +ybglexp	GAM	0.74
Yellow-bellied glider	Neighbourhood	sp ~ s(temp,2) + s(rain,2) + unmod2000 + s(ybglexp2000, 3)	GAM	0.76
Sooty owl	Local	sp ~ sowlexp x rain + undmod x rain	GLM	0.74
Sooty owl	Neighbourhood	sp ~ s(rain, 2) + rugg500 + s(sowlexp2000,3) + s(ter1000, 2) + unmod2000cl	GAM	0.86
Squirrel glider	Local	sp ~ sqglexp x unmod	GLM	0.78
Squirrel glider	Neighbourhood	sp ~ s(rugg500, 3) + sqglexp500 + s(unmod500cl, 2)	GAM	0.80

7.2.2. Habitat loss model

I calculated the average rate of increase of urban populations with the most recent data available on each major urban centre in the study region (2001 - 2004, Australian Bureau of Statistics 2006). I assumed that the population density stayed constant during the 20-year planning period. Therefore, the extent of each urban settlement increased at the same rate as its population. I also assumed that the growth rate from 2001 to 2004 continued over the 20-year simulations. The annual radius of expansion was that of a circle equal in size to the urban settlement at the start of the land use simulations multiplied by its annual rate of expansion. Settlements adjacent to Lake Macquarie and the Pacific Ocean are constrained from expanding eastward so I doubled their westward rates of expansion to compensate. To derive a continuous probability surface for urban development (“vulnerability”), I used a dispersal kernel with the formula:

$$P = \exp(-\alpha \cdot d) \qquad \text{(eq. 7.2.1)}$$

where *d* is the distance between a cell and a settlement. The parameter α was a characteristic specific to each urban settlement related to its rate of expansion. I calculated α by assigning a probability of 0.5 to a distance equivalent to the estimated average annual distance of expansion for each settlement and solved equation 1 for α. When a cell was within the expansion radius of more than one settlement its probability of conversion was the maximum possible given by equation C1 for all the settlements of interest.

I reclassified the continuous urban vulnerability map into four classes. I did this by applying cut-off values at 1, 2 and 3 standard deviations of urban vulnerability. I subsequently eliminated the first class (values from 0 to 1 standard deviation), because it consisted of areas far from existing urban settlements and with probabilities of conversion that were approximately zero. This class was redundant given that no area in private land was considered to have a null probability of conversion to agriculture.

For each 1 ha cell of native vegetation in private land, I assigned the highest value from the maps of agricultural and urban vulnerability. For planning units that covered more than one vulnerability class, I allocated vulnerability values to planning units as the rounded average vulnerability class of the cells it contained. I used average rather than maximum values within planning units to avoid overestimating probability of loss of vegetation in planning units containing 1 ha cells with variable vulnerabilities.

7.2.3 Planning unit cost

I assumed that the sale value of a planning unit (its acquisition cost) was equal to the discounted flow of net revenue that the planning unit is expected to generate into the future (its opportunity cost). I estimated the cost using a the formula proposed by Naidoo and Adamowicz (2006):

$$EV = \sum_{k=1}^{K} \sum_{c=1}^{C} P_{ck} R_k \qquad \text{(eq. 7.2.2)}$$

Where EV is the estimated land value equal to the sum across all the k possible land uses and all the 1 ha cells c within the planning unit of the return R_k associated with land use k multiplied by the probability of conversion to that particular land use P_k . The rationale for the use of the probability of conversion in the formula is that land values are modeled as the expected value of land arising from all possible uses k, where the expectation is taken over the probability that the land is converted to use k. In this case, I considered land uses related to urban and agricultural activities. The average values of land associated with each activity were available at the resolution of local government areas (LGAs) from the Australian Bureau of Agricultural and Resource Economics (ABARE 2000).

I estimated urban value by calculating the mean value across all urban land uses (defined here as Business, Industrial and Residential) weighted by their proportional extent in the LGA. Because the two LGAs intersected by the planning region (Cessnock and Lake Macquarie) had different land values for both urban and agricultural uses, I applied a smoothing technique to avoid an abrupt difference in land values at the boundary between the LGAs. I did this for urban land value by placing a point in the centre of each urban settlement within each LGA and using an inverse distance weighted interpolation to generate a cost surface for the entire planning region. For agricultural value the interpolation was based on points placed in the centre of each LGA. I calculated the acquisition cost surface by adding the urban and agricultural values together.

7.2.4. Additional results

Table 7.3 Fifth, 50th and 95th percentiles of persistence values (proportion of occurrences still extant at a given time) for all species and all strategies at years 10, 20, 30, 40. For the simulations that terminated before years 30 or 40, the year is indicated in parentheses. PA and PR are the abbreviations for Pattern and Process. MG and ML are the abbreviations for MaxGain and MinLoss. The letters “l” and “r” follow the same coding as in Figure 3.4

YELLOW BELLIED GLIDER				
10	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.887,0.894,0.898	0.887,0.896,0.901	0.887,0.894,0.907	0.889,0.897,0.904
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.885,0.894,0.905	0.881,0.894,0.899	0.882,0.889,0.900	0.877,0.887,0.895
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.584,0.599,0.609	0.591,0.598,0.604	0.592,0.601,0.609	0.591,0601,0.627
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.591,0.603,0.618	0.590,0.603,0.610	0.593,0.603,0.617	0.589,0.602,0.608
20	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.769,0.790,0.797	0.781,0.793,0.807	0.779,0.785,0.801	0.802,0.809,0.815
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.782,0.787,0.806	0.778,0.790,0.798	0.776,0.789,0.798	0.758,0.775,0.791
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.385,0.387,0.395	0.380,0.388,0.398	0.385,0.391,0.398	0.414,0.426,0.436
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.385,0.390,0.394	0.381,0.392,0.400	0.380,0.389,0.394	0.389,0.395,0.397
30	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.678,0.692,0.707	0.683,0.694,0.709	0.696,0.700,0.715	0.685,0.710,0.714
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.665,0.683,0.709	0.665,0.672,0.676	0.676,0.692,0.701	0.662,0.675,0.696
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	NA	NA	NA	NA
LAST	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.607,0.614,0.629	0.608,0.616,0.626	0.616,0.625,0.642	0.619,0.638,0.647
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.595,0.608,0.629	0.584,0.596,0.602	0.607,0.619,0.633	0.591,0.600,0.617
	PA-MG-LR (27th year)	PA-ML-LR (25-26th year)	PR-MG-LR (27th year)	PR-ML-LR (24-25th year)
	0.296,0.296,0.298	0.303,0.308,0.312	0.299,0.301,0.305	0.362,0.376,0.382
	PA-MG-Lr (27-28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)
	0.293,0.293,0.294	0.293,0.294,0.296	0.292,0.292,0.293	0.301,0.304,0.305

