

Metapopulation Modeling and Optimal Habitat Reconstruction for Birds in the Mount  
Lofty Ranges, South Australia

by

Michael Ian Westphal

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Committee in charge:

Professor Wayne M. Getz, Chair  
Professor Hugh P. Possingham  
Professor Steven R. Beissinger  
Associate Professor Cherie J. Briggs

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The dissertation of Michael Ian Westphal is approved:

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Metapopulation Modeling and Optimal Habitat Reconstruction for Birds in  
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## Abstract

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The use of decision theory and optimization tools has been rather wanting in conservation biology. The goal of my dissertation has been to apply a decision theory framework to metapopulation management and landscape-level optimal habitat reconstruction. I used stochastic dynamic programming to evaluate habitat restoration strategies, such as patch enlargement, patch creation and connectivity via corridors, for a metapopulation of the Critically Endangered Southern Emu-wren (*Stipiturus malachurus intermedius*) in South Australia. I also applied this model to optimal mowing of butterfly meadows in Germany. My results show that the state-dependent stochastic dynamic programming solutions are substantially better than state-independent strategies derived by Monte Carlo simulations. Furthermore, I simulated hypothetical metapopulations, varying the extinction, recolonization, patch geometry and area allocation parameters, and used a simulated annealing optimization algorithm to maximize the time to extinction

for the metapopulation, evaluating various habitat restoration scenarios. No robust rules of thumb emerged for how to allocate habitat to metapopulations.

One of the most salient questions in landscape ecology is the degree to which landscape configuration, as opposed to just landscape area, is important in explaining species distribution patterns. Using South Australia Ornithological Association Bird Atlas data from 1984-1985, I conducted logistic regression analyses on the distribution patterns of 31 bird species in the Mount Lofty Ranges (MLR), an important 'biological' island in South Australia with only 16% of the original native vegetation remaining. While most species responded positively to landscape area, half of 25 species with sufficient discriminatory models responded negatively to landscapes with high patch isolation and low patch compactness. This is in accord with theory, which suggests that configuration becomes important where habitat area is a small proportion of the total landscape area. I applied these probability functions from the logistic regression analyses to computer programs that explore, using simulated annealing, which areas should be prioritized for restoration to maximize the probability of occurrence over all species and all restoration sites. These programs are flexible enough to incorporate different objective functions, cost constraints and probability functions and are a useful tool for conservation planning in the MLR, and the general methodology is applicable to general landscape design problems in other regions.

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Chair

Date

To all my relatives and ancestors before me  
who never had the privilege and pleasure of higher education.

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**The Gum Forest**  
by Les Murray

After the last gapped wire on a post,  
homecoming for me, to enter the gum forest.

This old slow battlefield: parings of armour,  
cracked dollars, elbows, scattered on the ground.

New trees step out of the old: lemon and ochre  
splitting out of the grey everywhere, in the gum forest.

In there for miles, shade track and ironbark slope,  
depth casually beginning all around, at a little distance.

Sky sifting, and always a hint of smoke in the light;  
you can never reach the heart of the gum forest.

In here is like a great yacht harbour, charmed to leaves,  
innumerable tackle, poles wrapped in spattered sail,  
or of an unknown army in reserve for centuries.

Flooded-gums on creek ground, each tall because of each.  
Now a blackbutt in bloom is showering with bees  
but warm blood sleeps in the middle of the day.  
The witching hour is noon in the gum forest.

Foliage builds like a layering splash: ground water  
drily upheld in edge-on, wax-rolled, gall-plucked  
leaves upon leaves. The shoal life of parrots up there.

Stone footings, trunk-shattered. Non-human lights.  
Enormous abandoned machines. The mysteries of the gum forest.

Delight to me, though, at the water-smuggling creeks,  
health tome, too, under banksia candles and combs.

A wind is up, rubbing limbs above the bullock roads;  
mountains are waves in the ocean of the gum forest.

I go my way, looking back sometimes, looking round me;  
singid oils clear my mind, and the pouring sound high up.

Why have I denied the passions of my time? To see  
lightning strike upward out of the gum forest.

# Acknowledgments

This litany of thanks may be reminiscent of an Oscars speech, but I am indebted to many along this circuitous path that has ended in this “What I did in graduate school” term paper. We are a confluence of experiences with others, a superposition of many other people’s ideas. First, I would like to thank my advisors, Hugh Possingham and Wayne Getz. Hugh took a chance on this brazen boy from Berkeley, with more confidence than competence, and first invited me to work in Australia after only one brief burrito lunch in Santa Barbara. Hugh’s idiot savantic passion for birds, ecology and conservation is inspirational. (Though his wine cask, white bread, and Channel 10 cultural ways may not be.) Hugh is a good scientist, but more importantly a great man, the quintessential public scientist who believes that the objectivity of science does not preclude activism, which indeed should be part of our compact with society as scientists. I learned not so much techniques or tools from Hugh, but more critically the process of science, the marketing of ideas. He gave me the ideas to nucleate upon. Wayne first accepted me to Berkeley when others didn’t, and showed understanding when I fledged and moved to Australia. Wayne is a true intellectual and scientific generalist (and gourmet), with whom I have always had stimulating coffee-pot discussions. Wayne has always been vigilant against intellectual sloppiness (especially notation!), and this has made me a sharper scientist.

I owe a debt of gratitude to my family – David, Rachel, Rebecca, and particularly to my parents, John and Mary, who have always made their children’s education their

highest priority. My brother was my first intellectual role model, the one who taught me Marxism and algebra and who used to mercilessly wallop me in chess and Squad Leader when I was very young. I was the sounding board for his developing subversive, heretical ideas. This PhD is the one he never finished. I apologize you, Rachel and Rebecca, for giving your Barbie dolls haircuts and throwing them in the sewer. My uncle and aunt, Walt and Mary Jane, served as surrogate parents during my time at Berkeley and selflessly always provided me with fine meals, bourbon, a place to crash and sweeping views of the San Francisco Bay. It is a pity that I didn't really know you in my youth.

I have had many good teachers in my time, starting with elementary school. We built a city with Mrs. Kielbasa and hatched chicks with Mrs. Rideout. Mrs. Corraine and her strong-arm grammar tactics have assured that I will always remember what gerunds, split infinitives, and dangling participles are and that I will always be able to diagram sentences blindfolded. I apologize for rolling an orange at your feet, locking you out of your house, and breaking the statue of St. Joseph, respectively. In high school, Mr. Kenney opened up a world of literature to me and instilled in me a love language – so much so that I knew I would never major in literature, though it was always my favorite subject in school. Mr. Lennon made sure that I would always find such historical episodes like the Whiskey Rebellion or the Treaty of Guadalupe Hidalgo interesting. At university, Drs. Jaenike, Adams and Fehn gave me my first opportunities to do scientific research, while Prof. Brett brought me the first hand experience of a brilliant, encyclopedic, eccentric academic who could discursively talk about history of the earth

off the top of his head. Dr. Brooks showed me Hinduism and Buddhism and how an academic can be a GQ model. (What is the essence of an onion?)

Of course, I would be remiss not to mention the support of my friends and colleagues. I have been very fortunate to have three wonderful partners during my academic time: Deanna, Stacey and Ulla, without which, perhaps I would not be finishing this dissertation now. Deanna, my high school sweetheart, was there during the formative years. Perhaps no one will ever understand so deeply where I came from. Stacey was my support during my qualifying exam and the academic wilderness years when I was searching for a project. I fondly recall the mystery spot and the sunset in Santa Cruz and getting lost with you (and van Gogh) on the coast. Ulla was there during those halcyon days in Adelaide. Ulla is also my teacher of the classics, German and *Kultur*, my favorite Bluestocking, the lover of poetry who elicits my literary side and my favorite travel partner. Thank you for the journey from Les to Lesvos. Thanks to all my friends from KLC in Adelaide, but especially the Port Elliot gang: Heike for showing me a world with your smile, my Fitzroy femme fatale, Perrie, for all those Outback ruins and never desolate conversation, and Joel for the limericks, haikus and mounds of glistening flesh. Greg, Stacy, fiddlin' Luscious Jackson and Miche (or Elie from Sofia?) from the University of Rochester have affirmed my belief that if you leave a phase in life with just a few close special friends, then your life is not depauperate.

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benefited immensely from the avatars of stats and computing – Drew and Wayne. I have been fortunate to be surrounded by such a fantastic ensemble of strong women. This may never be replicated again, and I will miss you all. What I consider mordant wit often is viewed as obnoxiousness and arrogance, and I thank everyone in the Spatial Ecology Lab for tolerating me, and I hope I brought a little entrainment if not any expertise. I appoint Norbert and Chris as my replacement as Statler and Waldorf and Emily shall be the new Hugh's Pitbull. Scott, my co-conspirator on the MLR work and interlocutor on matters of foreign policy and the Middle East, has restored some of my confidence in the Aussie male. Thank you for spending those house teaching me bird calls (which I have forgotten for security reasons) and for keeping Adelaide safe from the deleteriously cult of Maximus. I hope you find your white raisins of clarity. Renaissance men are not yet extinct.

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Valhalla of modeling. The members of my Qualifying Exam and Dissertation committees – Dale McCullough, Adina Merenlender, Steve Beissinger and Cherie Briggs have allowed me to get this far. I would like to thank everyone else at the University of Adelaide, the University of Queensland, the University of Natal-Pietermaritzburg (South Africa), and the University of Helsinki that I have met on the course of my peregrinations and who have made my stays so pleasant.

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*And the Lord God commanded the man, saying Of every tree of the garden thou mayest freely eat: But of the Tree of the knowledge of good and evil, thou shalt not eat it: for in the day that thou eatest thereof thou shalt surely die. (Genesis 2:16-17)*

Though some of the mysteries of world may be not just outside the outstretched hand of Tantalus but fundamentally beyond our ken, I am grateful that some at the mad margins of humanity have always had that insatiable yearning to peel away the layers of

the unknown. Without the Enlightenment and the edifice that it created, no PhD, dogmatically unfettered, would be possible. *Eppure si muove*.

This dissertation is my greatest accomplishment since I warmed the chair of the Nobel-Laureate, Czelaw Milosz, and the biggest blood-letting since I stuck a Matchbox wheel up my nose in the first grade.

*Science tells what we can know, but what we can know is little, and if we forget how much we cannot know we become insensitive to many things of very great importance.*

- Bertrand Russell, *History of Western Philosophy*

*Our knowledge of nature must be supplemented with a knowledge of human society if we are to use our knowledge of nature in a human way.*

- Bertold Brecht, *The Messingkauf Dialogues*

# Summary

The leitmotif of my dissertation is the use of decision theory tools in conservation biology. I have focused on habitat reconstruction, but the tools I have employed, namely stochastic dynamic programming and iterative heuristics, can be applied more generally to landscape design problems. While decision theory tools have been used previously in conservation, it is rather sparse territory. There has often been a chasm between economics and conservation ecology. With exiguous resources available for conservation, however, it is essential that there is a melding of the two. In order to maximize the conservation value to cost ratio of management actions, a decision theory framework must be adopted.

Conservation biology is a fairly nascent discipline, and I think it has often been plagued by the over-preoccupation with the activity of stamp-collecting - the cataloging of species - and the estimation of the rate of hemorrhaging of biodiversity. With an immense amount of biodiversity, it is Sisyphean effort to describe it all. Obviously, beyond the erudite merits, taxonomy and phylogeny have conservation importance as we must understand the pattern of diversity, but it alone is impotent to arrest species loss. Furthermore, the field historically has been dominated by the *small-population* paradigm (Caughley 1994), the focus on species at the precipice of the extinction threshold or beyond. Often times, resources have been imprudently devoted to the futile and the doomed – species that may not be able to be resuscitated. While these pursuits are noble, I believe more time should be spent on the prescriptive rather than the descriptive and

more resources devoted to the community or landscape-level level rather than the species-level.

Conservation biology has often dichotomized the world into the “sacred” and the “profane”, that is the mythical “pristine” (there is no wildness devoid of humanness) lands and the environmentally-degraded areas. Research in conservation biology has been concentrated in the former, the wellsprings of biodiversity such as tropical rainforests, while the “backyard biodiversity” of human-modified landscapes has been given disproportionately less attention. However, the greatest challenges in conservation generally lie outside those delineated natural park areas, and as conservation biology matures, it will focus more on creating/designing sustainable landscapes where there are manifold, competing land uses and socioeconomic forces. It is often the matrix, the interstitial space between natural parks areas, which are critical to holding things together.

This ethos has dictated the course of my PhD research. The tools that I have used are not novel in themselves. As ecology is a derivative discipline, its techniques usually have been appropriated from other fields, where they have been used for a long time. (Ecology rarely develops its own tools of analysis and is not a canonical science, contributing to other disciplines. An exception would be chaos theory, where some of the initial developments were made in Ecology - (May 1973, 1974, 1976)). Both stochastic dynamic programming (SDP) (Bellman 1957) and the iterative heuristic that I have used, simulated annealing (Metropolis et al. 1953), ultimately have their roots in WWII, during the seminal developments in Operations Research. SDP has been used extensively in behavioral ecology (Mangel and Clark 1988, Clark and Mangel 2000) and more recently

in applied ecology (Lubow 1996, Possingham 1996, Johnson et al. 1997, Milner-Gulland 1997, Possingham 1997, Spencer 1997, Richards et al. 1999, Shea and Possingham 2000, Moore and Possingham 2001). Simulated annealing has been applied to reserve design (Ball 1999, Possingham et al. 2000, Andelman 2002, McDonnell et al. 2002) and used in other areas of natural resource management, such as forestry (Liu 2000, Meilby 2001, Baskent 2002, Ohmann 2002, Von B. W. Chen 2002). In fact, forestry is much more progressive than ecology when it comes to the use of decision theory tools.

In Chapter 1, I develop a Markov-chain metapopulation model and use SDP to explore optimal habitat reconstruction strategies (i.e. patch enlargement and creation of corridors) for a real metapopulation of the Critically Endangered Southern Emu-wren (*Stipiturus malachurus intermedius*). If one decision can be made at each time step, then the problem is an optimal sequencing problem in Operations Research, and only SDP can find the exact optimum. For every population state (pattern of occupancy of the patches) and landscape state (patch areas, presence of corridors) at every point in time, the model gives the best strategy for reducing the probability of extinction, given that in the future the optimal decisions are made. My results show that the sequence of decisions can be very complex and certainly impossible to intuit with any great robustness. The best strategy is highly dependent on the occupancy pattern of the metapopulation. The SDP state-dependent decisions were found to reduce the extinction probability over 30 years by 50 – 80%, compared to up to 30% by state-independent sets of strategies. In Chapter 2, I modify the model and do a “warm up” analysis of optimal mowing strategies for a hypothetical Levins-type (Levins 1969, 1971) butterfly metapopulation. Mowing is necessary as the habitat quality declines with time since mowing; however, mowing

extirpates the subpopulation with some probability. The idea is to find that “Goldilocks” mowing frequency, and the optimal decision depends on the time before some endpoint, the habit quality of the patches, and the pattern of occupancy. Even for this simple hypothetical metapopulation, under varying mowing extirpation probabilities, the state-dependent set of strategies derived from the SDP results in survival probabilities that are 0.35 – 0.55 greater than the state-independent strategies derived from Monte Carlo simulations.

The Southern Emu-wren work led me to explore the notion of rules of thumb in general for habitat reconstruction for metapopulations. In Chapter 3, I simulate many hypothetical metapopulations with varying patch configurations and size distributions, and then use a formula for the approximation of the time to extinction (Frank and Wissel 1998, Frank 2003) and simulated annealing to explore whether any rules of thumb can be distilled on which patches become connected by corridors or enlarged to the greatest extent. Based simply on the extinction submodel, it is expected that one should preferentially enlarge the smallest patch; that is, the smallest patch should have the largest absolute change in area. This is due to the fact that the smallest patch has the largest marginal value in terms of adding area to it. However, my results indicate that the complexity of patch geometry casts doubt on the robustness of rules-of-thumb, as over all runs, no simple rule was fulfilled much more than 50% of the time.

In the final three chapters, I move to multi-species optimal habitat reconstruction at the landscape scale, specifically focusing on birds in the Mount Lofty Ranges, South Australia. Single-species conservation really is a luxury, and in most cases we will be concerned with designing, reserving or restoring landscapes to maximize the viability or

occurrence of a whole suite of species. While the Mount Lofty Ranges is not particularly speciose, it is noteworthy because it is a 'biological island', a relatively wet region (500 – 800 mm rainfall) surrounded by more arid areas with many unique subspecies.

Moreover, it is the most western extent of the Eastern Australian bird fauna. About 16% of the region is native vegetation, comprised mostly of small, easily-overlooked remnants (mean size 13 ha) in a matrix of cropland, vineyards and pastureland. Having experienced land clearance earlier than most regions of Australia, it is also poised to deal with revegetation first; thus, it may serve as a template for strategic revegetation elsewhere in Australia.

With the advent of the cognizance of the potential importance space in ecology (Tilman and Kareiva 1997), one intriguing question is the degree to which the spatial configuration of habitat, the geometry alone, is important as a determinant of species occupancy or viability. In a simulation study Fahrig (1997, 1998) found that when the percentage of habitat in a landscape exceeds 20%, then species persistence was virtually assured, regardless of the spatial configuration of the habitat. A review of birds and mammals by Andr n (1994) also suggests that habitat patch isolation only becomes important in terms of species richness or abundance when the percentage of habitat decreases below a 20-30% threshold. In Chapter 4, I conduct logistic regression analyses on the effect the spatial pattern on the distribution of 31 woodland bird species. As is expected, most of the species responded positively to the amount of native vegetation area. However, the spatial configuration cannot be ignored. Considering a set of candidate models for which there is reasonable support (Akaike weights > 0.10), 12 species responded negatively to landscapes with highly linear and isolated patches.

Once you have those probability functions for occurrence in the landscape from the logistic regression, the next step is to explore how one can most efficaciously put habitat back into the landscape to maximize the probability of occurrence of species. Only considering the local scale in habitat restoration can be mistaken. I liken it to viewing a Seurat pointillist painting at too close a perspective - it is a meaningless collection of dots. It is only when one takes a step back, that the dots form a coherent pattern. In chapters 5 and 6, I use programs that I have written using a simulated annealing algorithm and a greedy iterative heuristic to answer this question for 22 and 29 species, respectively. The coding of these programs is not a trivial task. I first chose 31 species that were considered isolated or partially isolate in the region (Paton et al. 1994) and eliminated those species for which the models had inadequate discrimination (ROC area under the curve values of  $\geq 0.60$  - Hanley and McNeil 1982, Fielding and Bell 1997, Pearce and Ferrier 2000). In Chapter 5, I consider simply a binary landscape, but explore an array of budget sizes, cost scenarios and objective functions. The products of many runs of the algorithm are priority sites (high summed irreplaceability values) and benchmarks for aspects of landscape configuration. Under scenarios assuming equal site costs, my results suggest that revegetation in the region should strive to create landscapes with a mean revegetated patch size ranging from 1770 – 3170 ha and with the connectivity increased from 60 – 87 % over the present unvegetated landscape. With property values incorporated as site costs, connectivity is not significantly different from the present landscape, but the average size of revegetated patches is still ten times greater than the average patch size of the unvegetated landscape. Adding variable site costs (using property value as a surrogate) shifts the highly irreplaceable sites away from the

more vegetated main spine of the MLR near Adelaide to farther east in the region, where there are more inexpensive sites.