SQUIRREL GLIDER				
10	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.943,0.945,0.948	0.944,0.947,0.952	0.944,0.948,0.949	0.944,0.947,0.950
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.942,0.946,0.952	0.943,0.946,0.948	0.942,0.945,0.949	0.940,0.943,0.950
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.740,0.744,0.750	0.748,0.754,0.760	0.741,0.747,0.755	0.750,0.753,0.758
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.739,0.740,0.749	0.739,0.747,0.756	0.738,0.744,0.753	0.742,0.746,0.750
20	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.881,0.887,0.891	0.888,0.892,0.899	0.887,0.889,0.895	0.886,0.892,0.896
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.883,0.887,0.895	0.884,0.886,0892	0.881,0.885,0.893	0.877,0.885,0.893
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.483,0.488,0.501	0.524,0.530,0.535	0.481,0.486,0.491	0.545,0.548,0.556
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.467,0.469,0.476	0.485,0.489,0.493	0.473,0.477,0.484	0.482,0.488,0.491
30	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.820,0.825,0.837	0.831,0.836,0.843	0.826,0.830,0.840	0.819,0.833,0.837
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.817,0.824,0.836	0.814,0.824,0.832	0.817,0824,0.834	0.816,0.823,0.829
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	NA	NA	NA	NA
LAST	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.763,0.768,0.778	0.776,0.784,0.789	0.768,0.774,0.782	0.764,0.781,0.785
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.760,0.768,0.773	0.761,0.768,0.774	0.756,0.766,0.780	0.760,0.765,0.774
	PA-MG-LR (27th year)	PA-ML-LR(25-26th year)	PR-MG-LR (27th year)	PR-ML-LR (24-25th year)
	0.367,0.370,0.385	0.434,0.438,0.441	0.364,0.367,0.371	0.457,0.460,0.465
	PA-MG-Lr (27-28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)
	0.351,0.362,0.364	0.363,0.364,0.365	0.351,0.352,0.353	0.364,0.364,0.366

SOOTY OWL				
10	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.906,0.921,0.931	0.915,0.921,0.930	0.907,0.921,0.944	0.908,0.918,0.936
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.894,0.908,0.929	0.884,0.919,0.932	0.905, 0.912,0.930	0.900,0.919,0.935
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.673,0.703,0.725	0.696,0.717,0.723	0.688,0.708,0.722	0.692,0.707,0.727
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.689,0.716,0.727	0.695,0.707,0.717	0.684,0.700,0.728	0.695,0.702,0.717
20	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.830,0.843,0.856	0.823,0.854,0.870	0.822,0.839,0.860	0.840,0.852,0.867
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.808,0.849,0.869	0.815,0.840,0.858	0.812,0.846,0.858	0.814,0.836,0.867
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.521,0.532,0.542	0.521,0.533,0.556	0.525,0.534,0.546	0.544,0.563,0.571
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.523,0.536,0.546	0.507,0.536,0.551	0.510,0.534,0.540	0.531,0.540,0.549
30	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.771,0.781,0.793	0.755,0.785,0.800	0.761,0.781,0.805	0.779,0.793,0.811
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.724,0.769,0.788	0.753,0.773,0.783	0.745,0.771,0.792	0.748,0.761,0.788
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	NA	NA	NA	NA
LAST	PA-MG-lR	PA-ML-lR	PR-MG-lR	PR-ML-lR
	0.714,0.728,0.736	0.709,0.726,0.748	0.701,0.730,0.736	0.730,0.740,0.759
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.678,0.710,0.735	0.692,0.712,0.738	0.698,0.713,0.749	0.688,0.710,0.738
	PA-MG-LR (27th year)	PA-ML-LR (25-26th year)	PR-MG-LR (27th year)	PR-ML-LR (24-25th year)
	0.430,0.431,0.433	0.438,0.447,0.454	0.430,0.433,0.436	0.518,0.537,0.546
	PA-MG-Lr (27-28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)
	0.426,0.427,0.430	0.426,0.429,0.433	0.425,0.425,0.426	0.438,0.445,0.449

7.3 Appendices chapter 4

7.3.1 Objective function and constraints for MaxGain and MinLoss

The abundance of each feature *f*, in each area *n*, at each point in time *t*, was denoted B_{nft}. Managers made decisions using either MinLoss or MaxGain. At each point in time *t*, MaxGain maximizes the objective function:

$$\sum_{n=1}^{N}\sum_{f=1}^{F} B_{nft} Cmg_{ft} x_{nt} \qquad \text{(eq. 7.3.1)}$$

while MinLoss maximizes:

$$\sum_{n}^{N}\sum_{f}^{F} P_{nt} B_{nft} Cml_{ft} x_{nt} \qquad \text{(eq. 7.3.2)}$$

where x_{nt} was a boolean variable indicating whether area *n* at time *t* was reserved; an area could be reserved ($x = 1$) or developed ($d = 1$) only once during the planning period and remained in that state permanently.

P_{nt} denoted the probability of an area *n* at time *t* was equal to the cumulative probability of the area being lost from time *t* to the end time *T*

$$P_{nt} = 1 - \left(1 - P_{n0}\right)^{T-t} \qquad \text{(eq. 7.3.3)}$$

where P_{n0} was the probability of loss of an area in the following year (see next paragraph). Cmg_{ft} and Cml_{ft} were the complementarity weightings of feature *f* at time *t* for MaxGain and MinLoss respectively. In target based reserve selection the principle of complementarity is used to select new reserves whose features are further from having reached their conservation objectives with the current reserve network. In MaxGain, complementarity (Cmg_{ft}), was a feature weighting based on the ratio between the representation of the feature in the set of reserves *R* at time *t* and the total amount of the feature initially extant (B_{fnt0}) .

$$Cmg_{ft} = 1 - \frac{\sum_{r}^{R} B_{frt}}{\sum_{n}^{N} B_{fnt_0}}, \qquad \text{(eq. 7.3.4)}$$

This equation allocated a low complementarity weighting to features that were already well-represented in the existing reserve system.

I applied a new measure of complementarity for retention with MinLoss that considered all extant areas *E*, both reserved and unreserved:

$$Cml_{ft} = 1 - \frac{\sum_{e}^{E} B_{fet}(1 - P_{et})}{\sum_{n}^{N} B_{fnt_0}} \qquad \text{(eq. 7.3.5)}$$

The contribution of an extant area *e* to protecting feature *f* at time *t*, B_{fet}, was weighted by the probability of the feature persisting in the area until the end of the planning period (1-P_{et}). The denominator was the same as in eq. S1,4. This weighting shifted conservation attention away from features that had high levels of protection already, or were at low risk of losing additional habitat.

Both approaches operated under the budgetary constraint that:

$$\sum_{n}^{N} x_{nt} \leq RR_t \quad \forall t \in T \qquad \text{(eq. 7.3.6)}$$

meaning that each year the number of new reserves could not exceed the reservation rate, *RR*, set to a constant 20 areas.

I used Matlab 2009b (The MathWorks Inc. 2009) to simulate habitat loss, generate the landscape scenarios, and iteratively select areas according to equations 1 and 2.

7.3.2 Estimation of the initial loss rate with the inhibition model

The probability of an area *n*, with vulnerability V_n, being lost is equal to the probability that a random variable U, from a uniform distribution, is lower than V_n*LR where *LR* is the habitat loss rate. Substituting V_n*LR for *y* I have

$$P(U < y) = \frac{y - a}{b - a}, \qquad \text{(eq. 7.3.7)}$$

where *a* and *b* are the lower and upper bounds of the uniform random variable. In this case they are 0 and 1, respectively. Thus: $P(U<y)=y$.