In Chapter 6, I consider a heterogeneous landscape, where the landscape is divided into coarse habitat types: stringybark (e.g. *Eucalyptus leucoxylon*, *Eucalyptus fasciculosa*) vs. non-stringybark (e.g. *Eucalyptus baxteri*, *Eucalyptus obliqua*) overstorey and open forest, woodland, low woodland, and shrubland/heathland structural types. Moreover, I now explore scenarios where the unrestored site can become any habitat type or constrained to be only the most probable type as determined from a multinomial regression analysis, where the explanatory variables were climate and soil variables. The size of the patches in which the restored sites were imbedded ranged from 122 – 598 ha. Maximizing the amount stringybark or non-stringybark woodland (as opposed to low woodland, shrubland or open forest) maximizes the probabilities of occurrence of the species considered, but the exact proportion depends on the assumptions of the available habitat type for each site. Other heuristics for landscape restoration, such as just creating large patches or accreting area to the largest existing patch, performed poorly, with objective function values that ranged from 48 - 73% of that of the near-optimal solutions. Likewise, I analyzed the solutions for three focal species separately (Brush Bronzewing (*Phaps elegans*), Brown Treecreeper (*Climacteris picumnus*) and Scarlet Robin (*Petroica multicolor*) and found that one has to be cautious about using surrogates of the whole community. The objective function value for the single-species scenarios ranged from 63 – 91% of that of the multi-species solution objective function value.

It is my hope that this dissertation will contribute meaningfully to the corpus of decision theory in conservation biology. The multi-species, landscape-level habitat

reconstruction in this dissertation is the first instance of such research, and the software and methodology have applicability to species and regions outside the Mount Lofty Ranges. My focus has been on habitat reconstruction, but the techniques and the decision theory edifice can be applied to other problems in conservation.

The capacity to explicitly solve problems – the exploration of management decisions with an awareness of costs, as opposed to generating data and theory, has been wanting in conservation biology. Of course, there are many limitations to my work, which I have delved into more deeply in each chapter, but I will highlight here. Most are of the data limitation flavor. It must be emphasized that the decision theory tools that I have employed are flexible and are able to incorporate a wide variety of underlying data and models.

The work on the landscape-level Mount Lofty Ranges habitat reconstruction (Chapters 5-7) should be viewed as work in process, a skeletal framework that can be fleshed out with additional or more refined data, a modified objective function, and changes in the constraints or planning unit size. The Sword of Damocles hangs over many species in conservation, and decisions must be made with limited data. The failure to make a decision in the hope of collecting more data is a management action in itself. The probability of occurrence functions are based on South Australian Ornithological Association Bird Atlas from the mid 1980s, and while it has the advantage of being comprehensive in spatial extent, it has limited fine-scale resolution and the ‘usual suspects’ errors associated with varying survey effort and area, spatial autocorrelation, etc. I did not intend to privilege landscape-level variables over patch-level variables in my study; this is due to inconsistencies in the scale of individual surveying that precluded

the inclusion of patch-level variables. The relative importance of both can vary significantly across a community (Lee et al. 2002). An objective function incorporating viability over some time horizon instead of simply species occupancy would be preferable; however, in most regions, and particularly for non-charismatic species, anything beyond distribution data is a luxury. Over short time scales for some species, though, distribution data may be an adequate proxy for viability (Gates 2000, Araujo 2002). The most critical need for the habitat reconstruction program in the MLR is to test the landscape models I have presented with new data and the development of models that include patch-level variables. Besides the limitations and errors associated with the species distribution models, the other need is to derive more accurate revegetation costs, which would vary across the region due to ownership, land-use type, distance from the city of Adelaide, and environmental variables, such as soil type and topography.

The metapopulation-level work (Chapters 2-5) uses the area-connectivity, SPOM (stochastic patch occupancy model) approach as the fulcrum for the optimization analysis. Most spatially-structured populations do not perceive the landscape in simple binary terms, and the “Hanski-type” metapopulation paradigm is only relevant for a small subset of species, such as some butterflies (e.g. Glanville fritillary – Hanski and Kuussaari 1994, Hanski et al. 1994, Hanski and Thomas 1994, Hanski et al. 1995), frogs (Sjogren and Ray 1996, Vos and Stumpel 1996), American pika (Moilanen et al. 1998), and a very few birds (Westphal et al. 2003). Even if a species exists as a “classical metapopulation”, the area-dispersal distance model may not be correct; other factors, such as habitat quality, may be more important (Fleishman et al. 2002). Finally, with regard to using stochastic dynamic programming (SDP) for state-based decision problems

in conservation, while SDP does find the exact optimum, it is severely limited by the ‘curse of dimensionality’ (Bellman 1957). The number of matrix calculations grows by a factor of four with every doubling of the state space. SDP does not have the facility to solve large problem with many states (large number of patches and population states), and the question remains as to whether the exact optimum is really needed for most problems. Neuro-dynamic programming (Bertsekas 1996) is a state-based method that approximates Bellman’s equation, the essence of SDP, and I plan to pursue its application in conservation biology in the future, most notably the optimal mowing of butterfly meadows presented in Chapter 2.

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# Chapter 1

## **Optimal landscape reconstruction for a spatially-realistic metapopulation: an application of stochastic dynamic programming**

**Michael I. Westphal,<sup>\* +</sup> Marcus Pickett,<sup>¶</sup> Wayne M. Getz<sup>\*</sup> and  
Hugh P. Possingham<sup>+§</sup>**

<sup>+</sup>The Ecology Centre, Department of Zoology & Entomology, the University of  
Queensland, St. Lucia, Queensland 4072, Australia

<sup>\*</sup>Department of Environmental Science, Policy, & Management, University of California,  
Berkeley, CA 94720, U.S.A.

<sup>§</sup> Department of Mathematics, University of Queensland, Australia

<sup>¶</sup>Conservation Council of South Australia, Adelaide, South Australia

*Give me space and motion, and I will give you a world.*

- René Descartes

## **ABSTRACT**

A decision theory framework can be a powerful technique to derive optimal management decisions for endangered species. We build a spatially-realistic stochastic metapopulation model for the Mount Lofty Ranges Southern Emu-wren (*Stipiturus malachurus intermedius*), a Critically Endangered Australian bird. Using discrete time Markov chains to describe the dynamics of a metapopulation and stochastic dynamic programming (SDP) to find optimal solutions, we evaluate the following different management decisions: enlarging existing patches, linking patches via corridors, and creating a new patch. This is the first application of SDP to optimal landscape reconstruction and one of the few times that landscape reconstruction dynamics have been integrated with population dynamics. SDP is a powerful tool that has advantages over standard Monte Carlo simulation methods, because it can give the exact optimal strategy for every landscape configuration (combination of patch areas and presence of corridors) and pattern of metapopulation occupancy, as well as a trajectory of strategies. It is useful when a sequence of management actions can be performed over a given time horizon, as this the case for many endangered species recovery programs, where only a fixed amount of resources are available each time step. However, it is generally limited by computational constraints to rather small networks of patches. The model shows that optimal metapopulation management decisions depend greatly on the current state of the

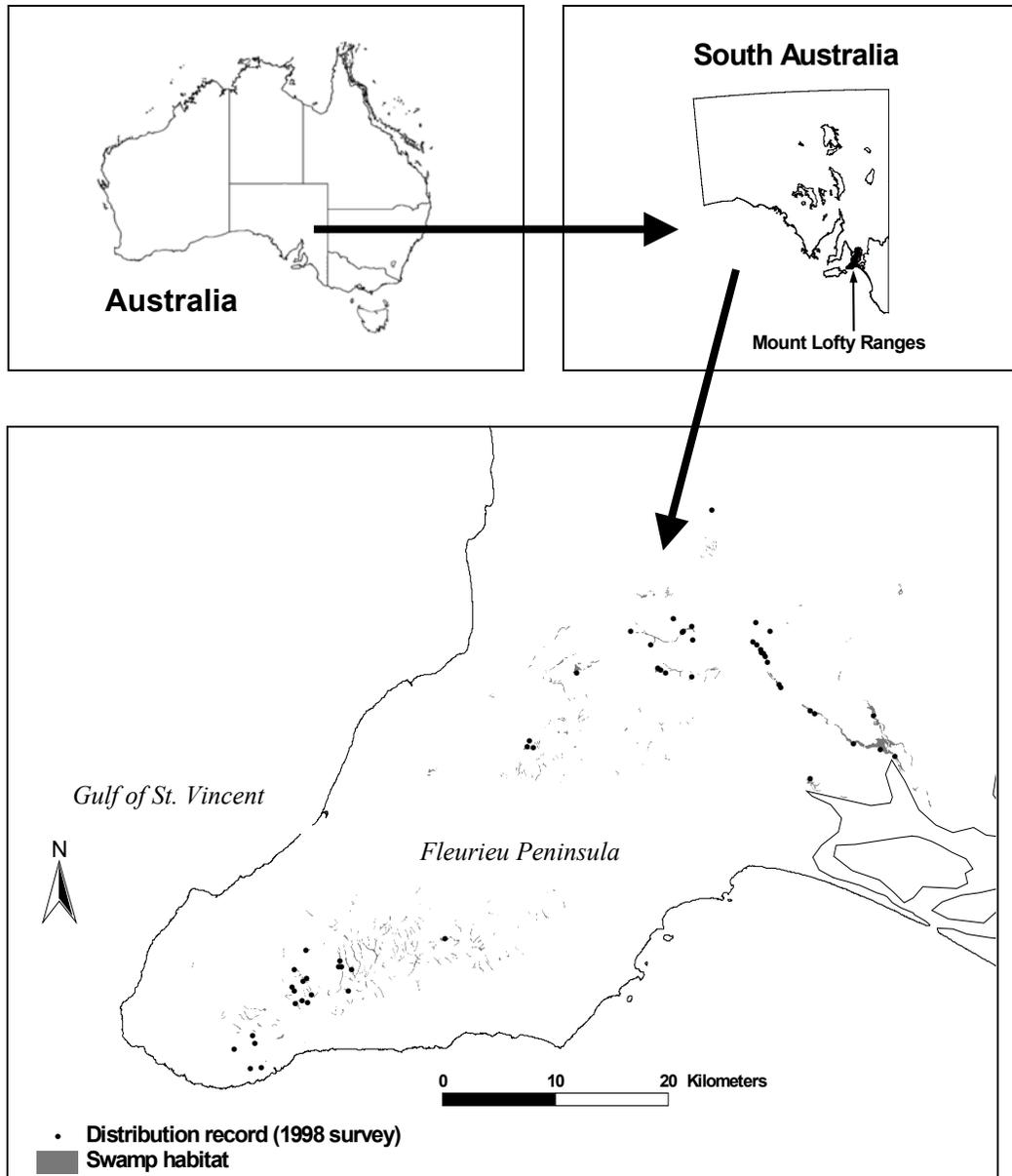
metapopulation, and there is no strategy that is universally the best. The extinction probability over 30 years for the optimal state-dependent management actions is 50-80% better than no management, while the best fixed state-independent sets of strategies are only up 30% better than no management. This highlights the advantages of using a decision-theory tool to investigate conservation strategies for metapopulations. It is clear from these results that the sequence of management actions is critical, and this can only be effectively derived from stochastic dynamic programming. The model illustrates the underlying the difficulty in determining simple rules of thumb for the sequence of management actions for a metapopulation. This use of a decision theory framework extends on the capacity of population viability analysis (PVA) to manage threatened species.

## INTRODUCTION

Decision theory has made important contributions to resource management, through the use of more qualitative methods like hierarchical ranking methods (Ralls and Starfield 1995) and quantitative techniques such as stochastic dynamic programming (SDP) (Mangel and Clark 1988, Clark and Mangel 2000). SDP has been used to find the best ways of harvesting populations (Johnson et al. 1997, Milner-Gulland 1997, Spencer 1997, Hanson and Ryan 1998), releasing a biological control agent (Shea and Possingham 2000), maintaining ecosystem diversity (Richards et al. 1999), translocating individuals between two populations to ensure persistence (Lubow 1996), and conserving a spatially-structured population (Possingham 1996).

In this paper, we use SDP and a presence-absence metapopulation model to explore the landscape reconstruction strategies for the Southern Emu-wren (*Stipiturus malachurus intermedius*), a threatened Australian bird. We consider and rank three management options: creating corridors, enlarging patches, and creating new patches. This is the first application of SDP to explicitly look at landscape reconstruction for a real metapopulation.

The Southern Emu-wren is made up of eight subspecies, one of which is confined to the Mount Lofty Ranges of South Australia (Schodde and Mason 1999). The Critically Endangered Mount Lofty Ranges Southern Emu-wren (IUCN Species Survival Commission 1994, Garnett and Crowley 2000) is restricted to swamp and heath habitats of the Fleurieu Peninsula in the southern Mount Lofty Ranges (Figure 1).



**Figure 1.** The location of Southern Emu-wren swamp habitat and distribution. The southern most points that do not correspond with swamps are heath habitat (Deep Creek Conservation Park).

About 25% of the original swamp habitat remains, most on private land. The majority of swamps (~75%) are less than 5 hectares. These swamps are characterized by dense vegetation in the 1-2 m. zone above the ground, composed of tea-tree (*Leptospermum* spp.), sedges (*Lepidosperma longitudinale*), rushes (*Baumea rubiginosa*, *Baumea*

*teragona*, *Juncus* spp.), and ferns (*Blechnum minus*, *Gleichenia microphylla*, *Pteridium esculentum*), often above a layer of peat (Littley and Cutten 1994). The swamps are either found along low-lying creeks, perched on hillsides and spring fed, or at the bottom of gullies.

The emu-wrens exclusively use the dense swamp vegetation to feed and nest in, not utilizing the surrounding pasture or eucalypt woodland matrix. The emu-wren is a poor flyer, and only engages in short bursts of flight. They have been called ‘button grass moths’, and their flight compared to that of a dragonfly (Schodde 1982). Thus, the emu-wren is thought to be a very poor disperser (Littley and Cutten 1994).

The metapopulation ecology framework (Nicholson 1933, Andrewartha and Birch 1954, den Boer 1968, Levins 1969, Levins 1971, Hanski 1998, Hanski 1999), where individual patches “wink” in and out but the spatially disjunct network persists as long as the patches are recolonized as quickly as they experience local extinctions, has developed into an important lens through which to understand spatially-structured populations. However, it cannot help us make sound management decisions without being embedded in a decision-making tool. For example, though metapopulation theory tells us that increasing the area and connectedness of habitat patches can attenuate the risk of extinction, it does not give us an ability to rank our decisions.

With a finite pool of resources and a certain exigency to immediately execute the most beneficial course of strategies for an endangered species, decision theory is needed to adjudicate among potential options. As conservation biology is a “triage” discipline, for it to mature there must be the development of a quantitative framework that can explicitly incorporate costs and benefits of management options and weigh them accordingly,

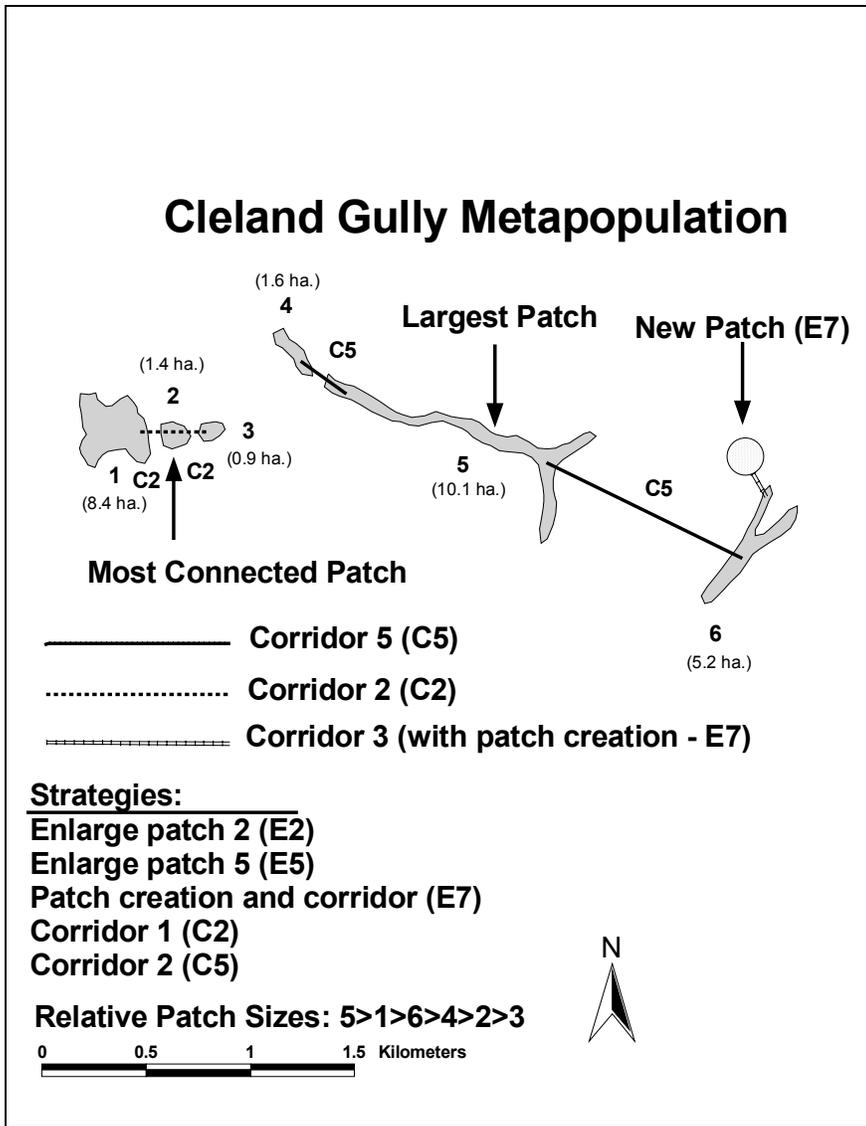
particularly with lacunas in data and a highly uncertain, stochastic world. This represents the integration of population viability analysis with optimization tools (Beissinger and Westphal 1998, Possingham et al. 2002).

In this paper, we first construct a discrete-time Markov chain model for the presence-absence dynamics of the metapopulation. With many endangered species, there is often a paucity of empirical data on density, and management decisions need to be expediently made without the necessary resources to gather detailed population demographic information. Stochastic patch occupancy models (SPOMS), which model only extinction and recolonization events in patches, ignoring population dynamics, can be formulated from snapshot data of patch occupancy (Hanski 1998, Moilanen et al. 1998, Hanski 1999). Second, we use stochastic dynamic programming to evaluate various conservation strategies, such as the enlargement of patches, the creation of new patches, and the construction of corridors between patches. This enables us to explore the optimal solution sets for different population states and patterns of metapopulation occupancy.

## **METHODS**

### *Formulation of the stochastic patch occupancy model (SPOM)*

We illustrate our methods using a Southern Emu-wren metapopulation in the Fleurieu Peninsula of South Australia (the Cleland Gully metapopulation) (Figure 2). We have partial survey information on patch occupancy from 1993 and 1998.



**Figure 2.** The Cleland Gully Southern Emu-wren metapopulation.

Our formulation of the SPOM follows Day and Possingham (1995). Let the population state of the metapopulation at any time,  $t$ , be the set of  $n$  patches that are occupied at time  $t$  ( $\leq n$  total patches). We can represent this as an  $n$ -dimensional vector,

$$\mathbf{u}(t) = [u_1(t), u_2(t), \dots, u_n(t)],$$

where the elements are binary variables,  $u_i(t) \in \{0, 1\}$ . If  $u_i(t) = 0$ , then patch  $i$  is empty and if  $u_i(t) = 1$ , then patch  $i$  is occupied.

Now, we can construct an extinction matrix,  $\mathbf{X}_n$  of dimension  $2^n \times 2^n$ , which represents the probabilities of transitions from any population state through extinction alone. The probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  by extinction in one time step is given by the product

$$x_{\mathbf{u}\mathbf{v}} = \prod_{i=1}^n I_1(u_i, v_i), \quad (1)$$

where the function  $I_1(u_i, v_i)$ , the probability that patch  $i$  goes extinct in a transition from  $\mathbf{u}$  to  $\mathbf{v}$ , is

$$I_1(u_i, v_i) = \begin{cases} 1 - E_i & \text{if patch } i \text{ remains occupied} \\ E_i & \text{if patch } i \text{ goes extinct} \\ 1 & \text{if patch } i \text{ remains empty} \end{cases} \quad (2)$$

$E_i$  is the patch-specific extinction probability. For instance, for a three patch system, if  $\mathbf{u}$  is  $[1, 1, 0]$  and  $\mathbf{v}$  is  $[1, 0, 0]$ , then,  $x_{\mathbf{u}\mathbf{v}} = (1 - E_1)E_2$ . The full matrix,  $\mathbf{X}_3$ , is given in the Appendix.

Similarly, we can construct a recolonization matrix,  $\mathbf{R}_n$ . The probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  by recolonization alone in one time step is given by the product

$$r_{\mathbf{u}\mathbf{v}} = \prod_{i=1}^n I_2(u_i, v_i), \quad (3)$$

where the function  $I_2(u_i, v_i)$ , the probability that patch  $i$  becomes recolonized in a transition from  $\mathbf{u}$  to  $\mathbf{v}$ , is

$$I_2(u_i, v_i) = \begin{cases} 1 - C_i & \text{if patch } i \text{ remains unoccupied} \\ C_i & \text{if patch } i \text{ becomes recolonized} \\ 1 & \text{if patch } i \text{ remains occupied} \end{cases} \quad (4)$$

$C_i$  is the patch-specific colonization probability.

Assuming that the order of events is first extinction then recolonization, the elements of the transition matrix,  $\mathbf{A}_n$ , represent the probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  through both extinction and recolonization:

$$a_{\mathbf{u}\mathbf{v}} = \sum_{\mathbf{w}} x_{\mathbf{u}\mathbf{w}} r_{\mathbf{w}\mathbf{v}}, \quad (5)$$

where  $\mathbf{w}$  is an intermediate state after extinction.

#### *Parameterization of the stochastic patch occupancy model (SPOM)*

To parameterize the SPOM, we use the functions for patch recolonization and extinction from the incidence function model (IFM) (Hanski et al. 1996, Hanski 1998, Moilanen and Hanski 1998, Moilanen et al. 1998, Hanski 1999). Assume the patch-specific extinction probabilities are inversely related to patch area:

$$E_i = \min\left[\frac{e}{A_i^\rho}, 1.0\right], \quad (6)$$

where  $A_i$  is the patch area ( $\text{m}^2$ ) for patch  $i$  and  $e$  and  $\rho$  are two parameters that scale area to extinction. We ignore the possibility of a rescue effect (Brown and Kodric-Brown 1977), in which immigration from neighboring patches leads to a decreasing risk of

extinction. To reduce the number of parameters, we assume that the extinction probability is 1.0 for patches below 2,000 m<sup>2</sup> (0.2 ha.), which is reasonable, as it is estimated the size of a pair's territory varies from several hectares to less than a half a hectare (MLR Southern Emu-Wren Recovery Team 1998).

We build a function for the probability of patch  $i$  becoming recolonized by first developing an expression for the relative number of dispersers reaching the patch,  $M_i$ . If we assume individuals have an exponentially declining probability of reaching a patch with distance, then the relative number of dispersers reaching a patch is:

$$M_i = \beta \sum_{j \neq i}^n \exp(-\alpha d_{ij}) p_j A_j, \quad (7)$$

where  $p_i$  equals 1 for occupied patches and 0 for empty patches,  $d_{ij}$  is the distance (total gap distance, using “stepping stone” dispersal) between patches  $i$  and  $j$ ,  $\alpha$  is a dispersal mortality parameter,  $\beta$  is a parameter that scales connectivity to the number of migrants reaching a patch, and  $n$  is the number of patches in the metapopulation. The area term effectively weights the number of dispersers originating from a patch by its size.

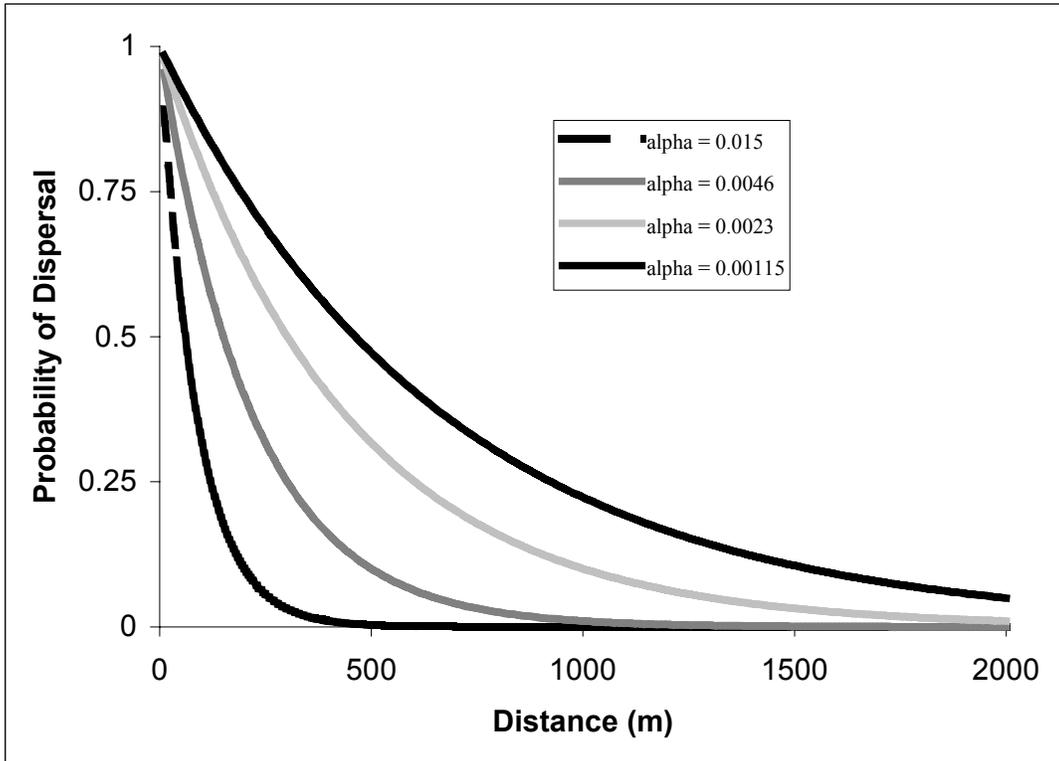
Let the per patch recolonization probability be sigmoidally related to the relative number of migrants reaching a patch:

$$C_i = \frac{M_i^2}{M_i^2 + \gamma^2}, \quad (8)$$

where  $\gamma$  is a location parameter. The squared term gives the curve a sigmoidal shape (Hanski et al. 1996, Hanski 1998, Moilanen and Hanski 1998, Moilanen et al. 1998, Hanski 1999). The parameter,  $\beta$ , effectively is subsumed within  $\gamma^2$ . One can envisage other functional forms, but it is reasonable to assume that the recolonization probability

will be related to the relative number of dispersers reaching a patch in a more complex manner than linearly.

We evaluated three dispersal different scenarios (Figure 3).



**Figure 3.** The dispersal curves for the three different scenarios considered and with the addition of corridors.

Under low dispersal conditions, we assumed  $\alpha$  to be  $0.015 \text{ m}^{-1}$ , which for a distance of 200 m gives a relative dispersal probability of only 0.1. This comes from the fact that emu-wrens are apparently unable to cross a matrix of pasture greater than 200 meters, though their movement would be facilitated by other vegetation, such as blackberry (*Rubus spp.*) (Little and Cutten 1994). Little and Cutten (1994) considered patches isolated if they were greater than 100 m apart, noting that emu-wrens were never seen flying more than 20 m at a time even when disturbed. Combined with a value of  $\gamma$  set to

$5 \times 10^5$ , this makes small patches (~1 ha.) essentially unable to recolonize neighboring patches (Table 1).

<b>Baseline Scenario</b>			<b>High Dispersal</b>		
<b>Patch</b>	<b>Extinction</b>	<b>Recolonization</b>	<b>Patch</b>	<b>Extinction</b>	<b>Recolonization</b>
1	0.11	0.17	1	0.11	0.49
2	0.31	0.71	2	0.31	0.84
3	0.41	0.69	3	0.41	0.85
4	0.29	0.73	4	0.29	0.86
5	0.10	0.13	5	0.10	0.49
6	0.14	0.02	6	0.14	0.24
<b>Lower Dispersal</b>			<b>Higher Extinction</b>		
<b>Patch</b>	<b>Extinction</b>	<b>Recolonization</b>	<b>Patch</b>	<b>Extinction</b>	<b>Recolonization</b>
1	0.11	0.03	1	0.33	0.17
2	0.31	0.45	2	0.56	0.71
3	0.41	0.32	3	0.64	0.69
4	0.29	0.42	4	0.54	0.73
5	0.10	0.02	5	0.31	0.13
6	0.14	0.00	6	0.38	0.02
<b>Lower Extinction</b>					
<b>Patch</b>	<b>Extinction</b>	<b>Recolonization</b>			
1	0.03	0.17			
2	0.18	0.71			
3	0.27	0.69			
4	0.16	0.73			
5	0.03	0.13			
6	0.05	0.02			

\*For the population state where all patches are occupied

**Table 1.** The extinction and recolonization rates under the various parameter scenarios considered.

Under the baseline (medium dispersal) scenario,  $\alpha$  is  $0.0046 \text{ m}^{-1}$ , which gives a relative probability of dispersal of 0.1 for 500 m. All patches within 100 m of each other, have at least a 10% chance of recolonizing each other, and the first cluster of patches (1,2,3) have roughly about a 5% chance of recolonizing the second cluster (4,5) of

patches when no corridors are present and at their initial sizes. Finally, under the high dispersal scenario,  $\alpha$  is 0.0023, giving a relative dispersal probability of 0.1 for 1000 m. Each patch has at least a 10% chance of recolonization, as long as one patch is occupied. The value of  $\gamma$  is the same for all three scenarios. Though there is uncertainty in the emu-wren recolonization ability, it would fall within this range of possibilities.

To get an estimate for  $\alpha$  when corridors are present, we fitted a negative exponential distribution to dispersal data from banding studies of emu-wrens in the nearby Nangkita metapopulation in the Fleurieu Peninsula (Pickett 2000). A total of 19 interpatch movements were recorded among 7 patches, which are effectively connected via vegetative corridors, giving a value of  $0.0015 \text{ m}^{-1}$  for  $\alpha$ .

Though we have survey data from 1993 and 1998, some patches were not surveyed in both years. Assuming the most optimistic extinction scenario we used Maximum Likelihood techniques (Moilanen 1999) to derive  $\rho$ , the parameter scaling patch area to extinction rate, giving a value of 0.6. We varied this parameter by  $\pm 50\%$ . The extinction and recolonization parameters represent plausible scenarios.

### *The Objective and Stochastic Dynamic Programming Equations*

Stochastic dynamic programming is a state-based, backwards iteration method that explicitly computes the optimal strategy at any time step, based on the state of the system and the time horizon, assuming that optimal strategies are subsequently made (Mangel and Clark 1988, Clark and Mangel 2000). We assume that the goal of the optimization is to maximize the probability that the metapopulation will remain extant at

the end of a time period,  $T$ . From the SPOM, the total number of population states (patterns of patch occupancy) is  $S = 2^n$  (Day and Possingham 1995). For this emu-wren metapopulation, there are 7 patches, including the newly created patch, so  $S = 128$ .

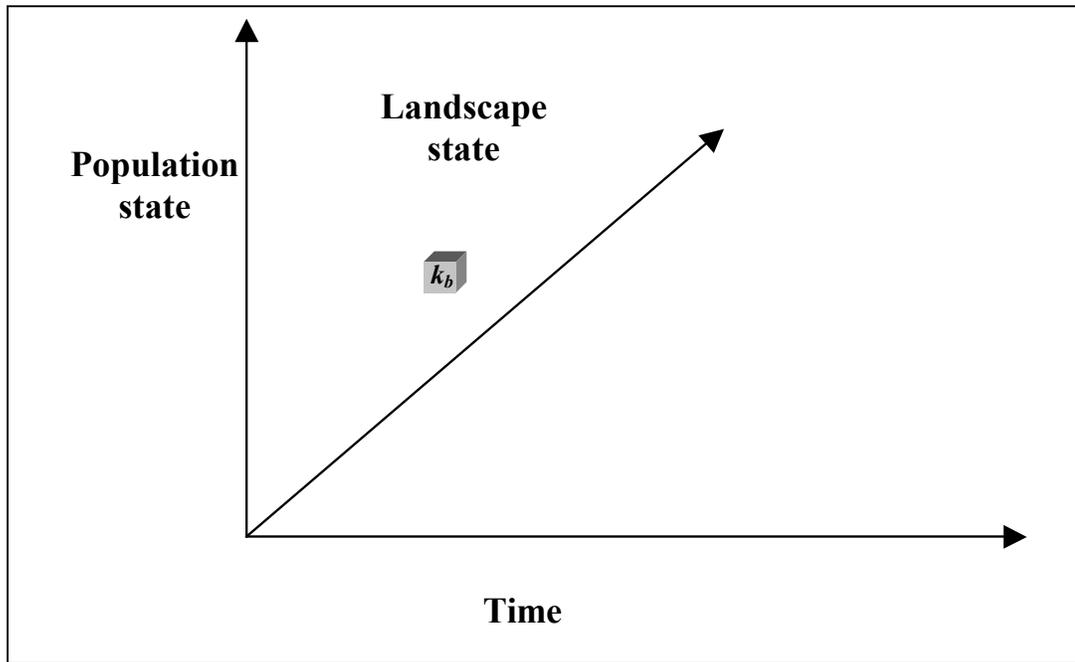
To implement the SDP we must assign a value to the state of the system when the strategy is evaluated. We let the value of the metapopulation be 1.0, if at least one patch is occupied at the end of the time period (the metapopulation is extant), and 0 otherwise. Suppose there exists  $k$  conservation strategies that can be implemented at each time step for the emu-wren, which include the enlargement of patches, the creation of new swamp patches, and connections between patches via corridors. Finding the optimal strategy involves backwards iteration. If we know the value of the metapopulation state at the terminal time,  $T$ , then we can calculate the value of any state in the previous time step, which is given by the dynamic programming equation (Mangel and Clark 1988, Clark and Mangel 2000):

$$V(\mathbf{u}, \mathbf{z}, t, T) = \max_k \left[ \sum_{\mathbf{v}=1}^S a_{\mathbf{u}\mathbf{v}}(\mathbf{y}) V(\mathbf{v}, \mathbf{y}, t+1, T) \right] \quad (9)$$

where  $V(\mathbf{u}, \mathbf{z}, t, T)$  is the value of population state  $\mathbf{u}$  and landscape state  $\mathbf{z}$  at time  $t$ ,  $T$  is the terminal time,  $a_{\mathbf{u}\mathbf{v}}(\mathbf{y})$  is an element of the transition matrix  $\mathbf{A}_k(\mathbf{y})$ , the probability of going from population state  $\mathbf{u}$  to  $\mathbf{v}$  given we implement the  $k$ -th management strategy with the metapopulation initially in the landscape state  $\mathbf{z}$ . The landscape state is the combination of possible patch areas and the presence/absence of corridors, and  $\mathbf{y}$  represents the new landscape state after the  $k$ -th strategy has been implemented,  $\mathbf{y} = F(\mathbf{z},$

*k*). Since each management strategy changes the patch areas and/or connection of patches, each combination of landscape state and population state has a different transition matrix for each management strategy. Therefore, the value term must be a function of both the population and landscape states. Because we set the value to 1 if the metapopulation remains extant and 0 if it goes extinct,  $V(\mathbf{u}, \mathbf{z}, 0, T)$  gives the exact extinction probability of the metapopulation for the  $\mathbf{u}$  population state and  $\mathbf{z}$  landscape state at the initial time. The SDP equation makes no assumptions about the functional forms of extinction and recolonization and simply gives the strategy that will maximize the persistence of the metapopulation at any time and for any state, given that in the future, optimal decision are made. In most cases for metapopulations, we are interested in modeling only the occupancy, and the main currency of interest is the probability of extinction for the entire metapopulation. One can think of the result of the SDP analysis as a 3-D matrix (Figure 4): at any point in time, landscape state and population state, the model derives an optimal strategy.

One can use this technique to determine an optimal trajectory of strategies. Since we are interested in the long-term optimal strategy, i.e. what management action we should perform now to minimize the long-term extinction, we have back-stepped to stationarity, that is, the point where the decision matrix, whose elements are the optimal strategy for each population and landscape state, no longer changes with time. This provides the strategy that maximizes long-term persistence of the metapopulation. For this metapopulation, it was found at 90 years.



**Figure 4.** The output of the SDP model. For every landscape state, population state and time, an optimal strategy,  $k_b$ , is calculated.

*The Management Strategies for the Southern Emu-wren*

We evaluate 6 landscape reconstruction strategies for the metapopulation (Figure 2): increasing the area of the largest patch, increasing the area of the most connected (and smaller) patch, the creation of a corridor from the largest patch to its two closest neighboring patches, the creation of a corridor from the most connected patch to its neighboring patches, the creation (and subsequent enlargement) of a new habitat patch with a corridor connecting it to the nearest patch, as well as executing no strategy.

An existing habitat patch, which is degraded habitat and unsuitable, has been chosen as the site for the patch creation. Though there are an infinite number of possible points across the landscape where one could model creating new habitat, sites of degraded patches are the most likely places with suitable habitat to be restored. Habitat for the emu-wren only occurs in topographic depressions, which would hydrologically facilitate the creation of swamps.

In each time step, the manager can execute one strategy; therefore, we have standardized the “cost” of each strategy to be equivalent to about 0.9 ha. of revegetated area. This is the amount of area needed to create the largest corridor, assuming the requisite corridor width of 10m (MLR Southern Emu-Wren Recovery Team 1998). For the strategy of creating a new patch, this amount is added, minus the amount of area needed for the construction of a corridor to the nearest patch. We assume as well that once a patch is enlarged, the new area will be suitable habitat within 5 years, the time step of the model; hence, there is no time delay. For the patch enlargements, each patch can be enlarged 6 times. This is justified by the fact there is only so much available land for habitat reconstruction. So, including the corridors, there exist a total of 1372 possible landscape states, or configurations,  $(7 \times 7 \times 7 \times 2 \times 2)$ , for which the best strategy is found at each time step and each population state.

Moreover, we have added the chance of catastrophic fire into the model, which is an important ecological process in most Australian ecosystems, though the fire frequency in the area is poorly understood. We have assumed that fire is an independent event in each patch, results in local extinction of the subpopulation, and does not spread to other patches. It occurs just after demographic extinction in the model. The occurrence of fire

probability is assumed to vary from once every one hundred years to once every one twenty years (extreme case). Once a subpopulation is extirpated by fire, the regeneration time is considered to be 5 years.