To calculate the overall proportion of areas lost, this probability needs to be integrated across all values of *y* (i.e., for all areas). Decomposing *y* again in V_n*LR and integrating for *V* I have

$$LR \int_{V} x f(x) dx, \qquad \text{(eq. 7.3.8)}$$

where *f(x)* corresponds to the beta probability distribution function of vulnerability and *x* is the random variable vulnerability. Note that

$$\int_V x f(x) dx = E(x)\,. \qquad \text{(eq. 7.3.9)}$$

The expected value of a beta distribution is

$$E(x) = \frac{\alpha}{\alpha + \beta}, \qquad \text{(eq. 7.3.10)}$$

where α and β are the shape parameters of the beta distribution. Since I simulated only symmetric distributions (i.e. $\alpha=\beta$), the resulting mean E*(x)* is equal to 1/2 for any value of α and β. Consequently equation 7.3.8 is equal to *LR/2*. Doubling the vulnerability values for the inhibition model is equivalent to multiplying the whole integral in eq. 7.3.8 by two. By doing so, I ensured that the initial habitat loss was the same for both types of habitat loss models.

7.3.3 Generation of the vulnerability distributions

The vulnerability values were drawn from a beta distribution whose parameters were set to $\alpha = \beta$ to give no skewness. The values of α were chosen to obtain vulnerability variances incrementing from 0.004 to the maximum of 0.083 (with a uniform distribution U[0,1] which is equal to Beta [1,1]). A scenario with zero vulnerability variance was not included because it would not have been possible or informative to derive different correlations between the abundances of five features and constant vulnerability values. Frequency distributions of the vulnerability values for each of the 21 variances tested are in Figure 7.2.

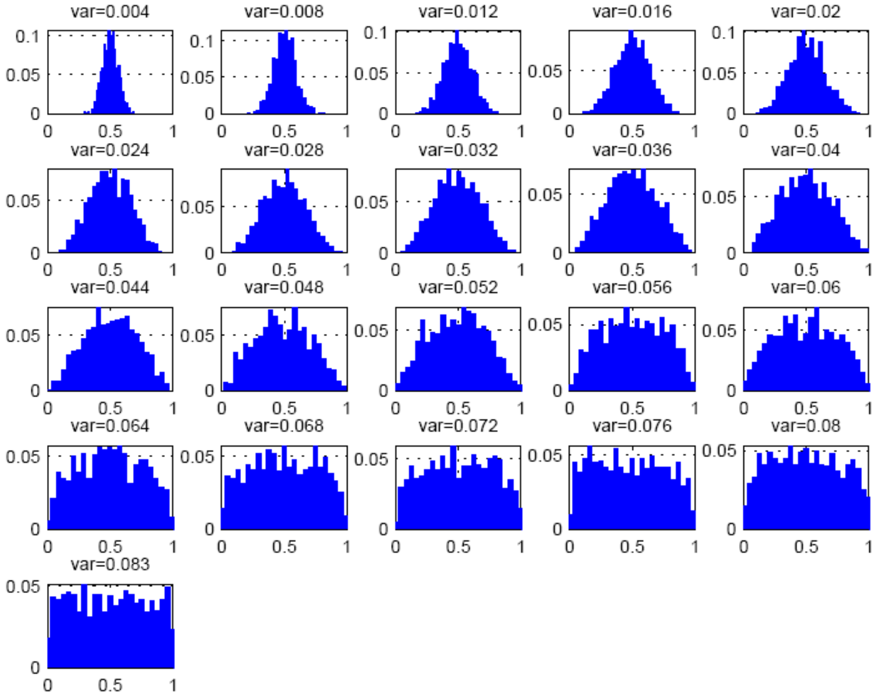


Figure 7.2. An example of the vulnerability distributions tested with different variances. On the *x* axes are the vulnerability values and on the *y* axes their frequency in the simulated landscape.

7.3.4 Alternative method for applying vulnerability uncertainty and associated results for reduced rates of loss

As an alternative approach to deriving values for “estimated” vulnerability, V_e, I randomly altered the “real” vulnerability, V_r, of each planning unit by a random value *Un* such that

$$V_e = V_r + Un$$

Un was drawn from the distribution U~[*lb,ub*]. The lower bound, *lb*, was always a negative value and the upper bound, *ub*, always a positive value.

$$\begin{cases} lb = -Vr; ub = Ul + lb & \text{for } Vr - Ul/2 < 0 \\ lb = -(Ul - ub); ub = 1 - Vr & \text{for } Vr + Ul/2 > 1 \\ lb = -Ul/2; ub = Ul/2 & \text{otherwise} \end{cases} \qquad \text{(eq. 7.3.11)}$$

Ul is the level of uncertainty which I increased from 0 (complete certainty) to 1 (complete uncertainty) at intervals of 0.1 (10%). This application of uncertainty respects two axioms: 1) Ul = |lb| + |ub|; and 2) $Vr + lb \geq 0$, $Vr + ub \leq 1$. As an example, applying an uncertainty level of 90% with two different real vulnerability values, the lower and upper limit of uncertainty and the range of vulnerability estimates would be as follows:

Vr	***Ul*** *(level of uncertainty)*	***lb (lower bound)***	***ub (upper bound)***	***Range of possible Ve values***
0.3	0.9	-0.3	0.6	0-0.9
0.9	0.9	-0.8	0.1	0.1-1

When *Ul* reached 100%, the estimated vulnerability V_e could take any value from 0 to 1 for any value of the real vulnerability V_r.

This application of uncertainty yielded qualitatively similar results to the permutations of vulnerability values (Figure 4.2). However, the uncertainty frontier at which MaxGain became the best model shifted to values closer to 100%, meaning that MinLoss was superior across almost the entire parameter space.

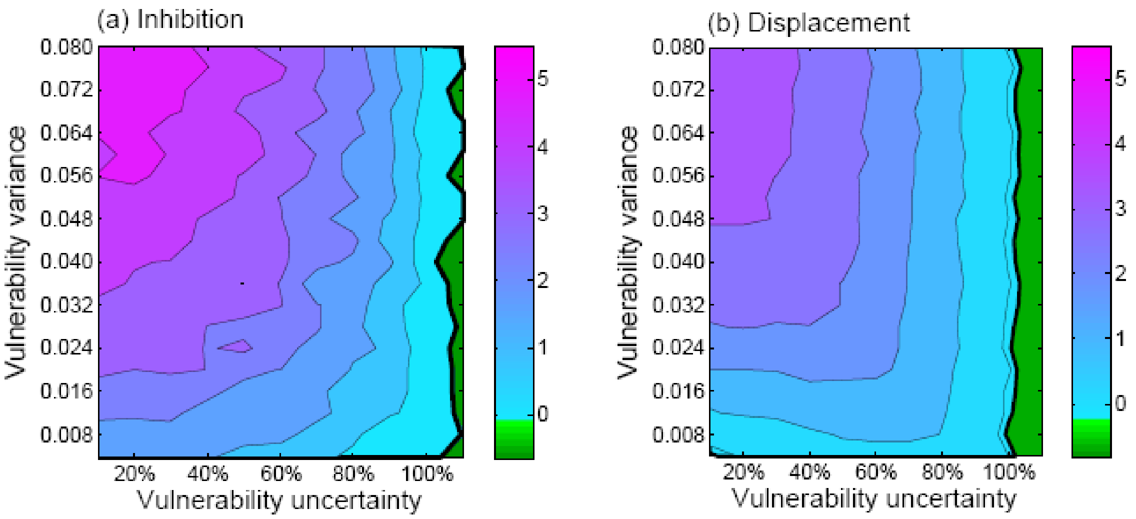


Figure 7.3 Absolute difference between MinLoss and MaxGain in minimum retention across 5 biodiversity features, using an alternative application of uncertainty about estimated vulnerability.