We have compared the 30-year extinction probability of the optimal strategy from the SDP analysis to that of some fixed population state-independent strategies, which have the same financial costs. By this we mean that the sequence of strategies is executed regardless of the population and landscape state, something that the stochastic dynamic programming approach explicitly considers. These strategies disregard what patches are occupied at any given time. The “big patch” strategy is to simply enlarge the largest patch six times. The actions for the “corridor focused” strategy are in order: construct a corridor connecting the largest patch to its neighbors, construct a corridor connecting the most connected patch to its neighbors, enlarging the largest patch, enlarging the most connected patch, and the last two actions repeated again. The “risk spread” strategy involves first creating a new patch, followed by the construction of corridors in the same order as the “corridor focused” strategy, and then subsequently enlarging the patches in order of decreasing size. To calculate the extinction probabilities for the non-optimal, state-independent sets of strategies, we simply multiplied out the transition matrices. Other possible fixed set of actions can be envisaged, but these represent typical habitat reconstruction paradigms that a manager would be expected to use in the absence of applying SDP. It is worth noting that typical analyses of extinction risk involve Monte Carlo simulations to get an estimate of the probability distribution; however, this is unnecessary as the Markov chain metapopulation model gives the exact extinction probability.

## RESULTS

First we will look at the time and state-dependence of the optimal strategies and the trajectories of long-term optimal decisions, then we will compare fixed, state-independent strategies with the optimal one over a 30 yr. period. It is cumbersome to show the optimal strategy for each population state, so we have only presented four possible benchmark states: only the largest patch occupied, only the two largest patches occupied, all the patches occupied, and only the two smallest patches occupied.

One can see that the optimal solution at the initial time ( $t = 0$ ) varies depending on the population state of the metapopulation and the extinction and recolonization probabilities (Table 2). Some generalities can be gleaned for the extinction and recolonization parameters and the particular patch geometry of the model. When only small patches are occupied, the best initial strategy is to enlarge those patches. However, when a more extinction-resistant, large patch is occupied, connecting it to neighbors via corridors is the optimal initial strategy rather than enlarging it, except when dispersal is quite high. As more patches are occupied, the initial strategy varies with the extinction and recolonization rates. The higher the extinction rate, the more augmenting the size of the smaller patch is favored, while the lower the dispersal, the more building corridors is favored. Under high fire conditions, the extinction probability of all patches is greater. The optimal strategy as the number of occupied patches increases is either to increase the size of vulnerable patches or construct corridors, depending on the dispersal ability of the organism. Under very poor dispersal conditions, the shorter corridor is more beneficial. With only a short time frame, patch enlargement is always favored over connecting

patches, regardless of the extinction and recolonization parameters. The penultimate time ( $T-1$ ) is one step before the end of the time horizon, and the optimal strategy at this point is the strategy that minimizes the extinction probability over one time step. These results illustrate the time-dependent nature of the optimal solution.

It must be noted that the optimal initial strategies ( $t=0$ ) in Table 2 assume that the optimal strategy is executed at every time step in the future, in this model, 90 years into the future. This initial strategy is not the same as the best strategy if one could one perform only one strategy over the entire time horizon of the model. The essence of SDP is the backwards iteration, which allows one to calculate the optimal strategy now, taking into consideration all possible future states of the metapopulation. The optimal initial strategy does not tell the whole story, nor indicate what strategies should be performed in the future; this is determined by the future occupancy of the metapopulation.

The optimal trajectories at stationarity for the baseline model can also be evaluated (Figures 5-8). In reality, after each strategy is implemented, there is a chance that the metapopulation will transition to any other population state, as given by the elements of the matrix,  $\mathbf{A}_n$ . Since it is a Markov process, one cannot speak of there being only **one** optimal trajectory of strategies, because the transitions to new population states are probabilistic. What management strategy one should execute in the next time depends on which patches are occupied in that time step. Here we only show the trajectories of optimal solutions if and only if the metapopulation remains in that population state over time. The same pattern emerges, where if an occupied patch is relatively large, it is important to first connect it to corridors and then enlarge it. The smaller a patch is the more critical it is to enlarge it at an earlier stage. From the

trajectory, it is clear that there is a very complex interplay of strategies, and the course through time is not easily summarized. It is important to note that the optimal solutions may be quite different for alternative extinction and recolonization parameters, patch geometry and distribution of patch areas. This is underscored by Figures 9 and 10, which shows the optimal trajectory through time if all the patches remain occupied under the low extinction and high dispersal scenarios.

For the particular spatial location of the new patch and the parameters of the model, creating a new patch is not a very desirable option, though this would be expected to vary with the spatial arrangement of the metapopulation and the potential location of the new patch. We have not sought to exhaustively vary the location of the new patch around the landscape, but have only used the location of a degraded patch as the focal site. This result makes intuitive sense. Because of the nonlinear form of the relationship between area and patch extinction, the creation of a new patch would generally not be a good strategy unless the magnitude of an area-independent extinction (e.g. catastrophe) is great. In which case, “spreading the risk” by creating a new patch may be more favorable compared to augmenting the size of an existing patch, if the patch is close enough to receive dispersers. The occurrence of “do nothing” before all the active strategies have been exhausted indicates that the difference between the value of doing nothing and any active strategy is smaller than the numerical precision of our calculations.

Compared to fixed, population-state independent strategies, one can see that the optimal state-dependent set of strategies is superior (Figure 11), particularly with the most extinction vulnerable population state. Under low fire conditions, the optimal management set of strategies is 50 – 80% better than no management, while the best

state-independent set of strategies is only 10 - 30% better than no management. Simply increasing the size of the largest patch has the highest extinction probability of the strategy sets considered, though the generality of this result is open to speculation. This is strong evidence for the idea that the sequence of actions, not just the particular management actions, is paramount. It is worth emphasizing that the extinction probabilities between the unmanaged scenario and the scenarios with continued management at each time step would diverge over time (Figure 12).

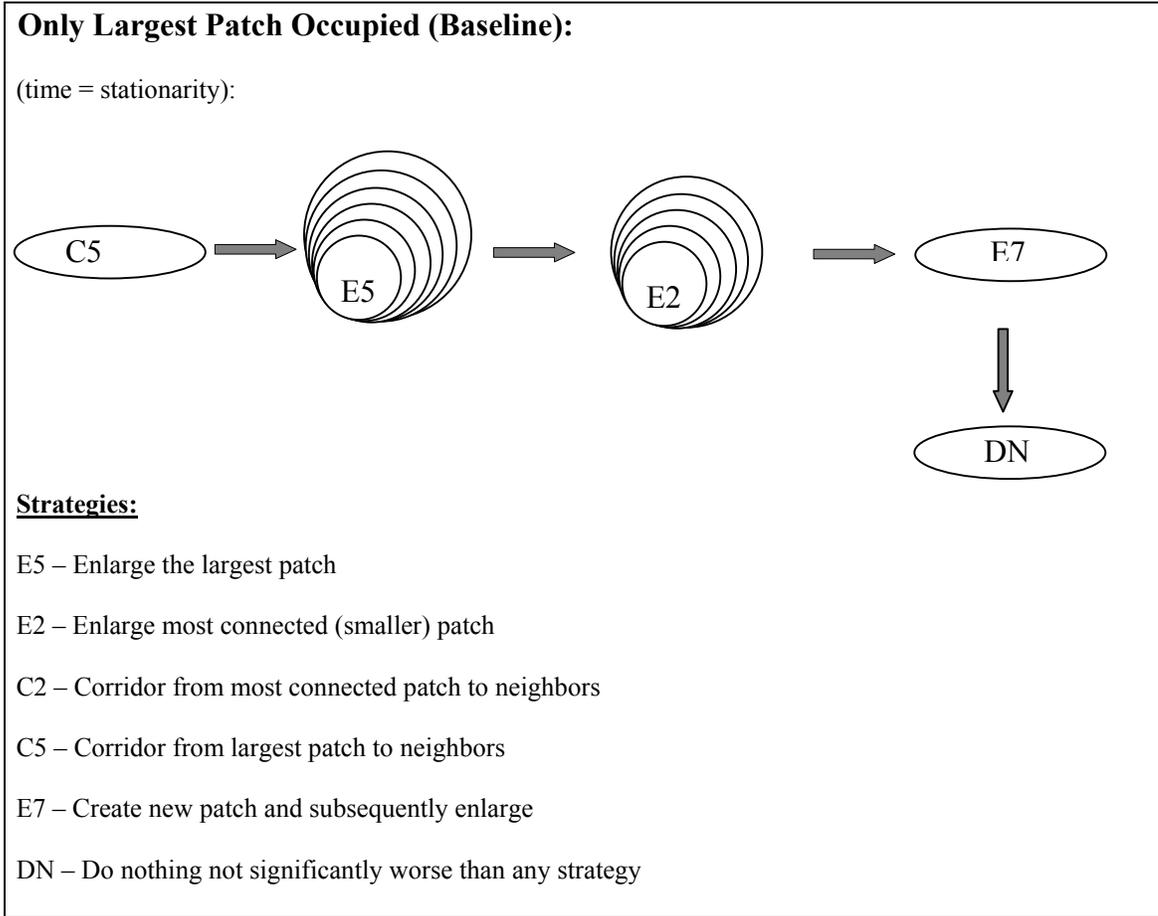
Table 3 shows the best strategy to perform if only one strategy could be executed over the 90 yrs under the baseline scenario, determined by multiplying out the transition matrices. As expected, this too is highly state-dependent. Connecting the largest patch to its neighbors is the most optimal strategy when the largest patch is occupied. When only enlargements are considered, enlarging the smallest patch is favored if it is occupied. These are not general results, but highly contingent on the model parameters and spatial configuration of the metapopulation. As the extinction vs. area curve is nonlinear, the patch whose marginal value for enlargement is greatest (greatest reduction in extinction per unit of area) will have the most benefit in terms of minimizing the metapopulation extinction. It is interesting to note that the best one-time strategy over a time horizon will not necessarily be the same as the initial optimal strategy nor the optimal strategy over one time step (the penultimate strategy).

<b>Optimal Metapopulation Strategy</b>						
<b>At the Penultimate Time (<math>t = T - 1</math>)</b>						
	<b>Baseline</b>		<b>Higher Dispersal</b>		<b>Lower Dispersal</b>	
	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>
<i>Only Two Smallest Patches (2,3) Occupied</i>	E2	E2	E2	E2	E2	E2
<i>Only Largest Patch Occupied</i>	E5	E5	E5	E5	E5	E5
<i>All Patches Occupied</i>	E2	E2	E2	E2	E2	E2
<i>Only Two Largest Patches Occupied</i>	E5	E5	E5	E5	E5	E5
<b>At Stationarity (<math>t = 0</math>)</b>						
	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>
<i>Only Two Smallest Patches (2,3) Occupied</i>	E2	E2	E2	E2	E2	E2
<i>Only Largest Patch Occupied</i>	C5	C5	E5	E5	C5	C5
<i>All Patches Occupied</i>	E2	E2	E2	E2	C2	C2
<i>Only Two Largest Patches Occupied</i>	C5	E2	C5	E2	C5	C2
<b>Strategies:</b>						
<b>E5 - Enlarge largest patch</b>						
<b>E5 - Enlarge the most connected (smaller) patch</b>						
<b>C2-Corridor connecting most connected (smaller) patch to neighbors</b>						
<b>C5-Corridor connecting largest patch to neighbors</b>						
<b>E7 - Create new patch and connect it to nearest patch (subsequently enlarge)</b>						
<b>DN - Do nothing not significantly worse than any strategy</b>						

**Table 2a.** The initial optimal management decision for various population states as calculated from stochastic dynamic programming.

<b>Optimal Metapopulation Strategy</b>				
<b>At the Penultimate Time (<math>t = T - 1</math>)</b>				
	<b>Lower Extinction</b>		<b>Higher Extinction</b>	
	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>
<i>Only Two Smallest Patches (2,3) Occupied</i>	E2	E2	E2	E2
<i>Only Largest Patch Occupied</i>	E5	E5	E5	E5
<i>All Patches Occupied</i>	E2	E2	E2	E2
<i>Only Two Largest Patches Occupied</i>	E5	E5	E5	E5
<b>At Stationarity (<math>t = 0</math>)</b>				
	<b>Low Fire</b>	<b>High Fire</b>	<b>Low Fire</b>	<b>High Fire</b>
<i>Only Two Smallest Patches (2,3) Occupied</i>	E2	E2	E2	E2
<i>Only Largest Patch Occupied</i>	C5	C5	C5	C5
<i>All Patches Occupied</i>	E2	E2	E2	E2
<i>Only Two Largest Patches Occupied</i>	C5	C5	E2	E2
<b>Strategies:</b>				
<b>E5 - Enlarge largest patch</b>				
<b>E5 - Enlarge the most connected (smaller) patch</b>				
<b>C2-Corridor connecting most connected (smaller) patch to neighbors</b>				
<b>C5-Corridor connecting largest patch to neighbors</b>				
<b>E7 - Create new patch and connect it to nearest patch (subsequently enlarge)</b>				
<b>DN - Do nothing not significantly worse than any strategy</b>				

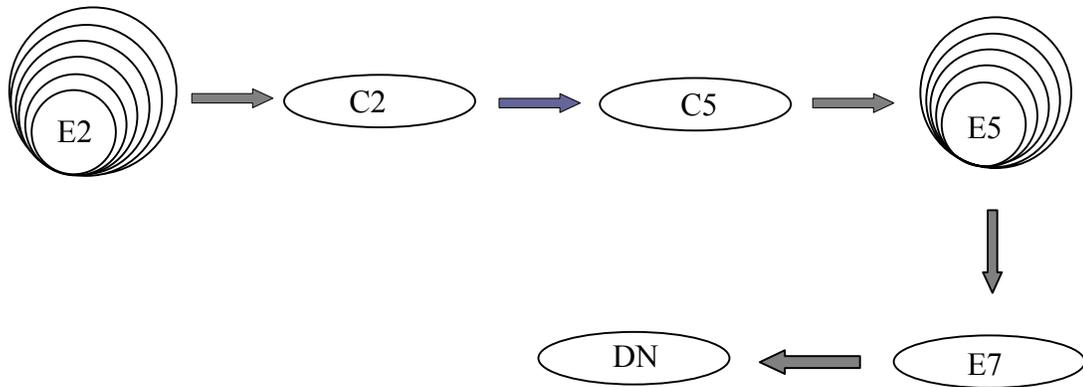
**Table 2b.** The initial optimal management decision for various population states as calculated from stochastic dynamic programming.



**Figure 5.** The trajectories of strategies at stationarity for the emu-wren metapopulation under low fire conditions. Each trajectory of strategies represents the long-term optimum for that population state, assuming the metapopulation remains in that population state throughout. Each circle represents one action. The concentric circles show the execution of the strategy a repeated number of times before the next strategy is implemented in the trajectory. The arrows show the course through time. The explanation is the same for subsequent Figures 6-10.

**Only Two Smallest Patches Occupied (Baseline):**

(time = stationarity):



**Strategies:**

E5 – Enlarge the largest patch

E2 – Enlarge most connected (smaller) patch

C2 – Corridor from most connected patch to neighbors

C5 – Corridor from largest patch to neighbors

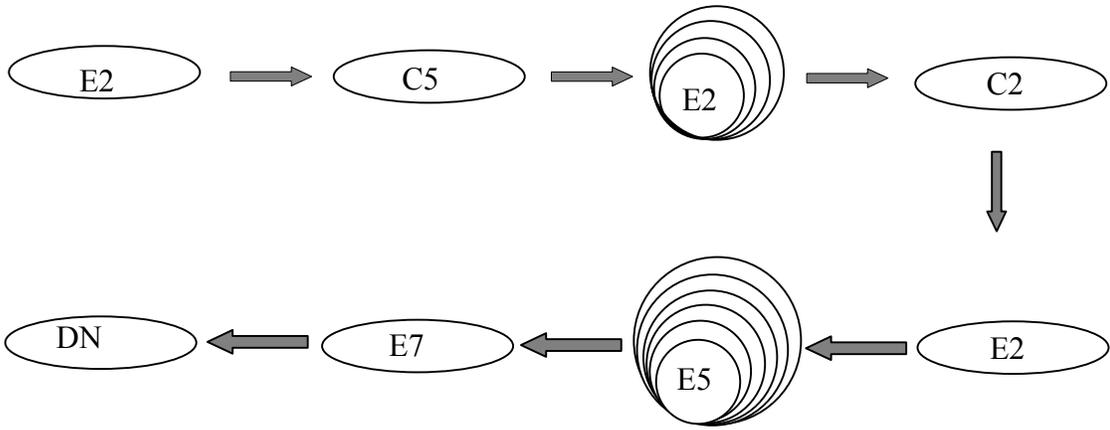
E7 – Create new patch and subsequently enlarge

DN – Do nothing not significantly worse than any strategy

**Figure 6**

**All Patches Occupied (Baseline):**

(time = stationarity):



**Strategies:**

E5 – Enlarge the largest patch

E2 – Enlarge most connected (smaller) patch

C2 – Corridor from most connected patch to neighbors

C5 – Corridor from largest patch to neighbors

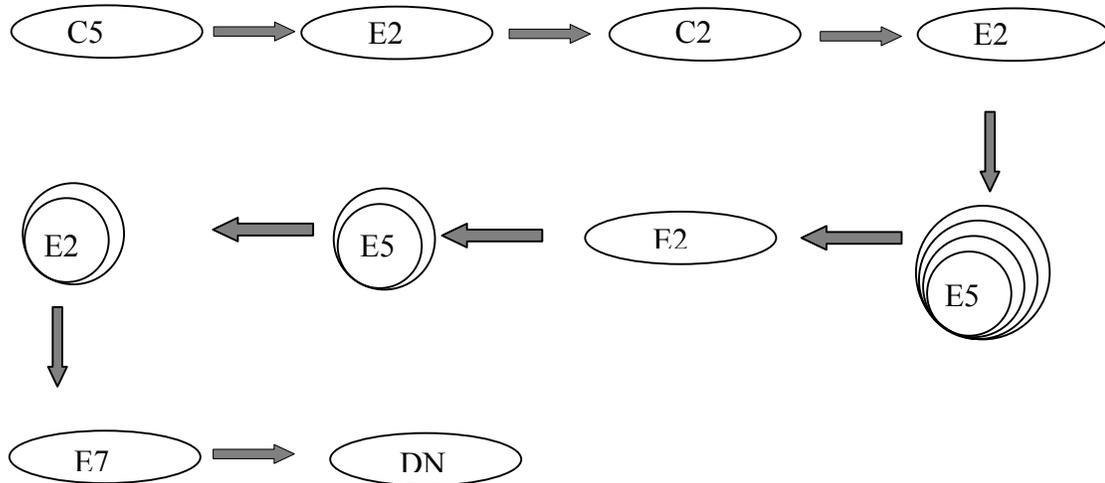
E7 – Create new patch and subsequently enlarge

DN – Do nothing not significantly worse than any strategy

**Figure 7**

**Only Two Largest Patches Occupied (Baseline):**

(time = stationarity):



**Strategies:**

E5 – Enlarge the largest patch

E2 – Enlarge most connected (smaller) patch

C2 – Corridor from most connected patch to neighbors

C5 – Corridor from largest patch to neighbors

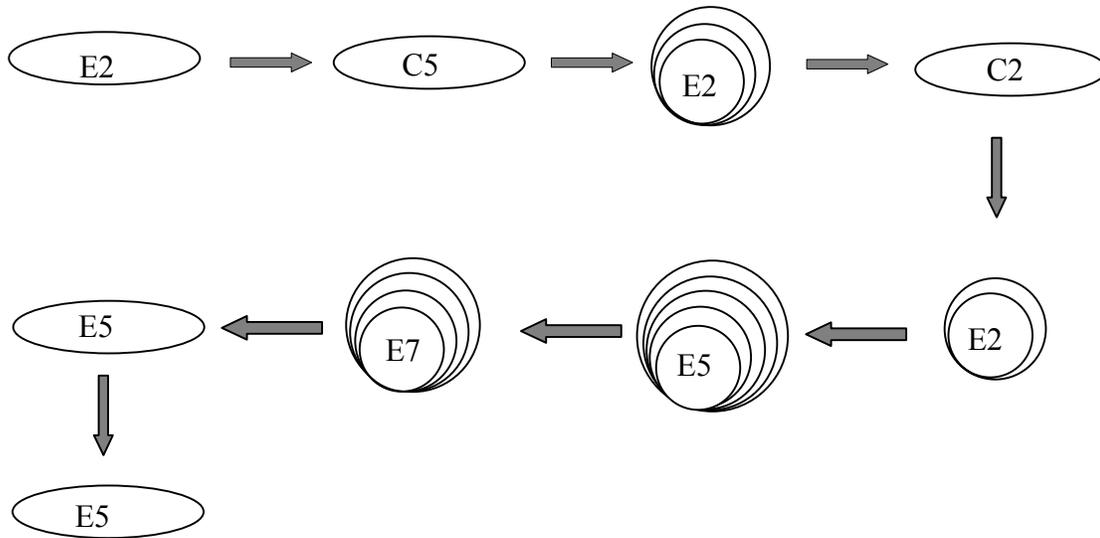
E7 – Create new patch and subsequently enlarge