These simulations are with a loss rate of 5% of the landscape. Retention was measured as the percentage of initial abundance still extant at the end of the planning period. I calculated percentage difference as MinLoss retention (%) – MaxGain retention (%), so positive values indicate higher retention for MinLoss. Each contour line represents a 0.8% increment. The thicker contour line represents zero difference. *x*-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). *y*-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape).

With this form of uncertainty, and for the permutation method, I repeated all simulations using a loss rate of 2% to test the sensitivity of the rules of thumb to the habitat loss rate. The results were qualitatively identical but the magnitude of the difference between best and worse approaches was reduced by approximately 50% in both cases. Figure 7.3 shows the results when using permutation-based uncertainty with a 2% loss rate. Figure 7.4 shows the results when using the alternative application of uncertainty described here with a 2% loss rate.

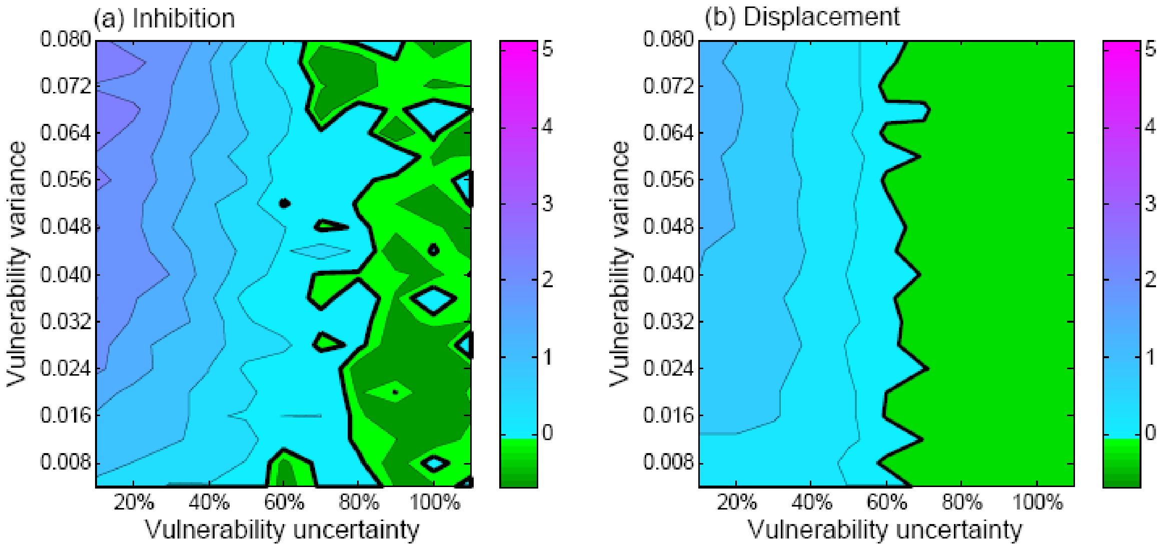


Figure 7.4. Difference between MinLoss and MaxGain in minimum retention across 5 biodiversity features with the permutation-based application of uncertainty about vulnerability estimates and 2% habitat loss rate.

Retention was measured as the percentage of initial abundance still extant at the end of the planning period. I calculated percentage difference as MinLoss retention (%) – MaxGain retention (%), so positive values indicate higher retention for MinLoss. Each contour line represents a 0.5% increment. The thicker contour line represents zero difference. *x*-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). *y*-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape). The scale bar is the same as in Figures 4.2 and 7.3 although the values here never exceed +2.7%

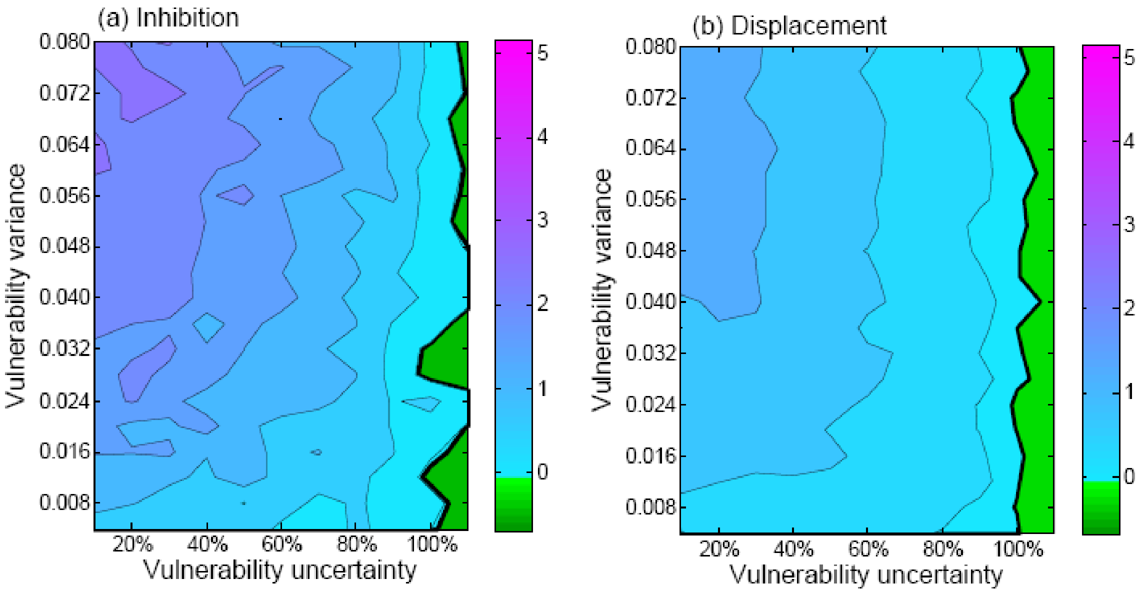


Figure 7.5. Difference between MinLoss and MaxGain in minimum retention across 5 biodiversity features with the alternative application of uncertainty about vulnerability estimates (described above) and 2% habitat loss rate.

Retention was measured as the percentage of initial abundance still extant at the end of the planning period. I calculated percentage difference as MinLoss retention (%) – MaxGain retention (%), so positive values indicate higher retention for MinLoss. Each contour line represents a 0.5% increment. The thicker contour line represents zero difference. *x*-axes show vulnerability uncertainty (difference between real vulnerability and estimated vulnerability provided to the MinLoss manager). *y*-axes show vulnerability variance (spatial variation in vulnerability values in the simulated landscape). The scale bar is the same as in Figures 4.2 and 7.3 although the values here never exceed +1.9%.