DN – Do nothing not significantly worse than any strategy

**Figure 8**

**All Patches Occupied (Low Extinction):**

(time = stationarity):



**Strategies:**

E5 – Enlarge the largest patch

E2 – Enlarge most connected (smaller) patch

C2 – Corridor from most connected patch to neighbors

C5 – Corridor from largest patch to neighbors

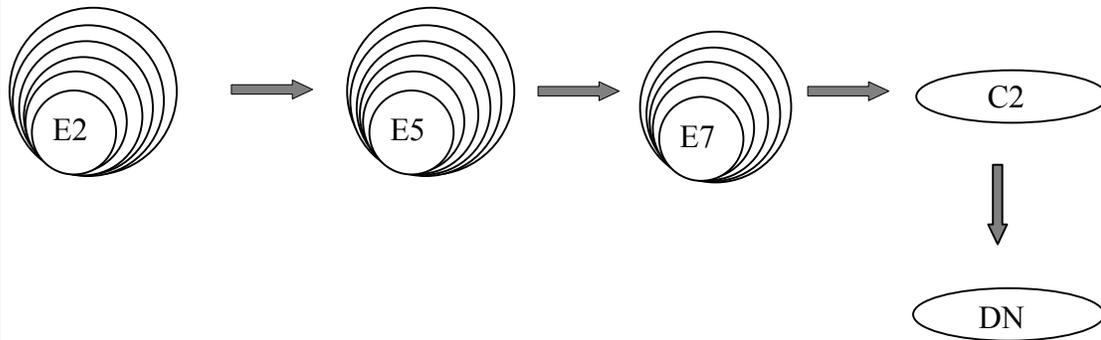
E7 – Create new patch and subsequently enlarge

DN – Do nothing not significantly worse than any strategy

**Figure 9**

**All Patches Occupied (High Dispersal):**

(time = stationarity):



**Strategies:**

E5 – Enlarge the largest patch

E2 – Enlarge most connected (smaller) patch

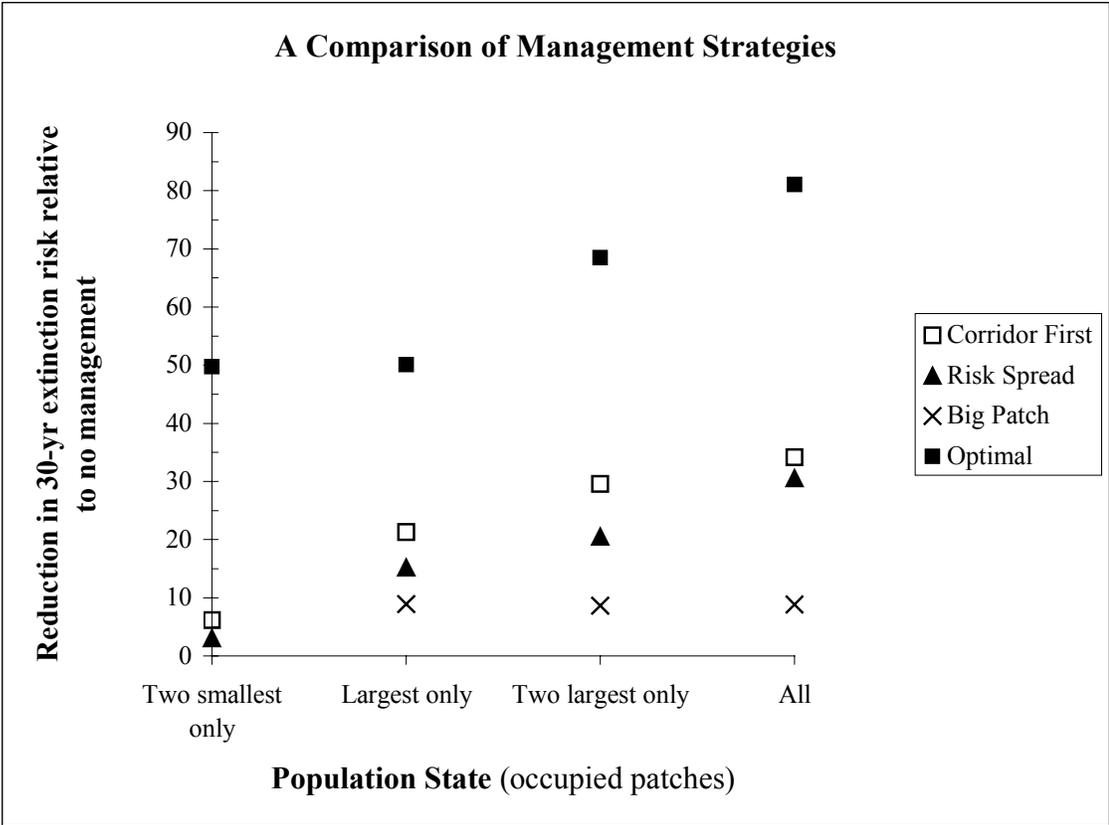
C2 – Corridor from most connected patch to neighbors

C5 – Corridor from largest patch to neighbors

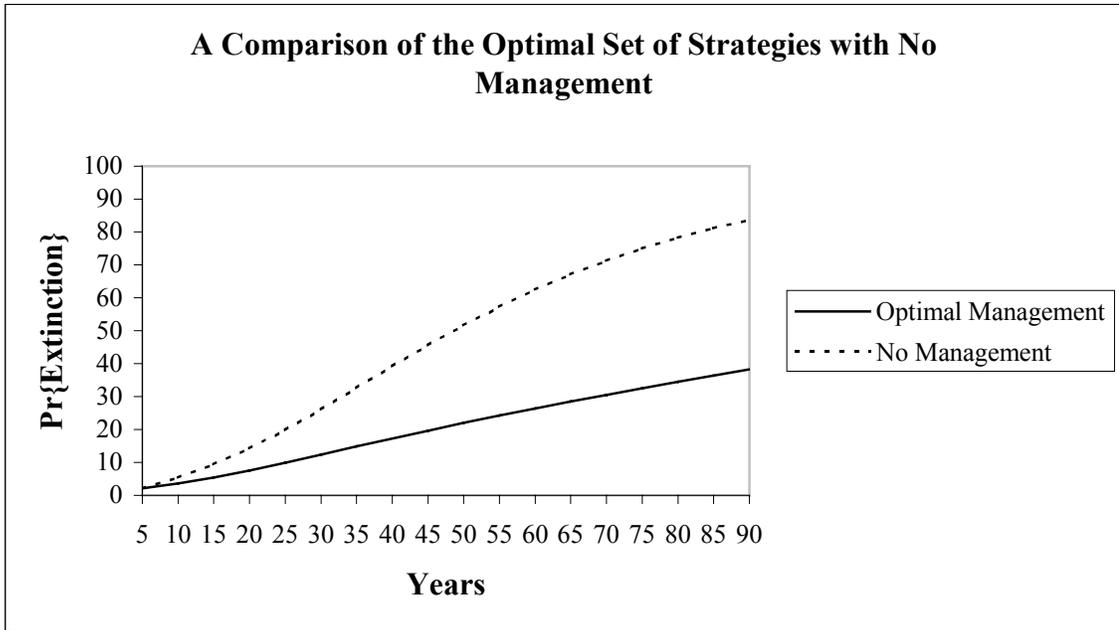
E7 – Create new patch and subsequently enlarge

DN – Do nothing not significantly worse than any strategy

**Figure 10**



**Figure 11.** A comparison of the 30 yr. extinction probabilities between the optimal, state-dependent (SDP) set of decisions and fixed, state-independent sets of decisions under low fire conditions.



**Figure 12.** A comparison of the optimal set of decisions with no management under the baseline parameter scenario of the model and low fire conditions. The extinction trajectories initially diverge over time, and then the difference remains constant, indicating the diminishing returns of the optimal strategies. The difference would be greater with more ambitious strategies. The extinction probabilities for all non-optimal decisions lie between the two curves.

<b>Baseline Scenario</b>			
	<b>All Strategies</b>	<b>Only Enlargement</b>	<b>Only corridors</b>
<b>Population state</b>	<b>Strategy</b>	<b>Strategy</b>	<b>Strategy</b>
<i>Only Two Smallest Patches (2,3) Occupied</i>	E2	E2	C2
<i>Only Largest Patch Occupied</i>	C5	E5	C5
<i>All Patches Occupied</i>	C5	E2	C5
<i>Only Two Largest Patches Occupied</i>	C5	E2	C5

**Table 3.** The optimal management decision for various population states when only one management action can be made (baseline model).

## DISCUSSION

We have shown how stochastic dynamic programming can be used to evaluate the optimal landscape reconstruction strategies for a real metapopulation. The technique has advantages over Monte Carlo simulations, because it would require an inordinate number of simulations to explore all the complex combinations of population and landscape states and find the optimal strategy for each time step. If one were simply interested in finding the best strategy to execute in order to minimize the extinction probability over one time step, then Monte Carlo simulation methods would be adequate. One would simulate the metapopulation dynamics for each management strategy a reasonable number of times to confidently differentiate the impacts of each strategy, perhaps 1000 times. However, the utility of SDP lies in its ability to explicitly find the optimal strategy at some initial time, considering the best decisions in the future. For the emu-wren metapopulation, in order to find the optimal decision at the initial time using Monte Carlo methods, one would have to simulate all possible strategy combinations over the entire time horizon. To find the optimal decision for all population states assuming the metapopulation is in the present landscape state, this would require (# strategy combinations over entire time horizon)  $\times$  ( $\sim 1000$  replicates) <sup>$t$</sup>   $\times$  (# population states) simulations, where  $t$  equals the number of time periods. Over 18 time periods as in our model, this equals an exorbitant number,  $(\sim 10^{12}) \times (1000)^{18} \times (128) \approx 1.28 \times 10^{34}$  simulations! It is often the case that resources for the conservation of a species are spread over many years, and it is not feasible to allocate area for habitat reconstruction all at once. In which case the sequence of actions becomes critical, and as indicated, this can only be efficaciously calculated

with stochastic dynamic programming. Moreover, stochastic dynamic programming gives the exact optimum, something that Monte Carlo methods can only approximate.

What lessons for metapopulation management can be learned from this analysis? Firstly, our results highlight the fact that the optimal decision is very state-dependent. Management strategies cannot be executed without cognizance of the pattern of metapopulation occupancy, landscape state and a good understanding of the extinction and recolonization rates. One cannot hope to effectively manage metapopulations without knowing which patches in the metapopulation are occupied. The complex interplay of strategies and the number of landscape and population state combinations in a spatially-realistic metapopulation model make a glib analysis difficult, like “it is always better to enlarge the biggest patch”. Secondly, the sequence of actions is critical, as is evident in our comparison of the optimal set of strategies with other sequences of actions. It is not simply what you do, but when you do it that matters. The population state-independent strategies can be significantly worse than the optimal strategy, even when compared to the optimal strategy under a short, 30-yr time horizon. This metapopulation management problem is akin to the optimal scheduling problem in Operations Research (Walker 1999), and as such stochastic dynamic programming is really the only tool that can solve it. With a limited amount of resources available for conservation, spread thinly among many endangered species programs, it is essential that the maximum benefit be obtained. If one has knowledge about the occupancy of the metapopulation and the rates of extinction and recolonization, then the use of the SDP framework will always be superior, as it is the only technique that can give the exact optimal set of strategies. Other

techniques or simple qualitative rules can only approximate the optimal solution and probably crudely at that.

Using an analytical metapopulation model for an idealized landscape, where all patches have equal sizes and extinction and recolonization rates, Etienne and Heesterbeek (2001) conclude that decreasing the extinction rate is more beneficial than increasing recolonization by the same amount. However, the unit of comparison for managers is given some fixed cost, which action is most beneficial. Our results indicate that for real landscapes the picture is a complex function of patch geometry, the distribution of patch areas, the extinction and recolonization functional forms, and most importantly, which patches are occupied. They further recommend, by varying the patch-specific rates but not including spatial-explicitness or variation in patch sizes, that if one is focusing on extinction, one should preferably decrease the lowest local extinction probability. Furthermore, if one is focusing on recolonization, then one should preferably increase the recolonization probability of the patch with the lowest local extinction probability. The former result is discordant with our result in Table 3, (though admittedly this is only one sample metapopulation) and casts doubt on those simple rules for real landscapes. Moreover, with species management it is seldom the case that only one action can be performed, but usually a suite of actions over a given time period. The focus should be on how to optimally schedule those management actions.

In fact, one salient point of our analyses is that it is not easy to glean simple rules of thumb on metapopulation management. Though intuitive general rules merge with regard to the first ( $t = 0$ ) management strategy to execute (Table 2), we have shown that the sequence of actions can be quite complicated, and it is impossible to distill qualitative

rules. Conservation has always sought for the holy grail of simple rules, as is evidenced by the SLOSS debate (Diamond and May 1981). This analysis shows that simple, robust rules about the whole sequence of management actions are chimeras due to the complexity of real landscapes. It is necessary to apply a quantitative decision theory framework for every species of concern.

To use this technique, a manager would need to fix the time horizon over which one is interested in minimizing a species' extinction probability. The various strategies need to be delineated, and any constraints on the number of times they can be executed. Here we have limited ourselves to habitat reconstruction, but in practice, many other possibilities could also be incorporated, such as fire management, predator control, and translocation of individuals into patches. In fact one of us (MIW) is using this SDP formulation to look at optimal mowing of pastures for butterfly metapopulations. The manager must then have some estimate of the extinction and recolonization rates, which can be parameterized easily with two snapshots of data (Moilanen 1999). The functional forms of extinction and recolonization can also be altered, but the population dynamics must eventually be described by a discrete time Markov chain. The model that we developed can be elaborated with more realism, such as including habitat quality, fire spread, time delays, additional species, and habitat succession. Explicit financial costs can even be incorporated into the dynamic programming equation. Here we have standardized the costs of each strategy. After the state space and metapopulation dynamics have been specified, the manager would then survey the occupancy of the metapopulation, and the model gives the exact optimal decision for the current time period and the state of the metapopulation. However, while the technique is quite

powerful, it is limited by the size of the state space to rather small networks of metapopulations (Clark and Mangel 2000).

How can our results help guide policy decisions for the emu-wren?

Unfortunately, as our results show, management should not be enacted blindly without regard to exactly which patches are occupied and an understanding of the extinction and recolonization rates. One could choose the most conservative extinction and recolonization scenario presented here, and then after a complete survey of the patches and a specification of the time frame of interest, this model will give the exact optimal strategy. As the parameters become more fine-tuned, this technique can be applied with more confidence for this metapopulation or other metapopulations of the emu-wren in the Fleurieu Peninsula. It must be emphasized that the optimal sequence of strategies is never known beforehand, because what one should do in the future is a function of which patches will be occupied, a probabilistic process. Our main goal in this paper was to formalize this approach and show how metapopulation management cannot be done without the stochastic dynamic framework. This decision-theory technique should be considered an important tool for metapopulation management in general and provides an “engineering”, cost-benefit approach that is needed in conservation (Possingham et al. 2002).

Previous recommendations for landscape planning have not considered the co-dynamics of the population and landscape. One method is to evaluate the relationship between landscape metrics (O'Neill et al. 1988, Turner et al. 1989, Gustafson and Parker 1994, McGarigal and McComb 1995) and species occupancy and design landscapes with a spatial pattern that would have a high probability of species occurrence. Frank and

Wissel (1998) make general recommendations about patch placement in the landscape with regard to dispersal range and the correlation length of the metapopulation dynamics. Vos et al. (2001) have proposed using ecologically scaled landscape indices (ESLI) of average patch carrying capacity and connectivity as guides for landscape planning. Hanski and Ovaskainen (2000) have presented a measure of metapopulation capacity, which is the dominant eigenvalue of a matrix of interpatch connectivity measures. The effect of patch alteration or creation can be evaluated by assessing the change in metapopulation capacity. Lambeck (1997) has promoted the focal species approach for landscape reconstruction, where habitat is created that satisfies the ecological requirements of the most area-limited, resource-limited, dispersal-limited, and process-limited (e.g. fire) species. While these methods may be important in providing end-goals or final characteristics of landscapes, they provide no tack through time. They decouple landscape dynamics and population dynamics and tacitly assume that the latter occurs at a much faster time scale. Our model is a novel, dynamic approach to landscape reconstruction and is the first attempt to explicitly include these two processes. By analyzing the co-dynamics we find that the optimal decision logically depends on the current state. Moreover, one cannot talk about optimal metapopulation management only in terms of which actions to undertake, but the sequence of those actions. Stochastic dynamic programming is the only method that can effectively solve this problem.

## APPENDIX

Below is the extinction matrix for a three-patch system, where  $E_i$  is the patch-specific extinction probability. The order of the population states is:  $[0,0,0]$ ,  $[0,0,1]$ ,  $[0,1,0]$ ,  $[0,1,1]$ ,  $[1,0,0]$ ,  $[1,0,1]$ ,  $[1,1,0]$ ,  $[1,1,1]$ .

$$\mathbf{X}_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ E_3 & 1-E_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ E_2 & 0 & 1-E_2 & 0 & 0 & 0 & 0 & 0 \\ E_2E_3 & E_2(1-E_3) & (1-E_2)E_3 & (1-E_2)(1-E_3) & 0 & 0 & 0 & 0 \\ E_1 & 0 & 0 & 0 & 0 & 0 & 1-E_1 & 0 \\ E_1E_3 & E_1(1-E_3) & 0 & 0 & 0 & 0 & (1-E_1)E_3 & 0 \\ E_1E_2 & 0 & E_1(1-E_2) & 0 & 0 & 0 & (1-E_1)E_2 & 0 \\ E_1E_2E_3 & E_1E_2(1-E_3) & E_1(1-E_2)E_3 & E_1(1-E_2)(1-E_3) & 0 & 0 & (1-E_1)E_2E_3 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ (1-E_1)(1-E_3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & (1-E_1)(1-E_2) & 0 & 0 & 0 & 0 & 0 & 0 \\ (1-E_1)E_2(1-E_3) & (1-E_1)(1-E_2)E_3 & (1-E_1)(1-E_2)(1-E_3) & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

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## **Chapter 2**

### **From Lofty birds to lowly meadows: optimal mowing strategies for butterfly metapopulations**

**Michael I. Westphal,<sup>\* +</sup> and Martin Drechsler<sup>§</sup>**

<sup>\*</sup>Department of Environmental Science, Policy, & Management, University of California,  
Berkeley, CA 94720, U.S.A.

<sup>+</sup>The Ecology Centre, Department of Zoology & Entomology, the University of  
Queensland, St. Lucia, Queensland 4072, Australia

<sup>§</sup> Department of Ecological Modelling, UFZ – Centre for Environmental Research,  
Leipzig-Halle Ltd., PO Box 500135, Permoserstr. 15, D-04301, Leipzig, Germany

*Reality is just another replicate.*

- Tony Starfield

## **ABSTRACT**

We formulate a Markov chain metapopulation model for a hypothetical 4-patch butterfly metapopulation and use stochastic dynamic programming (SDP) to find optimal mowing strategies. Mowing a subpopulation initially extirpates it with a certain probability, but habitat quality and survival probabilities decrease with time since mowing. Under varying mowing extirpation probabilities, the state-dependent set of strategies derived from the SDP result in survival probabilities that are 0.35 – 0.55 greater than the state-independent strategies derived from Monte Carlo simulations. We show how the incorporation of budget size in the SDP formulation can be used to understand the cost-benefit ratio of optimal mowing strategies.

## INTRODUCTION

Over many centuries, the alteration of landscapes for agriculture in Europe has created open landscapes on a very large scale, resulting in the establishment of many species adapted to these human-modified landscapes, “cultural codependents”, including many butterfly species. However, due to the conversion of meadows into arable land, more intensive land use practices, and the abandonment and reforestation of meadows, the habitat of many butterfly species is declining and becoming more fragmented, leading to the concomitant decline in the populations of many butterfly species (Heath 1981, Rat der Europäischen Gemeinschaften 1992). Many butterfly species that live in European meadows exist as metapopulations (Hanski 1998, Hanski 1999). They prefer early successional habitat and in the absence of mowing, there is a diminution of habitat quality over time. However, the act of mowing extirpates or heavily reduces the subpopulation in a meadow. The difficult task of managers then is to derive a “Goldilocks” mowing strategy that is neither too frequent nor too seldom, while also being constrained by economic parameters of these agricultural landscapes.

In the Rhineland-Palatine region of Germany, two *Maculinea* butterflies are of conservation concern: *M. teleius* and *M. nausithous* (Kunz 2000). The region is also home to the White Stork (*Ciconia ciconia*), which has similar habitat requirements and whose population has been slowly decreasing since the middle of the 20<sup>th</sup> Century (Johst 2001, Johst et al. 2002). In the past few decades, whereas mowing used to take place throughout the whole summer, the mowing regime has been reduced to two 2-week periods separated by 6-8 weeks of vegetation regrowth. This synchrony in mowing is

due to the use of mowing machines, which allow farmers to mow simultaneously over large spatial scales (Johst et al. 2002). Like the White Stork, the *Maculinea* butterflies are threatened by the current mowing regime of meadows, and thus, alternative and cost-effective strategies are needed to prevent the species from going extinct.

In this paper, we have adapted the stochastic dynamic programming metapopulation model of Westphal et al. (2003) to compare state-dependent mowing strategies with state-independent strategies derived from Monte Carlo simulations. Like the conservation program for the White storks (Johst et al. 2002), the ultimate goal of this project is to aid in the development of an efficient compensation payment scheme to induce farmers to manage their meadows in a way that is more beneficial to the endangered *Maculinea* butterflies in Rhineland-Palatina. The development of this model will be the skeleton that will be fleshed out with life history information and field survey data.

## **METHODS**

### *Markov Chain Metapopulation Model*

Our formulation of the metapopulation follows Day and Possingham (1995) and Westphal et al. (2003). Let the population state of the metapopulation at any time,  $t$ , be the set of  $n$  patches that are occupied at time  $t$  ( $\leq n$  total patches). We can represent this as an  $n$ -dimensional vector,

$$\mathbf{u}(t) = [u_1(t), u_2(t), \dots, u_n(t)],$$

where the elements are binary variables,  $u_i(t) \in \{0, 1\}$ . If  $u_i(t) = 0$ , then patch  $i$  is empty and if  $u_i(t) = 1$ , then patch  $i$  is occupied.

Now, we can construct an extinction matrix,  $\mathbf{X}_n$  of dimension  $2^n \times 2^n$ , which represents the probabilities of transitions from any population state through extinction alone. Let  $I_1(u_i, v_i)$  be the probability that any patch  $i$  goes extinct in the transition from  $\mathbf{u}$  to  $\mathbf{v}$ . The probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  in one time step, considering only the extinction process is

$$x_{\mathbf{u}\mathbf{v}} = \prod_{i=1}^n I_1(u_i, v_i), \quad (1)$$

where the function  $I_1(u_i, v_i)$  is

$$I_1(u_i, v_i) = \begin{cases} 1 - E_i & \text{if patch } i \text{ remains occupied} \\ E_i & \text{if patch } i \text{ goes extinct} \\ 1 & \text{if patch } i \text{ remains empty} \end{cases} \quad (2)$$

$E_i$  is the patch-specific extinction probability. For instance, for a three patch system, if  $\mathbf{u}$  is  $[1, 1, 0]$  and  $\mathbf{v}$  is  $[1, 0, 0]$ , then,  $x_{\mathbf{u}\mathbf{v}} = (1 - E_1)E_2$ .

Similarly, we can construct a recolonization matrix,  $\mathbf{R}_n$ . Let  $I_2(u_i, v_i)$  be the probability that any patch  $i$  becomes recolonized in the transition from  $\mathbf{u}$  to  $\mathbf{v}$ . The probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  by the recolonization process alone in one time step is given by the product

$$r_{\mathbf{uv}} = \prod_{i=1}^n I_2(u_i, v_i), \quad (3)$$

where the function  $I_2(u_i, v_i)$ , the probability that patch  $i$  becomes recolonized in a transition from  $\mathbf{u}$  to  $\mathbf{v}$ , is

$$I_2(u_i, v_i) = \begin{cases} 1 - C_i & \text{if patch } i \text{ remains unoccupied} \\ C_i & \text{if patch } i \text{ becomes recolonized} \\ 1 & \text{if patch } i \text{ remains occupied} \end{cases} \quad (4)$$

$C_i$  is the patch-specific colonization probability.

Assuming that the order of events is first extinction, then recolonization, the elements of the transition matrix,  $\mathbf{A}_n$ , represent the probability of going from any population state  $\mathbf{u}$  to  $\mathbf{v}$  through both extinction and recolonization:

$$a_{\mathbf{uv}} = \sum_{\mathbf{w}} x_{\mathbf{uw}} r_{\mathbf{vw}}, \quad (5)$$

where  $\mathbf{w}$  is an intermediate state after extinction.

Let us consider a hypothetical 4-patch spatially-implicit butterfly metapopulation, where recolonization is of the Levins-type (Levins 1969, 1971), that is, panmictic dispersal makes the recolonization probability independent of the exact spatial coordinates of a patch. Assume the habitat state of patch  $i$ ,  $h_i \in \{1,5\}$ , is equal to the number of time steps since mowing, with  $h_i = 5$  the maximum value. The probability occupied patch  $i$  going extinct is a function of the habitat quality of a patch:

$$E_i = \min\left(\frac{1}{H - ((h_i - 1)2.5)}, 1.0\right) + \left[1 - \min\left(\frac{1}{H - ((h_i - 1)2.5)}, 1.0\right)\right] m_i \quad (6)$$

where  $H$  is a carrying capacity parameter that implicitly scales habitat quality to population size and  $m_i$  is the probability that the subpopulation in patch  $i$  is extirpated if it is mowed. Let  $H = 10$ , such that in the absence of mowing, the minimum extinction probability is 0.1 in the first year after a mowing event and 1.0 in the fifth year after a mowing event. It is assumed that demographic extinction occurs before mowing.

Likewise, the number of dispersers produced by a patch is proportional to its habitat quality. Let us assume that recolonization probability of patch  $i$  is an average of the ‘recolonization production’ of the occupied neighboring patches:

$$C_i = \frac{\sum_{j \neq i} (1 - (0.25(h_j - 1)))u_j}{n - 1} \quad (7)$$

A patch mowed in the same time step cannot produce dispersers, nor become recolonized if it escapes extirpation by mowing.

### *Stochastic Dynamic Programming*

Dynamic programming is a state-based programming technique in Operations Research for determining an optimal scheduling of decisions (Bellman 1957). At any point in time, each decision imparts some immediate cost (or value) but also alters the future state of the system and thus affects the future cost (or value) incurred in future time steps. Stochastic dynamic programming (SDP) refers to the fact that for some systems, the future state of the system due to some decision is not deterministic, but probabilistic. SDP has been employed in behavioral ecology and more recently in applied ecology (Mangel and Clark 1988, Lubow 1996, Possingham 1996, Johnson et al. 1997, Milner-

Gulland 1997, Possingham 1997, Spencer 1997, Hanson and Ryan 1998, Richards et al. 1999, Clark and Mangel 2000, Shea and Possingham 2000, Moore and Possingham 2001). SDP is a backwards iteration procedure and begins by evaluating the system at the penultimate time,  $T - 1$ . For our metapopulation, let us assign a value of 1.0 if the metapopulation remains extant over the time period  $T$ , and 0 otherwise. Suppose there are  $k$  mowing strategies, that is, how many and which of the  $n$  patches are mowed. At  $T - 1$ , the value of the system in state  $\mathbf{u}$  is a sum of the values for each possible  $\mathbf{v}$  state at time  $T$  that the system could transition to given one of the  $k$  management actions, weighted by the transition probabilities. The algorithm subsequently backsteps to find the strategy that maximizes the value of any  $\mathbf{u}$  state at any time step. The objective is a modification of Bellman's equation (Bellman 1957):

$$V(\mathbf{u}, \mathbf{w}, t, T) = \max_k \left[ \sum_{\mathbf{v}=1}^S a_{\mathbf{u}\mathbf{v}}(\mathbf{x}) V(\mathbf{v}, \mathbf{x}, t + 1, T) \right] \quad (8)$$

where  $V(\mathbf{u}, \mathbf{w}, t, T)$  is the value of population state  $\mathbf{u}$  and habitat state  $\mathbf{w}$  at time  $t$ ,  $T$  is the terminal time,  $a_{\mathbf{u}\mathbf{v}}(\mathbf{x})$  is an element of the transition matrix  $\mathbf{A}_n(\mathbf{x})$ , the probability of going from population state  $\mathbf{u}$  to  $\mathbf{v}$  given we implement the  $k$ -th management strategy. Because each patch can be in one of 5 habitat states, there  $5^n$  (625) total habitat states. The habitat state  $\mathbf{x}$  represents the new habitat after the  $k$ -th strategy has been implemented. Because we set the value to 1 if the metapopulation remains extant and 0 if it goes extinct,  $V(\mathbf{u}, \mathbf{0}, T)$  gives the exact extinction probability of the metapopulation for the  $\mathbf{u}$  population state at the initial time.

## *Scenarios*

The number of possible mowing strategies is equal to the number of population states,  $k = 2^n$ . We have evaluated various values of  $m$ , the probability of extirpation by mowing: 1.0, 0.5, 0.25, and 0.01. We have compared the state-dependent optimal strategies derived from the SDP with state-independent strategies derived from Monte Carlo simulations. In the simulations, the probability that a patch is mowed at any time step is static, regardless of its occupancy or habitat state. We have varied this probability of mowing,  $p$ , from 0.0 to the trivial case of 1.0.

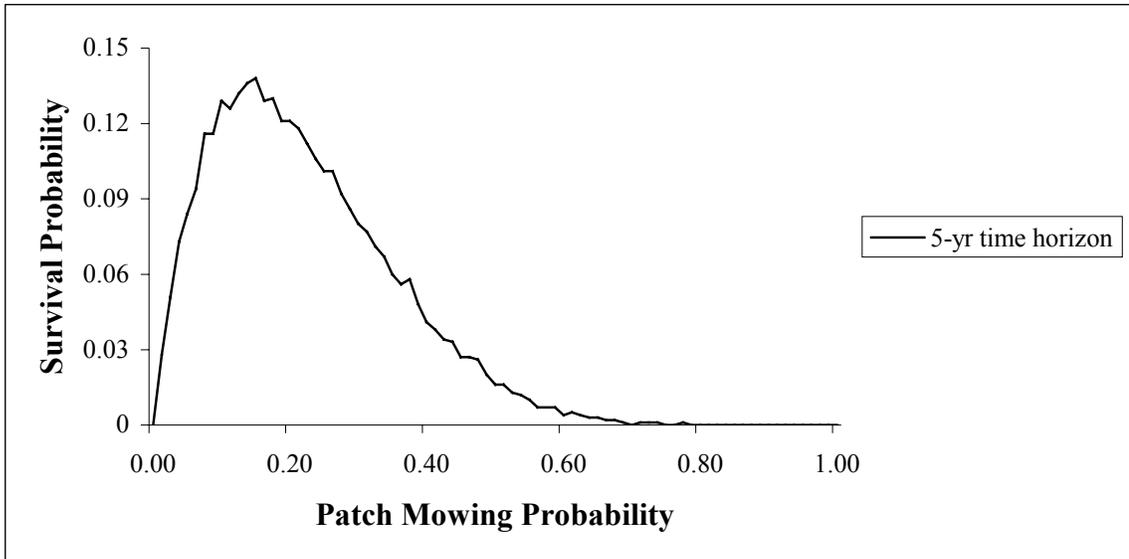
A tradeoff often exists between the economic costs of management and the conservation values. The reconciling of these often-disparate ‘currencies’ is not a trivial task (the subject of Multi-criteria Decision Analysis - Bana e Costa 1990, Beinat and Nijkamp 1998), driven largely by sociopolitical concerns. We could modify the objective function directing by including a penalty term, but this brings up the difficulty of the appropriate conversion from mowing costs into viability. Moreover, the penalty term should be time varying most likely. An  $q$  % increase in viability due to mowing at the penultimate time probably is not equivalent in terms of cost to an  $q$  % increase in mowing at  $t = 0$ . Moreover, the utility of decreasing the extinction probability from 1.0 to 0.95 would not be the same as the utility in decreasing the extinction probability from 0.5 to 0.45. A less abstruse method is to simply include a budget ceiling, which can be varied to analyze of the conservation benefit per unit cost. The objective function in equation (8) becomes:

$$V(\mathbf{u}, \mathbf{w}, y, t, T, B) = \max_k \left[ \sum_{v=1}^S a_{\mathbf{u}\mathbf{v}}(\mathbf{x}) V(\mathbf{v}, \mathbf{x}, z, t+1, T, B) \right] \quad (9)$$

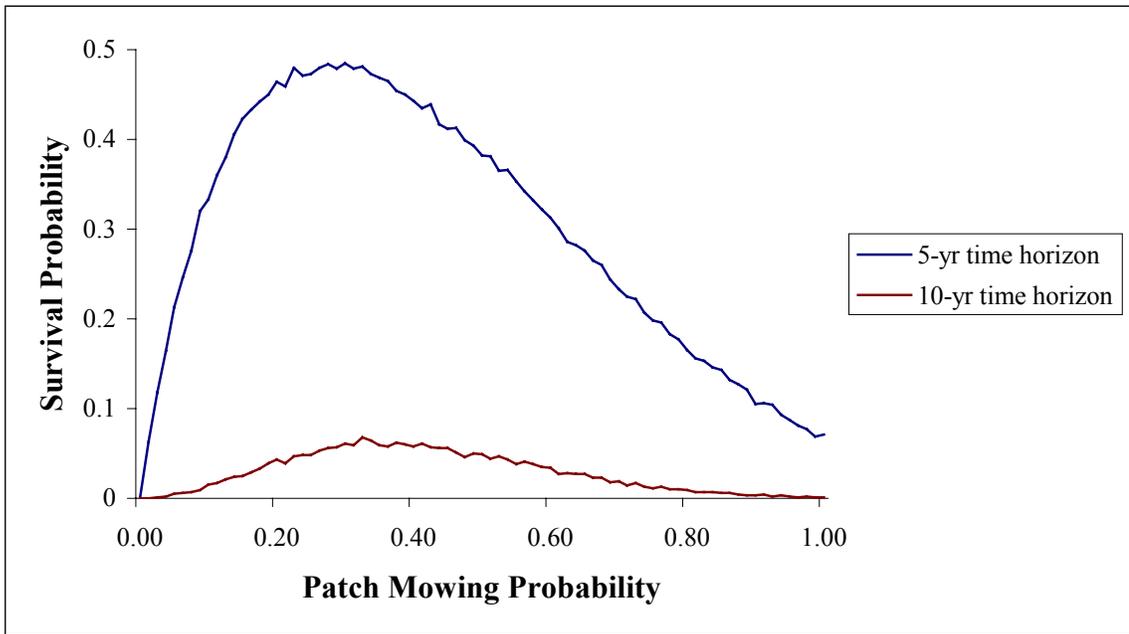
where  $y$  and  $z$  are the costs (i.e. number of mowings) accrued from time 0 to time  $t$  and  $t + 1$ , respectively, for the particular population and habitat states with a budget ceiling of  $B$ . The available budget at any time is  $B - y$ . Now the state space effectively becomes three-dimensional: population state, habitat state and cost state. It is necessary to explicitly keep track of the cost state (i.e. number of mowings available), because the number of mowings is bounded.

## RESULTS

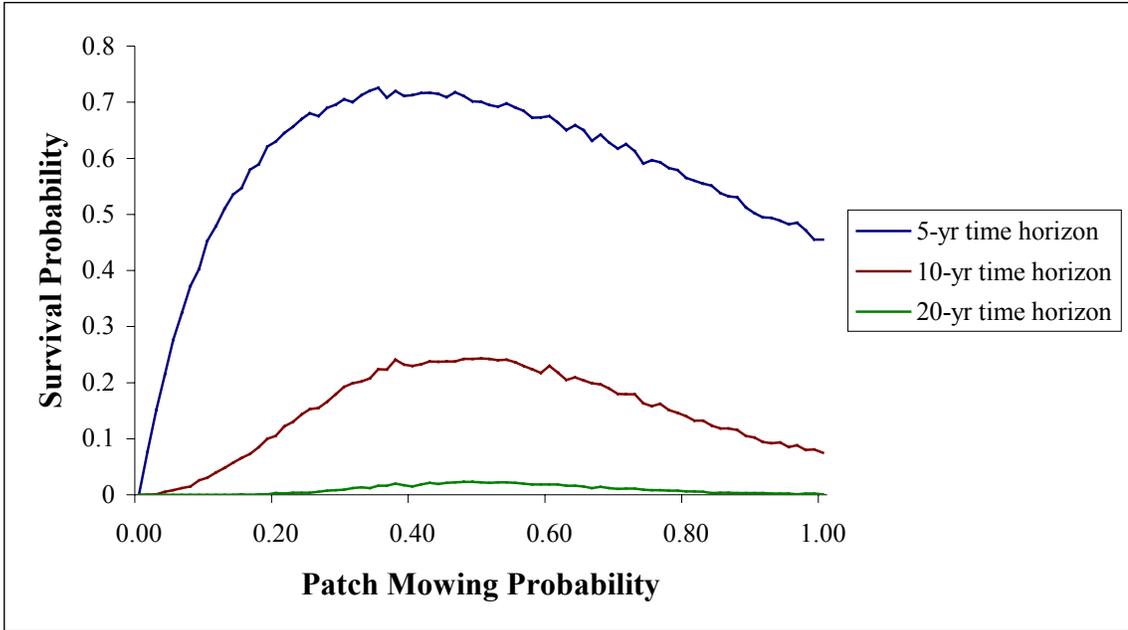
Figures 1-4 show the results of the state-independent Monte Carlo mowing strategies with the various extirpation probabilities. For each mowing probability and time step, the dynamics of the metapopulation were simulated 1000 times. The lower the extirpation probability of the mowing and the longer the time horizon, the higher the patch mowing probability that maximizes the survival probability of the metapopulation. With a very low  $m$ , the metapopulation is invulnerable to mowing, so a high frequency of mowing assures that the patches are continuously in a favorable, early-successional state.