7.3.5. Supplementary discussion on third order interactions

Increasing uncertainty worsened the relative performance of MinLoss for negatively correlated features in the inhibition scenarios (Figure 4.4a) and improved it in the displacement scenarios (Figure 4.4b). With higher uncertainty, it increases the likelihood that a MinLoss manager might overestimate the vulnerability of unthreatened areas and mistakenly reserve them. This shifts reservation towards negatively correlated features and, due to budgetary constraints, leaves threatened features less protected. This “uncertainty-driven” shift occurred regardless of the habitat loss model; however, its effects were model-specific. With displacement, this incidental protection of unthreatened areas was beneficial to positively correlated features because any increment of protection reduced the likelihood of those areas being part of the sample that was lost. However, it also perversely shifted additional vulnerability onto high-threat areas because these became more likely to be part of the constant proportion of the landscape lost. With inhibition, this uncertainty-driven shift in reservation toward less vulnerable areas did not necessarily provide additional protection to that happening *de facto* in these areas (because of their low real vulnerability *Vr*). On the contrary, even negatively correlated features had lower retention with increased uncertainty because these features also occurred in areas of high vulnerability, albeit at lower abundance, and more of these areas were lost through the uncertainty-driven shift in reservation.

7.4 Appendices chapter 5

7.4.1 HYDE 3.0 Land use change model

The GLOBIO/HYDE land use change model works in two phases. In the first phase, the model calculates how much crop and pasture is available in each IMAGE region. For the year 2000, the 30" resolution GLC2000 map (Bartholomé & Belward 2005) was first up-scaled to 6’ resolution. The proportions of all land cover types were retained as attributes, for each raster cell. Then the model recalculates cropland area in each raster cell by joining cropland proportions from GLC-cropland (class 16) and GLC-mosaics (classes 17 and 18) into one new cropland class (equation 1).

crop: $0.9*glc16 + 0.5*glc17 + 0.3*glc18 + 0.5*glc23$ (eq. 7.4.1)

The land use change codes are in table 7.4.

The model also calculated pasture areas in each raster cell, joining proportions of GLC-grassland classes (classes 12, 13, 14) and proportions of GLC-cropland and GLC-mosaic classes into a new pasture class (equation 7.4.2 below).

pasture: $0.5*glc12 + 0.9*glc13 + 0.9*glc14 + 0.6*glc18 + 0.1*glc16 + 0.3*glc17 + 0.5*glc23$

These formulas were calibrated by Klein Goldewijk et al. (Klein Goldewijk et al. 2007) to best approximate the current distribution of crop and livestock at the country level from FAO (Food and Agriculture Organization of the United Nations 2005) based on a mix of GLC land use classes.

Table 7.4 Classes in Global landcover classification 2000 (GLC2000)

CLASS	**Global Extent**	**Description**
12	11.3 Mkm^2	Shrub cover, closed/open, deciduous
13	13.2 Mkm^2	Herbaceous cover, closed/open (shrubland), vast grassland areas
14	13.7 Mkm^2	Sparse herbaceous and sparse shrub cover
16	17.1 Mkm^2	Cultivated and managed areas (over 50% of cropland and grassland)
17	3.48 Mkm^2	Cropland/tree cover/nature mosaic (less than 50% of cropland)
18	3.11 Mkm^2	Cropland/shrub or herbaceous cover (less than 20% cropland)
23	-	No land use specified

The resulting total area of cropland and pastures still yielded slightly different estimates than reported in FAOSTAT (Food and Agriculture Organization of the United Nations 2009) so that, at the regional level, an area surplus or deficit appeared in the 6’ resolution land cover map. The area of cropland and pasture land in each raster cell was therefore adjusted by subtracting or adding areas proportionally over each raster cell within a region, so that the total cropland and pasture land was equal to the reported areas in FAOSTAT. For regions with a surplus of cropland or pasture land, the subtraction was distributed proportionally over all natural land use classes present in the raster cells, except bare areas (class 19), water bodies (class 20) snow/ice (class 21) and urban areas (class 22). For regions with a deficit of agricultural land, the cropland and pasture areas were corrected by proportionally subtracting areas from the natural vegetation land cover classes.

For future projections, the total cropland and pasture areas for each region were derived from the integrated assessment model IMAGE 2.2 (Bouwman et al. 2007) used for the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005). Cropland and pasture estimates were derived from the quantitative, spatially explicit models of patterns and trends in human population growth, consumption, production and productivity at 30’ resolution that were used in the IMAGE framework. The resulting areas of cropland and pasture were summed for each IMAGE region. T refer to these regional totals as crop and pasture land “claims”. Subsequently these regional totals were redistributed to the 6’ resolution map by adding or subtracting areas to the cropland and pasture classes respectively, in the proportions described above for the year 2000. This was done sequentially starting with cells and vegetation types more suitable for conversion. The sequence was as follows:

For Crop:

1) Try to allocate crop to non-forest GLC classes in cells that already contain cropland.

2) If all the claim has not been allocated, then try to allocate the remainder in non-forest GLC classes in any 6' cell classified as agricultural land in IMAGE.

3) If all the claim has still not been allocated, then try to allocate the remainder in forest GLC classes in those cells that already contain cropland.

4) If all the claim has still not been allocated, then try to allocate the remainder in forest GLC classes in 6' cells classified as agricultural land in IMAGE, then in cells of other IMAGE classes, beginning with grassland and continuing with shrubland, then forests. Cells classified in IMAGE as bare areas, water bodies, snow and ice and artificial surfaces were excluded.

For Pasture:

1) Try to allocate pasture to non-forest GLC classes in those cells that already contain cropland.
2) If all the claim has not been allocated, then try to allocate the remainder in non-forest GLC classes in any 6' cell classified as agricultural land in IMAGE.
3) If all the claim has still not been allocated, then try to allocate the remainder in forest GLC classes in those cells that already contain pasture.
4) If all the claim has still not been allocated, then try to allocate the remainder in forest GLC classes in 6' cells classified as agricultural land or extensive grassland (respectively land use classes 1 and 2 in IMAGE), and then in cells of other IMAGE classes, beginning with grassland and continuing with shrubland, and then forests. Cells classified in IMAGE as bare areas, water bodies, snow and ice and artificial surfaces were excluded.

Natural vegetation regrowth and effect of Protected Areas

If the projected land claim for pasture or cropland was smaller than the existing amount of cropland or pasture (i.e. there would be a reduction in crop and/or pasture in the region), then the surplus crop and/or pasture was assigned to the dominant land cover in the 6' cell. This was done in reverse order with respect to the allocation of crop and pasture, that is, starting with cells classified in IMAGE as natural vegetation first and then moving to agricultural land, on the assumption that land abandonment would happen first in areas with lower crop/pasture suitability.

Protected areas were assumed to be immune from land cover change. This assumption might be invalid in some regions with poor enforcement but t had no explicit model to account for spatial variation in protected area effectiveness.