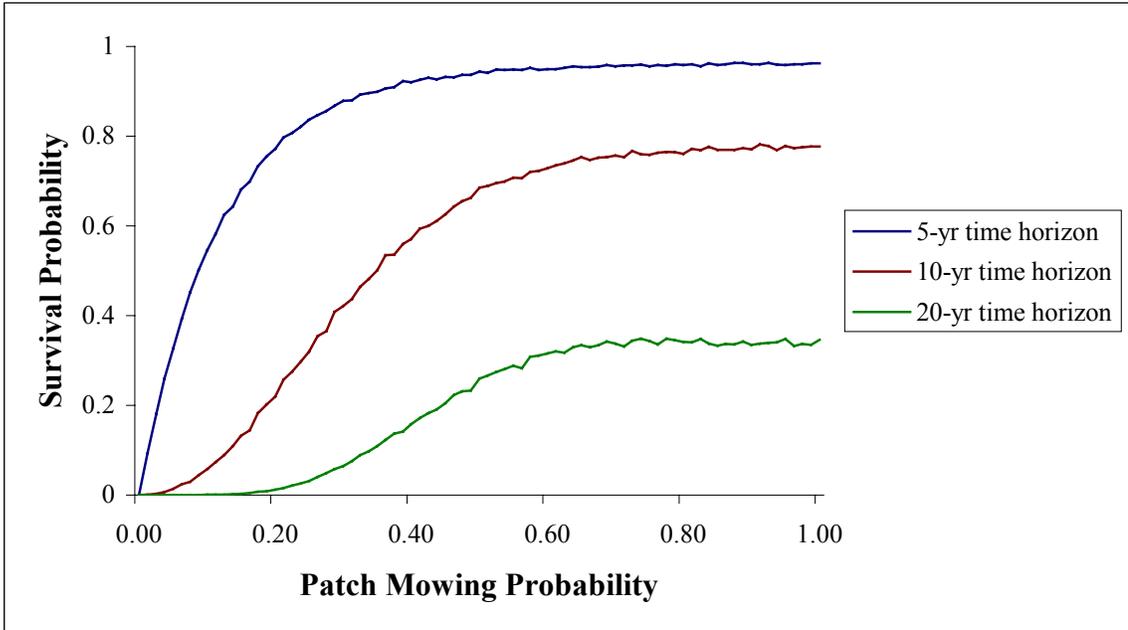
**Figure 1.** Metapopulation survival probability versus mowing intensity, where the probability of extirpation due to mowing ( $m$ ) is 1.0.



**Figure 2.** Metapopulation survival probability versus mowing intensity, where the probability of extirpation due to mowing ( $m$ ) is 0.5.



**Figure 3.** Metapopulation survival probability versus mowing intensity, where the probability of extirpation due to mowing ( $m$ ) is 0.25.



**Figure 4.** Metapopulation survival probability versus mowing intensity, where the probability of extirpation due to mowing ( $m$ ) is 0.01.

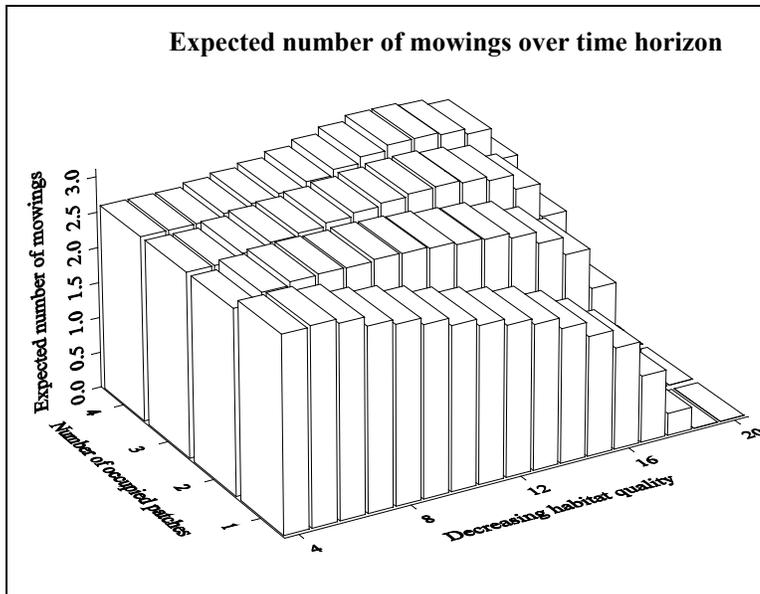
Table 1 shows the comparisons of the best state-independent Monte Carlo strategies with the state-dependent set of strategies as calculated by the SDP. Even for a relatively small number of patches and over a short time horizon, the SDP performs dramatically better, with increases in survival probabilities from 0.35 – 0.55 over the state-independent strategies. Moreover, not only does the SDP set of strategies result in higher survival probabilities, but also they are more efficient in terms of costs (number of mowings).

	Best state-independent strategy			SDP strategy	
Mowing extirpation probability ( <i>m</i> )	Survival probability		Expected number of mowings	Survival probability	
1.0	0.14	(5 yr.)	3.00	0.51	(5 yr.) 2.61
0.5	0.06	(10 yr.)	12.00	0.49	(10 yr.) 7.17
0.25	0.02	(20 yr.)	38.4	0.51	(20 yr.) 21.90
0.01	0.35	(20 yr.)	62.4	0.90	(20 yr.) 34.49

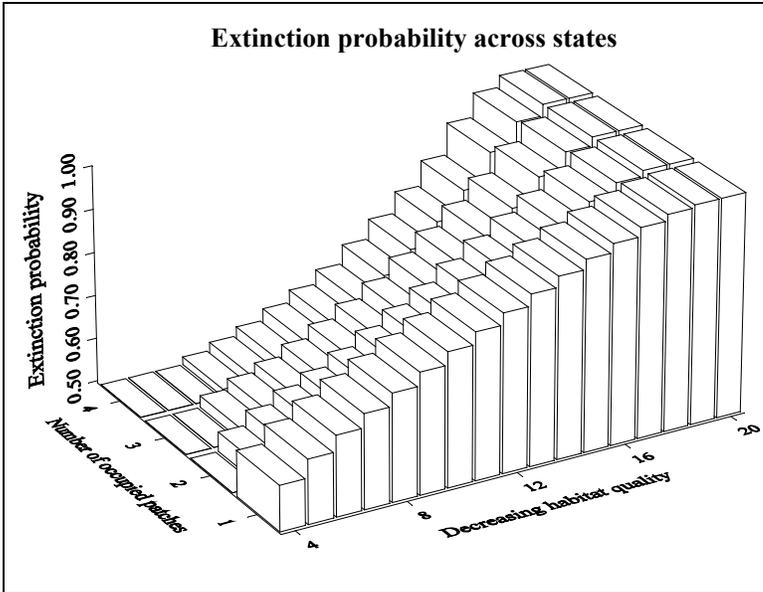
**Table 1.** Comparison of the best state-independent strategies with the optimal SDP sequence of actions with an unlimited budget.

With the inclusion of budget size, the output from the SDP is four-dimensional. For every population state, habitat state, budget size and time, an optimal solution is found. Figures 5-16 show the output for the four mowing extirpation scenarios. In general, the greater the number of occupied patches the greater the expected number of mowings over the entire time horizon. The expected number of mowings is low with a low aggregate habitat quality (i.e. summed habitat quality value across all patches) because a metapopulation with a low habitat quality has a higher chance of extinction over the time horizon. The lower the aggregate habitat quality of the metapopulation, the greater the number of mowings at the initial time ( $t = 0$ ). The number of expected

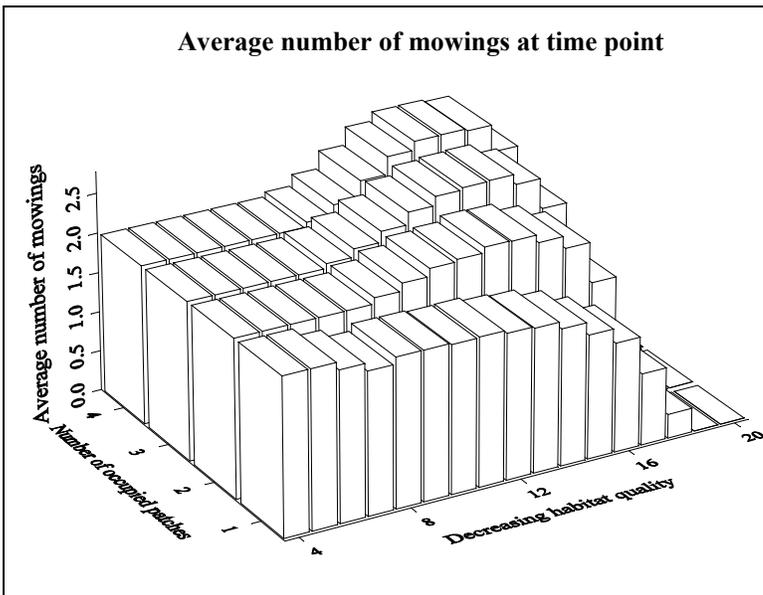
mowings over the time horizon and the initial number of mowings increases as the mowing extirpation probability decreases. There is interplay between the initial cost of mowing and the long-term benefits of maintaining an early successional state, and as  $m$  decreases, the latter becomes less of a factor.



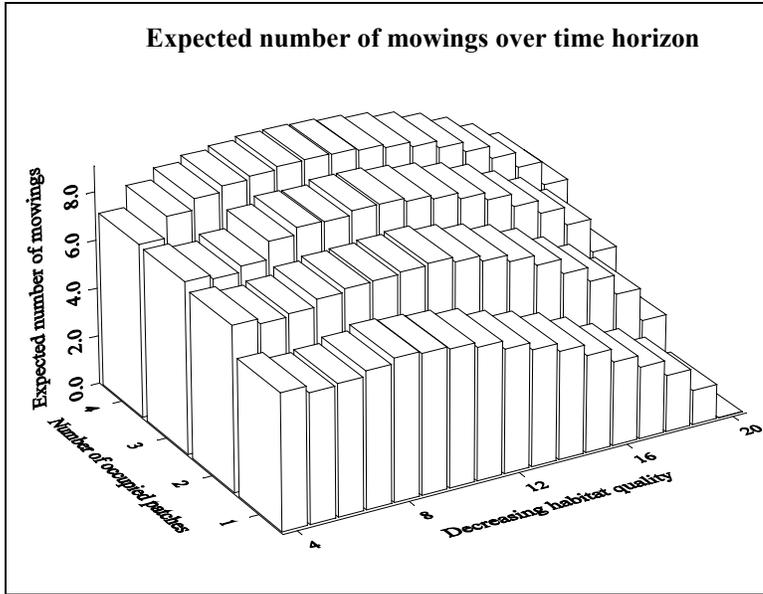
**Figure 5.** The expected number of mowings over the entire time horizon as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 1.0$ ,  $T = 5$ ,  $t = 0$ ,  $y = 0$ ).



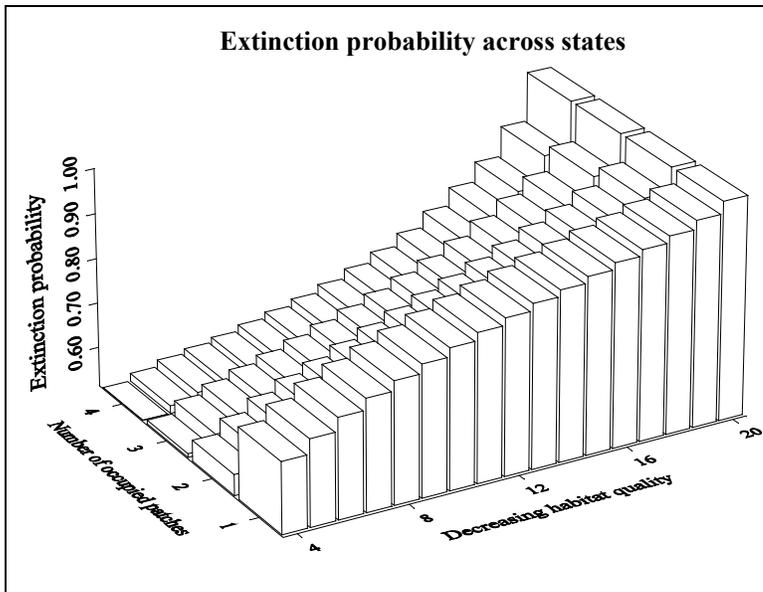
**Figure 6.** The extinction probability at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 1.0$ ,  $T = 5$ ,  $y = 0$ ).



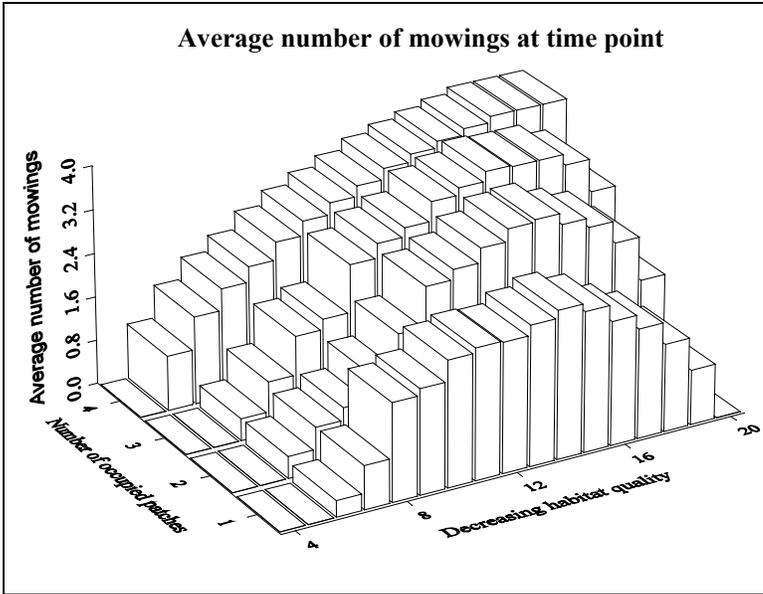
**Figure 7.** The average number of mowings at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 1.0$ ,  $T = 5$ ,  $y = 0$ ).



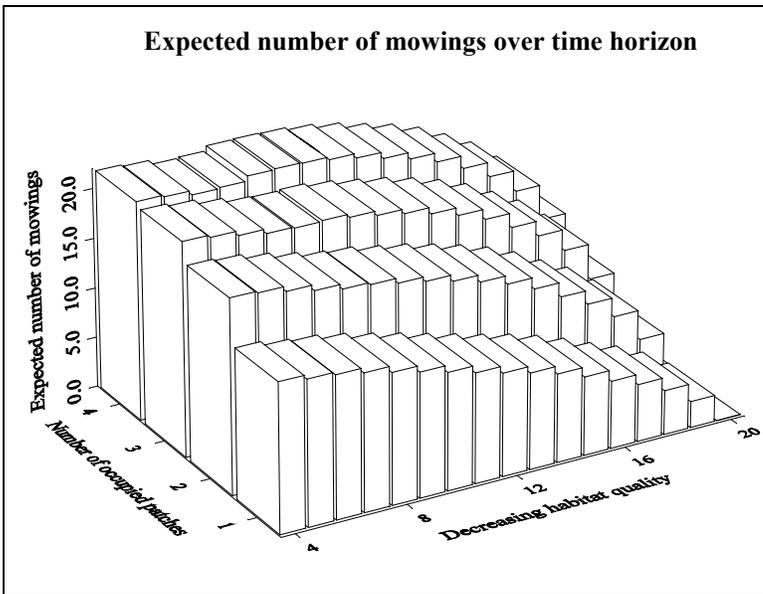
**Figure 8.** The expected number of mowings over the entire time horizon as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.5$ ,  $T = 10$ ,  $t = 0$ ,  $y = 0$ ).



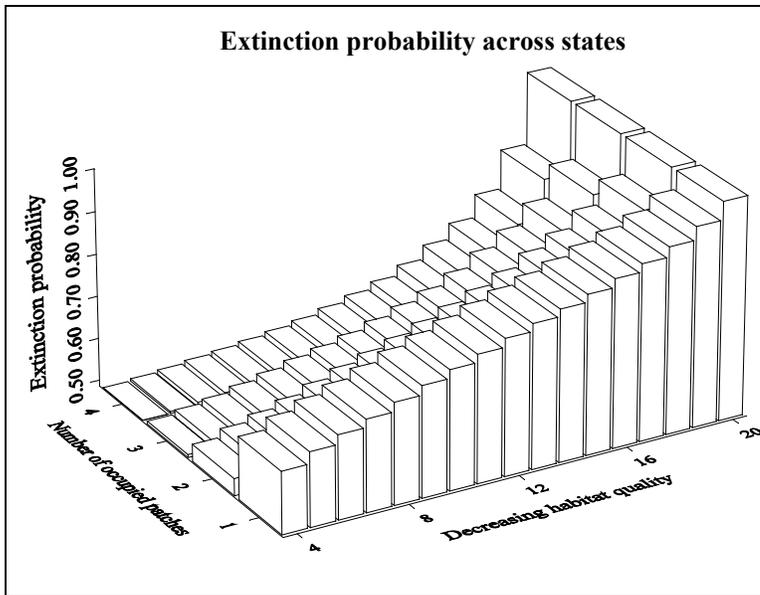
**Figure 9.** The extinction probability at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.5$ ,  $T = 10$ ,  $y = 0$ ).



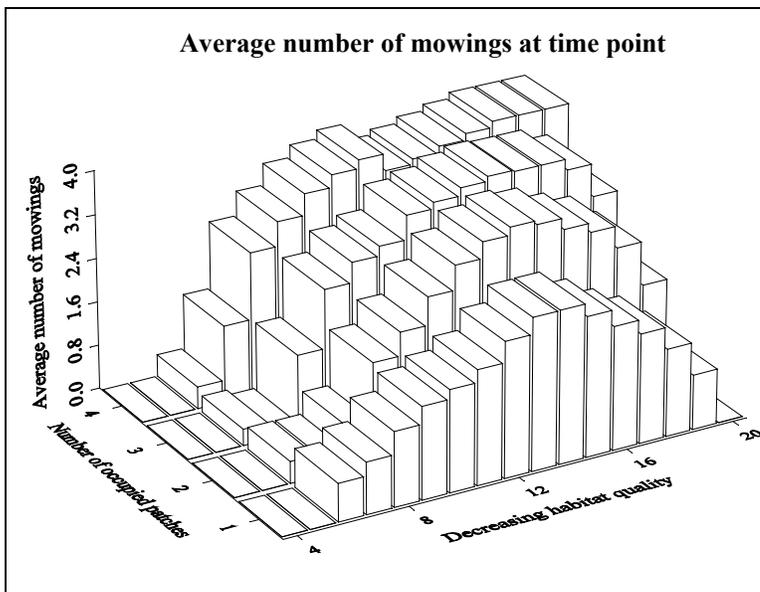
**Figure 10.** The average number of mowings at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.5$ ,  $T = 10$ ,  $y = 0$ ).