Climate change effect on land cover and land use

Climate change in IMAGE was simulated using the BIOME model (Prentice et al. 1992) which predicts the potential vegetation based on climate, soil, dispersal abilities and growth rates of different vegetation types at 30' resolution. However, in the downscaling process, the original IMAGE maps are only accounted for to preferentially allocate land claims to agricultural classes (steps 2 and 4) and to exclude regions classified as bare areas, water bodies, snow and ice (step 4). Therefore, only land cover changes involving these classes in IMAGE would be reflected in the downscaled maps.

Figure 7.6. Average number of declining species across all scenarios versus average National Contribution to Global Loss (NCGL). *y*-axis: average number of declining species across all scenarios, *x*-axis: average National Contribution to Global Loss (NCGL) across all species and scenarios Some labels have been removed to improve readability, others are abbreviated (Table 7.7).

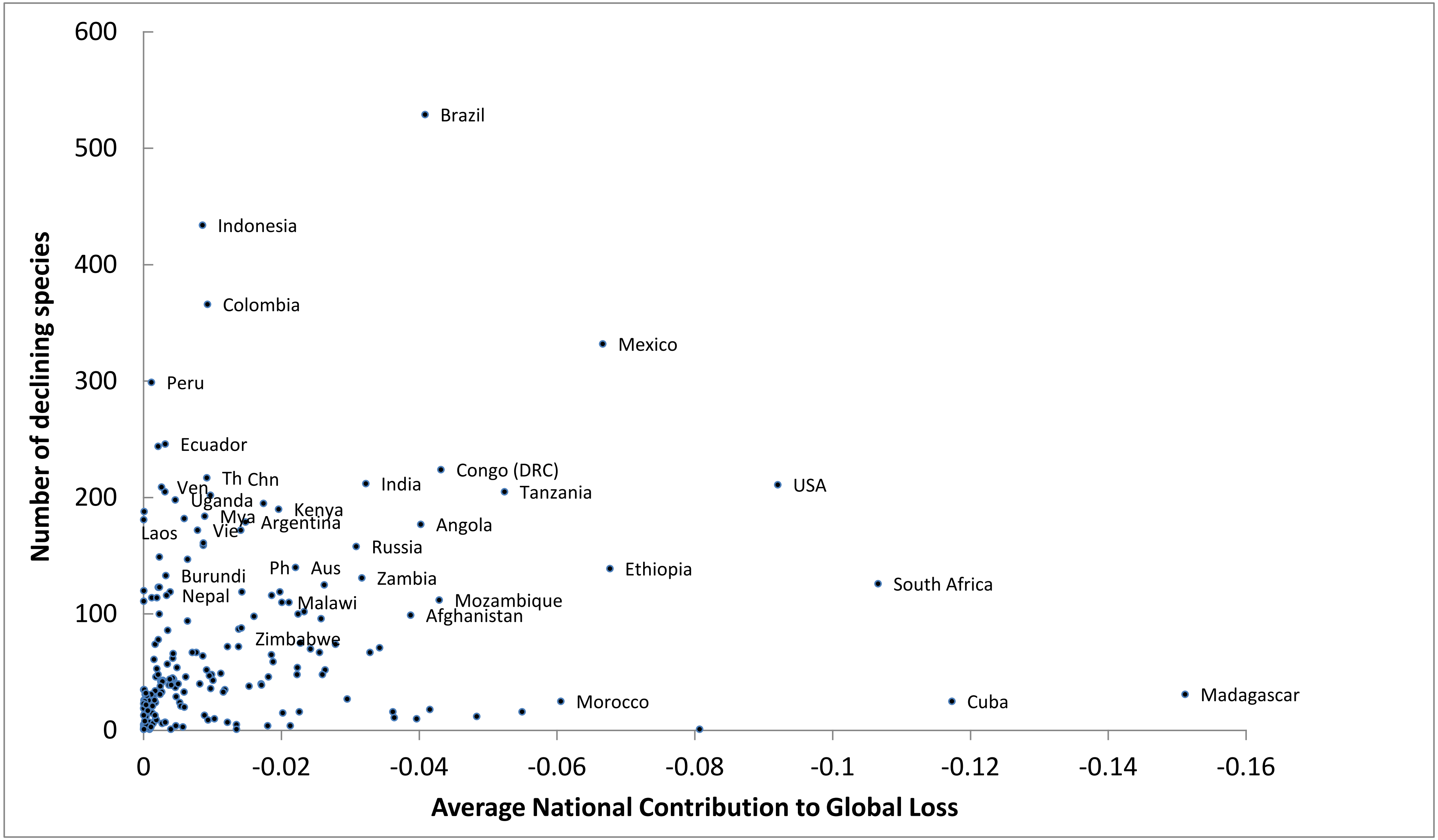


Table 7.5. Conversion of GLOBCOVER classes into GLC2000 classes for habitat suitability models

GLOBCOVER code	GLOBCOVER legend	GLC 2000 code	GLC2000 legend
40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (> 5m)	1	Tree Cover, broadleaved, evergreen
41	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest	1	Tree Cover, broadleaved, evergreen
42	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents	1	Tree Cover, broadleaved, evergreen
50	Closed (>40%) broadleaved deciduous forest (>5m)	2	Tree Cover, broadleaved, deciduous, closed
60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	3	Tree Cover, broadleaved, deciduous, open
92	Open (15-40%) needle-leaved evergreen forest (>5m)	4	Tree Cover, needle-leaved, evergreen
70	Closed (>40%) needle-leaved evergreen forest (>5m)	4	Tree Cover, needle-leaved, evergreen
80	Closed (>40%) needle-leaved deciduous forest (>5m)	5	Tree Cover, needle-leaved, deciduous
91	Open (15-40%) needle-leaved deciduous forest (>5m)	5	Tree Cover, needle-leaved, deciduous
100	Closed to open (>15%) mixed broadleaved and needleaved forest	6	Tree Cover, mixed leaf type
101	Closed (>40%) mixed broadleaved and needleaved forest	6	Tree Cover, mixed leaf type
102	Open (15-40%) mixed broadleaved and needleaved forest	6	Tree Cover, mixed leaf type
160	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily), fresh or brackish water	7	Tree Cover, regularly flooded, fresh water
161	Closed to open broadleaved forest on (semi-)permanently flooded land, fresh water	7	Tree Cover, regularly flooded, fresh water
162	Closed to open broadleaved forest on temporarly flooded land, fresh water	7	Tree Cover, regularly flooded, fresh water
170	Closed (>40%) broadleaved forest or shrubland permanently flooded, saline or brackish water	8	Tree Cover, regularly flooded, saline water
110	Mosaic forest or shrubland (50-70%) and grassland (20-50%)	9	Mosaic: Tree Cover / Other natural vegetation
120	Mosaic grassland (50-70%) and forest or shrubland (20-50%)	9	Mosaic: Tree Cover / Other natural vegetation
133	Closed to open (>15%) needle-leaved evergreen shrubland (<5m)	11	Shrub Cover, closed-open, evergreen
132	Closed to open (>15%) broadleaved evergreen shrubland (<5m)	11	Shrub Cover, closed-open, evergreen
131	Closed to open (>15%) broadleaved or needle-leaved evergreen shrubland (<5m)	11	Shrub Cover, closed-open, evergreen
134	Closed to open (>15%) broadleaved deciduous shrubland (<5m)	12	Shrub Cover, closed-open, deciduous
135	Closed (>40%) broadleaved deciduous shrubland (<5m)	12	Shrub Cover, closed-open, deciduous
136	Open (15-40%) broadleaved deciduous shrubland (<5m)	12	Shrub Cover, closed-open, deciduous
145	Lichens or Mosses	13	Herbaceous Cover, closed-open
142	Closed (>40%) grassland with sparse (<15%) trees or shrubs	13	Herbaceous Cover, closed-open
141	Closed (>40%) grassland	13	Herbaceous Cover, closed-open
143	Open (15-40%) grassland	13	Herbaceous Cover, closed-open
144	Open (15-40%) grassland with sparse (<15%) trees or shrubs	13	Herbaceous Cover, closed-open
140	Closed to open (>15%) herbaceous vgt (grassland, savannas or Lichens/Mosses)	13	Herbaceous Cover, closed-open
151	Sparse (<15%) grassland	14	Sparse herbaceous or sparse shrub cover
152	Sparse (<15%) shrubland	14	Sparse herbaceous or sparse shrub cover
153	Sparse (<15%) trees	14	Sparse herbaceous or sparse shrub cover
150	Sparse (<15%) vegetation	14	Sparse herbaceous or sparse shrub cover
186	Closed to open (>15%) grassland on temporarily flooded land	15	Regularly flooded shrub and/or herbaceous cover
187	Closed to open (>15%) grassland on permanently flooded land	15	Regularly flooded shrub and/or herbaceous cover
185	Closed to open (>15%) grassland on regularly flooded or waterlogged soil, fresh or brakish water	15	Regularly flooded shrub and/or

			herbaceous cover
184	Closed to open (>15%) woody vgt on waterlogged soil	15	Regularly flooded shrub and/or herbaceous cover
182	Closed to open (>15%) woody vgt on temporarily flooded land	15	Regularly flooded shrub and/or herbaceous cover
181	Closed to open (>15%) woody vgt on regularly flooded or waterlogged soil, fresh or brakish water	15	Regularly flooded shrub and/or herbaceous cover
180	Closed to open (>15%) grassland or woody vgt on regularly flooded or waterlogged soil, fresh, brakish or saline water	15	Regularly flooded shrub and/or herbaceous cover
183	Closed to open (>15%) woody vgt on permanently flooded land	15	Regularly flooded shrub and/or herbaceous cover
188	Closed to open (>15%) grassland on waterlogged soil	15	Regularly flooded shrub and/or herbaceous cover
13	Post-flooding or irrigated herbaceous crops	16	Cultivated and managed areas
16	Rainfed shrub or tree crops (cashcrops, vineyards, olive tree, orchards,…)	16	Cultivated and managed areas
11	Post-flooding or irrigated croplands (or aquatic)	16	Cultivated and managed areas
15	Rainfed herbaceous crops	16	Cultivated and managed areas
14	Rainfed croplands	16	Cultivated and managed areas
12	Post-flooding or irrigated shrub or tree crops	16	Cultivated and managed areas
10	Cultivated and Managed areas	16	Cultivated and managed areas
32	Mosaic forest (50-70%) / cropland (20-50%)	17	Mosaic: Cropland / Tree Cover / Other natural vegetation
30	Mosaic cropland (50-70%) / forest (20-50%)	17	Mosaic: Cropland / Tree Cover / Other natural vegetation
21	Mosaic cropland (50-70%) / grassland or shrubland (20-50%)	18	Mosaic: Cropland / Shrub and/or grass cover
31	Mosaic grassland or shrubland (50-70%) / cropland (20-50%)	18	Mosaic: Cropland / Shrub and/or grass cover
202	Non-consolidated bare areas (sandy desert)	19	Bare Areas
203	Salt hardpands	19	Bare Areas
201	Consolidated bare areas (hardpands, gravels, bare rock, stones, boulders)	19	Bare Areas
200	Bare areas	19	Bare Areas
210	Water Bodies	20	Water Bodies
220	Permanent Snow and Ice	21	Snow and Ice
190	Artificial surfaces and associated areas (Urban areas >50%)	22	Artificial surfaces and associated areas
140	Closed to open (>15%) herbaceous vgt (grassland, savannas or Lichens/Mosses)	30	Pastures and rangelands (grazing area)
141	Closed (>40%) grassland	30	Pastures and rangelands (grazing area)
142	Closed (>40%) grassland with sparse (<15%) trees or shrubs	30	Pastures and rangelands (grazing area)
144	Open (15-40%) grassland with sparse (<15%) trees or shrubs	30	Pastures and rangelands (grazing area)
143	Open (15-40%) grassland	30	Pastures and rangelands (grazing area)
21	Mosaic cropland (50-70%) / grassland or shrubland (20-50%)	30	Pastures and rangelands (grazing area)

Table 7.6 The 43 countries and territories excluded from this study because of small size (names accord with the International Organization for Standardization (ISO) standard 3166-1)

Åland Islands	Kiribati	Saint Helena, Ascension and Tristan Da Cunha
American Samoa	Macao	Saint Martin
Antarctica	Maldives	Saint Pierre And Miquelon
Bahamas	Marshall Islands	Samoa
Bermuda	Micronesia, Federated States Of	Seychelles
Bouvet Island	Moldova, Republic Of	South Georgia And The South Sandwich Islands
British Indian Ocean Territory	Monaco	Timor-Leste
Christmas Island	Montserrat	Tokelau
Cocos (Keeling) Islands	Nauru	Tonga
Cook Islands	Niue	Turks And Caicos Islands
French Polynesia	Norfolk Island	Tuvalu
French Southern Territories	Northern Mariana Islands	United States Minor Outlying Islands
Guam	Palau	Wallis And Futuna
Heard Island And Mcdonald Islands	Pitcairn	
Holy See (Vatican City State)	Saint Barthélemy	

Table 7.7 Country names and abbreviated labels in figure 5.2 and figure 7.4.1.

Country	Label
Afghanistan	Afg
Angola	Ang
Argentina	Arg
Australia	Aus
Brazil	Bra
Cameroon	Cam
Central African Republic	CAR
China	Chn
Colombia	Col
Congo	Con
Cuba	Cu

Congo (Democratic Republic of the)	DRC
Ethiopia	Et
Ghana	Gha
Guatemala	Gt
Guinea	Gui
India	Ind
Indonesia	Ins
Iran	Irn
Kazakhstan	Ka
Kenya	Ke
Liberia	Lir
Madagascar	Mad
Mali	Mal
Mexico	Mex
Malawi	Mlw
Morocco	Mor
Mozambique	Moz
Myanmar (Burma)	Mya
Namibia	Na
Nicaragua	Nic
Niger	Nig
Nigeria	Nir
Pakistan	Pak
Panama	Pan
Philippines	Ph
Russia	Ru
Rwanda	Rw
South Africa	SoA
Somalia	Som
Sudan	Su
Tanzania	Tan
Thailand	Th
Turkey	Tur
Uganda	Ug
United States	USA
Venezuela	Ven
Vietnam	Vie
Zambia	Za
Zimbabwe	Zim

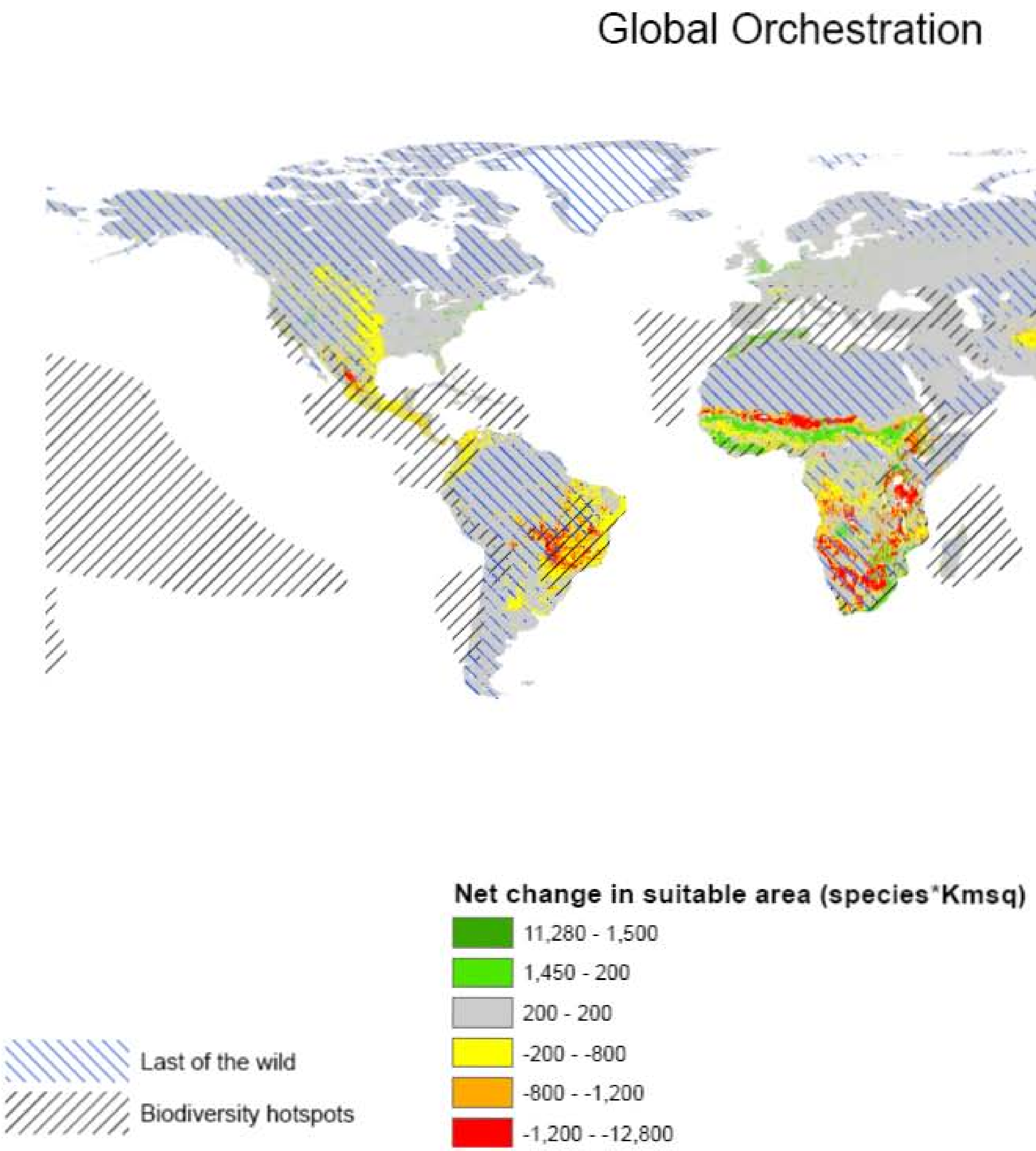


Figure 7.7. Present and future conservation priorities at 6' resolution. Net change in suitable habitat across all terrestrial mammals

between 2000 and 2050 for the scenario Global Orchestration overlapped with the Biodiversity Hotspots (example of reactive conservation) and the Last of the Wild (example of proactive conservation). The level of overlap between yellow and red areas and proactive and reactive conservation priorities is similar with other scenarios of human development (data not shown).

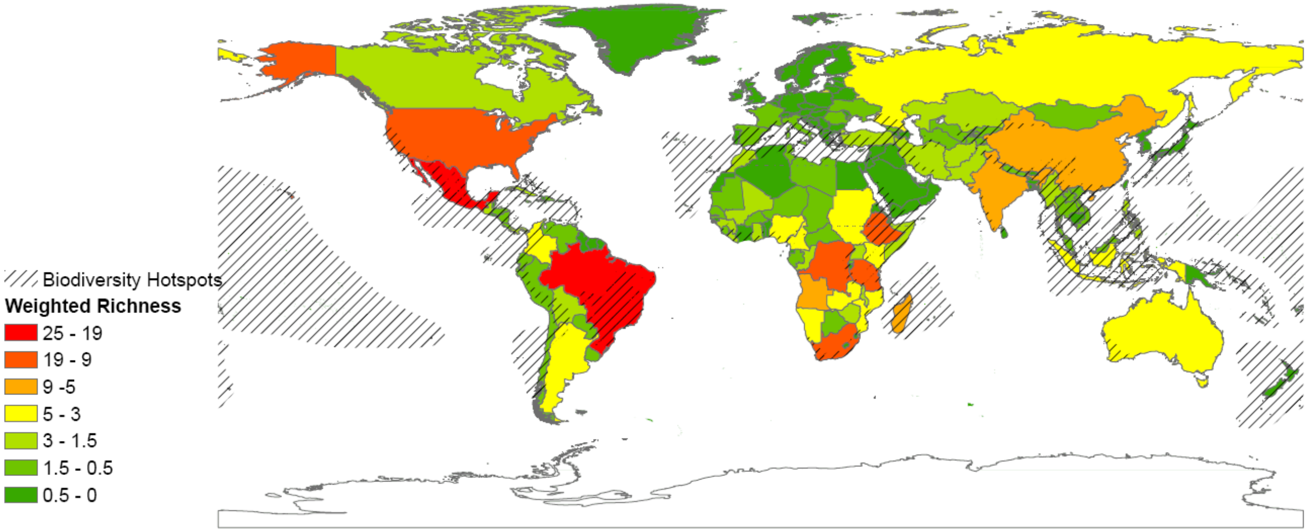


Figure 7.8. Mammal richness weighted by average global loss across the four scenarios and by the proportion of species range in each country (GLC). This richness is equivalent to the summation across the set of species *S* in country *c* of the global loss of habitat of each species *s*, multiplied by the proportion of its range in country *c*. $GLC_c = \sum_s^S GL_s P_{sc}$. Legend categories use natural breaks adjusted to the closest integer with ArcGis 10