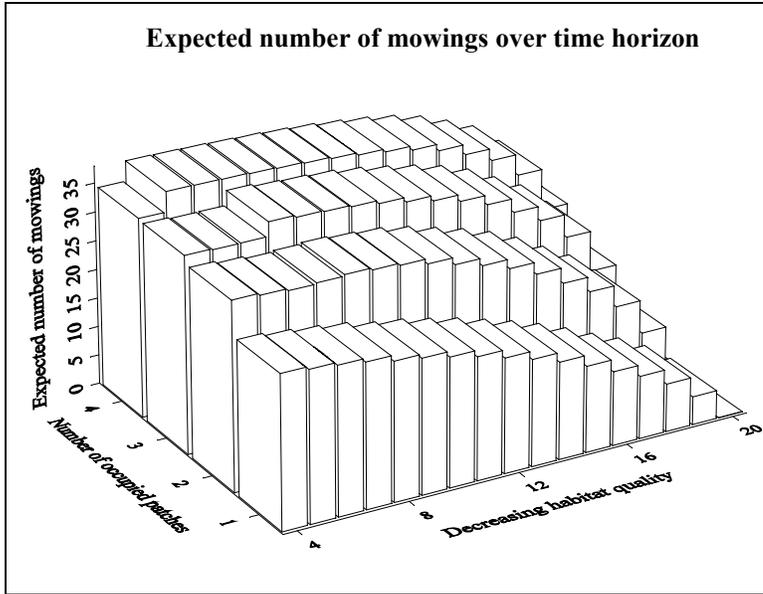
**Figure 11.** The expected number of mowings over entire time horizon as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.25$ ,  $T = 20$ ,  $t = 0$ ,  $y = 0$ ).



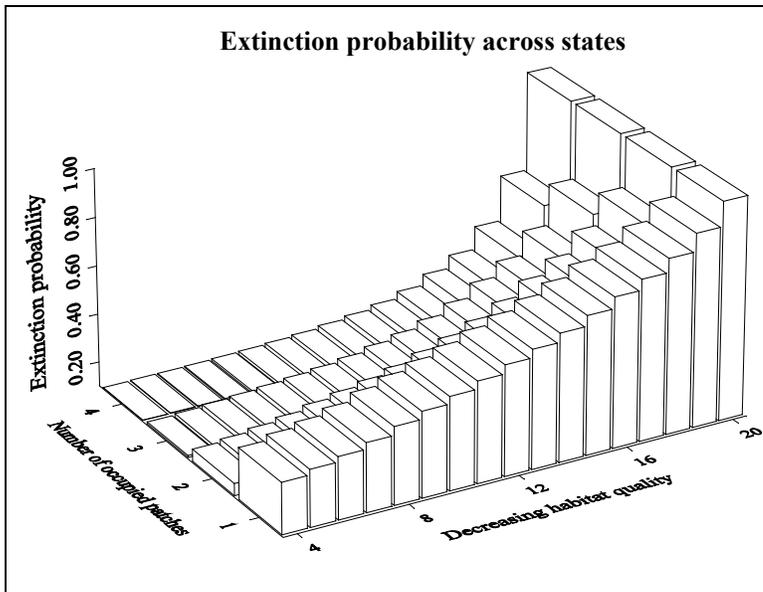
**Figure 12.** The extinction probability at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.25$ ,  $T = 20$ ,  $y = 0$ ).



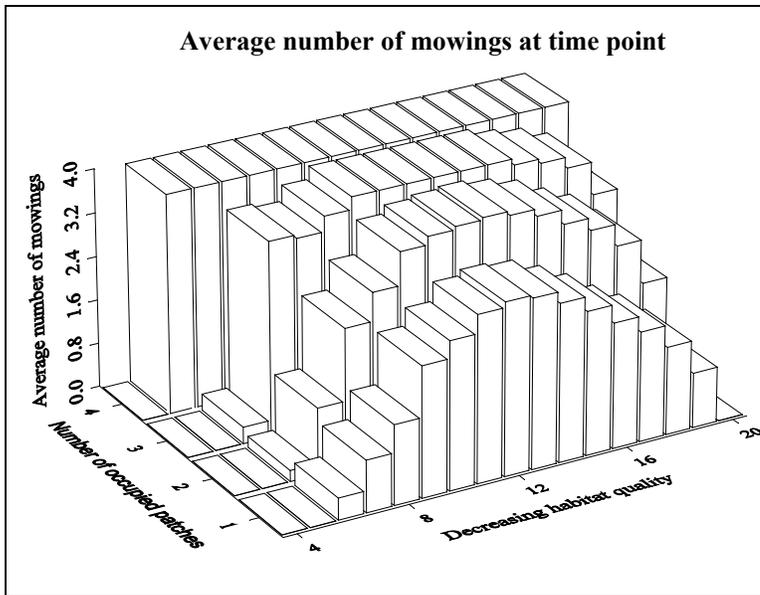
**Figure 13.** The average number of mowings at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.25$ ,  $T = 20$ ,  $y = 0$ ).



**Figure 14.** The expected number of mowings over entire time horizon as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.01$ ,  $T = 20$ ,  $t = 0$ ,  $y = 0$ ).

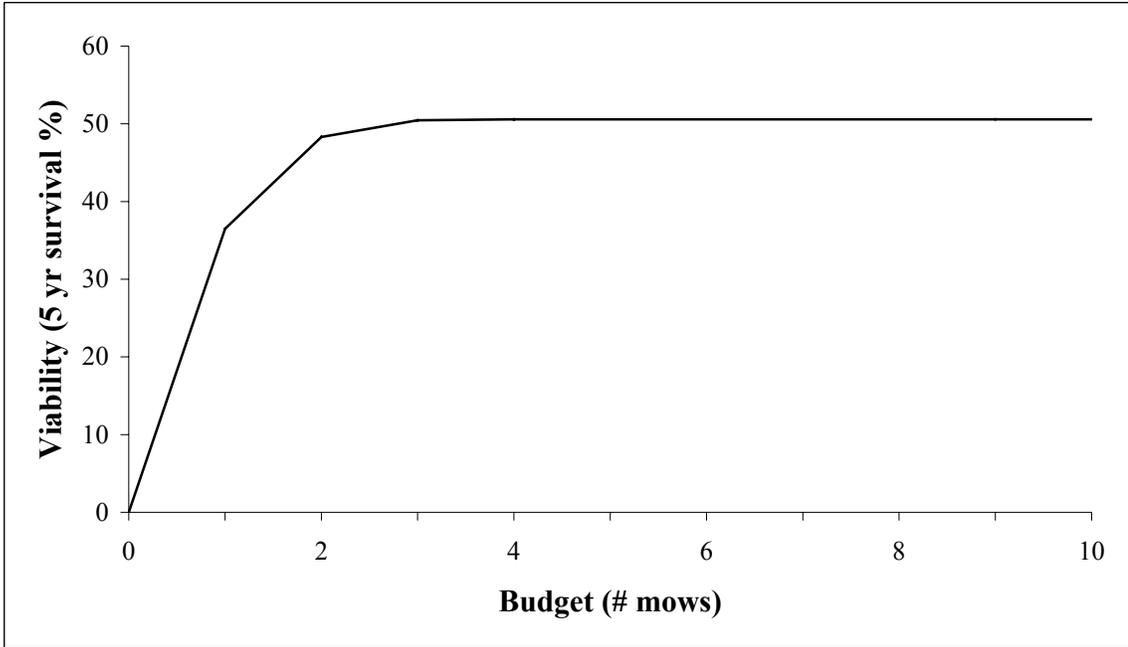


**Figure 15.** The extinction probability at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.01$ ,  $T = 20$ ,  $y = 0$ ).

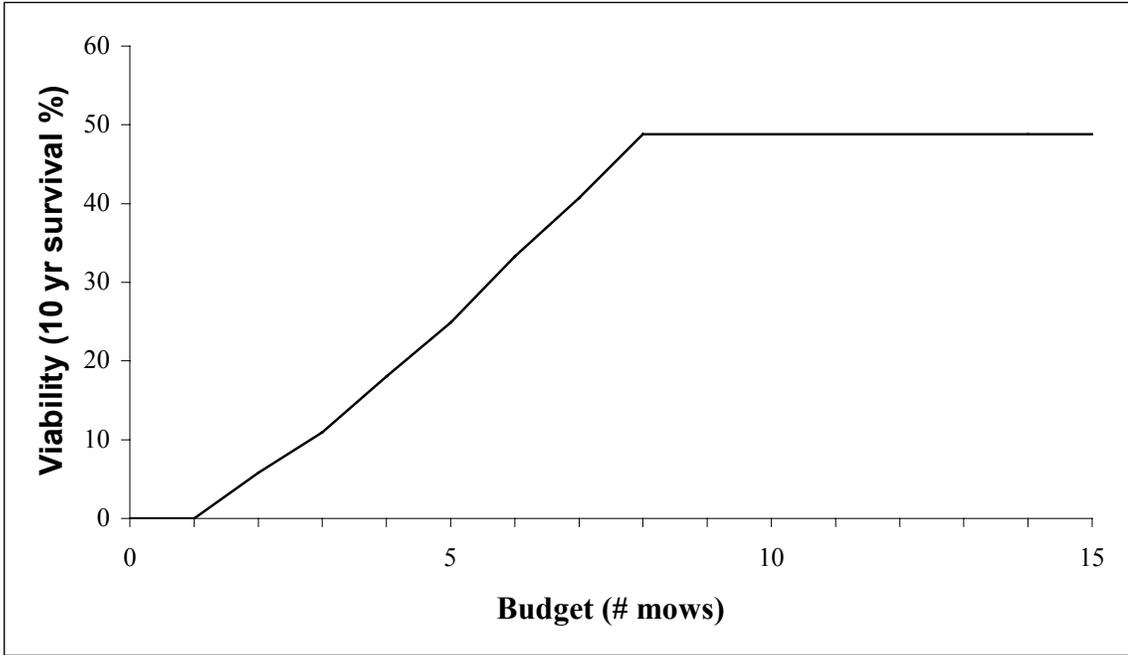


**Figure 16.** The average number of mowings at  $t = 0$  as a function of habitat quality (value summed across all patches) and number of occupied patches ( $m = 0.01$ ,  $T = 20$ ,  $y = 0$ ).

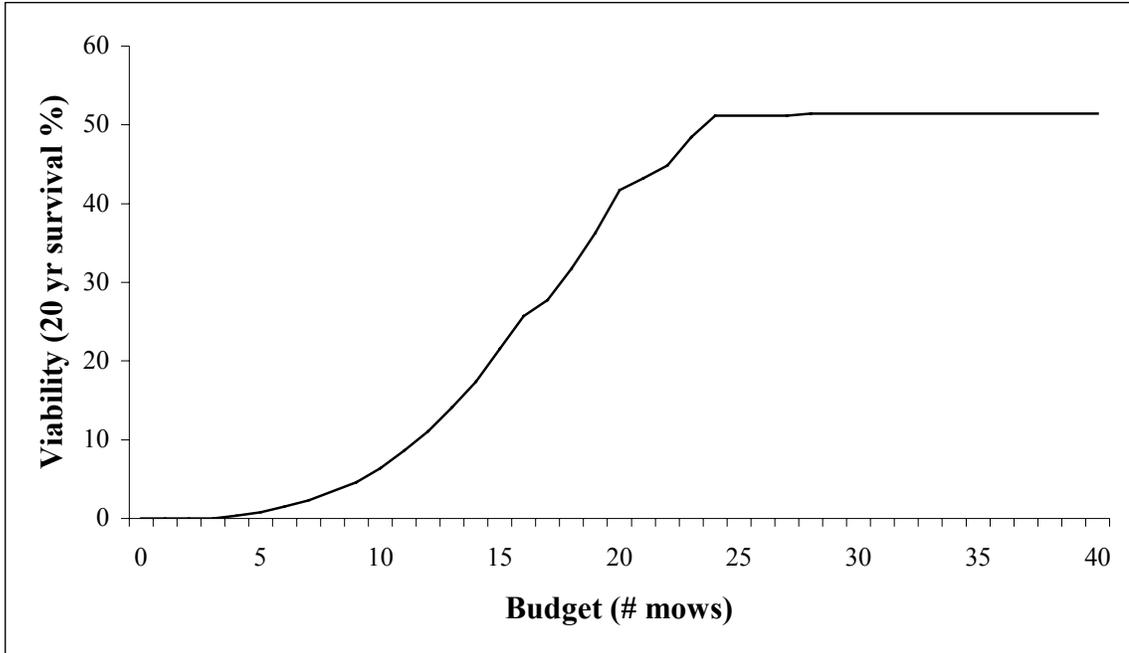
Of course, it is Pollyannaish to think that all conservation programs can be funded to the level that would result in the maximal conservation benefit, and like the principle of triage, only those programs whose conservation value per unit cost is high should be funded. Figures 17-20 show the metapopulation survival from the optimal SDP model as a function of budget size for the four mowing scenarios. For all four cases, there are some diminishing returns in conservation benefit. As total budget can easily be translated into monetary costs, these analyses can be used to select the expenditure that maximizes the viability per unit financial cost. This would be useful where a government agency has to manage several species conservation programs and the goal is to maximize some aggregate viability.



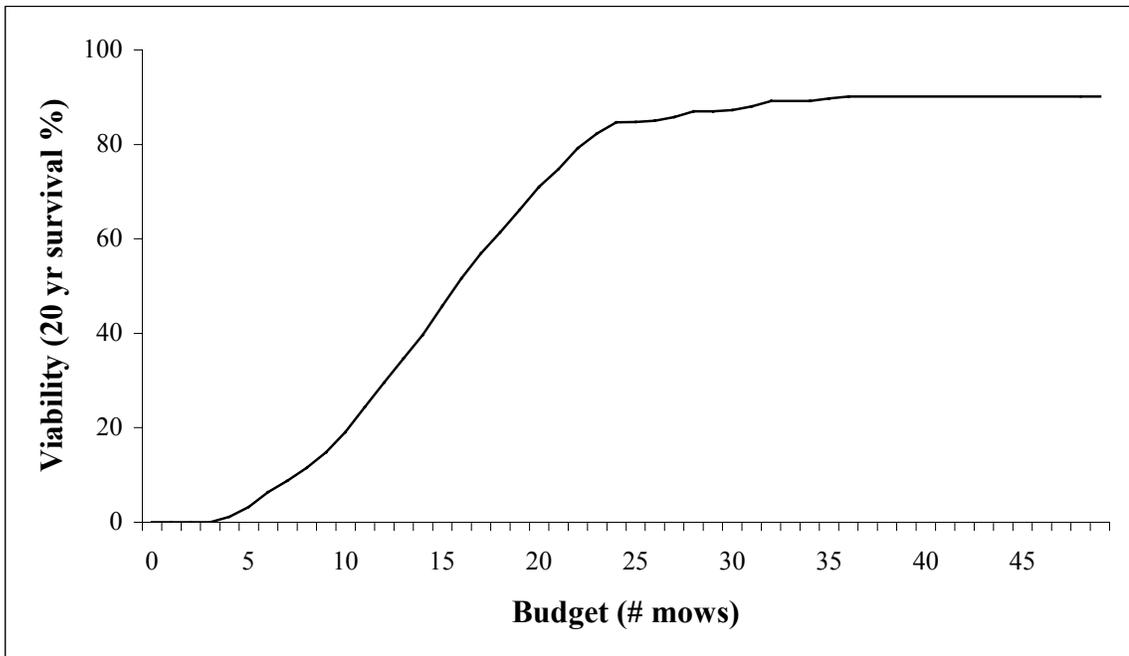
**Figure 17.** Metapopulation survival probability over 5 yrs. as a function of the total budget available, where the probability of extirpation due to mowing ( $m$ ) is 1.0. No management over the time horizon would result in a 0% chance of survival.



**Figure 18.** Metapopulation survival probability over 10 yrs. as a function of the total budget available, where the probability of extirpation due to mowing ( $m$ ) is 0.5. No management over the time horizon would result in a 0% chance of survival.



**Figure 19.** Metapopulation survival probability over 20 yrs. as a function of the total budget available, where the probability of extirpation due to mowing ( $m$ ) is 0.25. No management over the time horizon would result in a 0% chance of survival.



**Figure 20.** Metapopulation survival probability over 20 yrs. as a function of the total budget available, where the probability of extirpation due to mowing ( $m$ ) is 0.01. No management over the time horizon would result in a 0% chance of survival.

## DISCUSSION

We have shown how making state-dependent mowing strategies derived from SDP can have dramatic improvements over state-independent strategies in reducing extinction risk even for a 4-patch, idealized metapopulation. Clearly, one must be cognizant of the habitat and population states of the metapopulation to derive maximal benefit from mowing. This model will serve as a foundation for further analyses. We plan to fit models to occupancy data for a real landscape in the Rhineland-Palatina, using maximum likelihood techniques (Hilborn 1997, Hanski 1999, Moilanen 1999). It is possible to incorporate Bayesian learning when the extirpation probability of mowing is unknown (Hilborn 1997, Hauser 2002). The metapopulation model that we have formulated is rather simple, with Levins-like, spatially-implicit dispersal. It may be more realistic to include spatial-explicitness in the recolonization probabilities, as in the Southern Emu-wren work (Westphal et al. 2003).

The biggest limitation of SDP is the “curse of dimensionality”, as size of the state space grows by a factor of four with every increase in patch number, quickly making the problem intractable. Metapopulations with many subpopulations will not be amenable to exploration with this technique, unless the state space constraint can be circumvented by delineating relatively disjunct networks of subpopulations or using approximation methods. For the former, if there are distinct clusters largely disconnected from other such clusters, then a series of nested SDPs could be formulated. For any such cluster, only the number of occupied patches in a neighboring cluster, not the exact occupancy

pattern, may be relevant. In which case, the number of population states is  $2^nc$ , where  $c$  is the maximum number of occupied patches in the other clusters. This can be an aggregate value, or  $c$  can be further decomposed into a value for each neighboring cluster.

One promising technique to surmount state space limitations is neuro-dynamic programming (Bertsekas 1996). Bellman's dynamic programming equation calculates the strategy that maximizes the expected value of the current reward plus the reward of all future time steps. Neuro-dynamic programming uses techniques like neural networks to find good approximations of that future reward, without having to explicitly multiply the transition matrices for every state.

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# Chapter 3

## On rules of thumb for the design of metapopulations

**Michael I. Westphal,<sup>\* +</sup> and Karin Frank<sup>§</sup>**

<sup>\*</sup>Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, U.S.A.

<sup>+</sup>The Ecology Centre, Department of Zoology & Entomology, the University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>§</sup> Department of Ecological Modelling, UFZ – Centre for Environmental Research, Leipzig-Halle Ltd., PO Box 500135, Permoserstr. 15, D-04301, Leipzig, Germany

*Nature goes her own way and all that to us seems an exception is really according to order.*

- Johann Wolfgang von Göthe.

## **ABSTRACT**

We simulate many hypothetical metapopulations, varying the extinction and recolonization parameters, patch distribution and area allocation, and use simulated annealing optimization algorithms to find the optimal allocation of additional restoration area with the objective to maximize the time to extinction. We sought to examine whether rules can be distilled on which patches become connected by corridors or enlarged to the greatest extent. Over all runs, no simple rule was fulfilled much more than 50% of the time, casting doubt on the usefulness of rules of thumb for habitat restoration for metapopulations. Patch geometry and area distribution impinge in complex ways, rendering simple, robust rules illusory. Other restoration heuristics, such as maximizing the uniformity of patch size, adding area according to the degree of connectivity (highest immigration rate), or adding area according to the degree of isolation (lowest immigration rate) while maintaining the original patch number, generally do poorly in comparison, resulting in a time to extinction over all runs that is only about 70% of the near-optimal value derived from the simulated annealing algorithm. Our results do show, however, the utility of decision theory/optimization tools for habitat restoration for metapopulations.

## INTRODUCTION

The metapopulation ecology paradigm (Andrewartha and Birch 1954, Huffaker 1958, den Boer 1968, Levins 1969, 1971, Hanski 1998, Hanski 1999), whose development has been concomitant with the appreciation of spatial heterogeneity in ecology in general (Tilman and Kareiva 1997), has been an important lens through to understand spatially-structured populations. Though the term has been synonymous with any spatially-structured population, in a classical sense, metapopulation refers to the situation where subpopulation go extinct but the whole network persists due to continual recolonization from neighboring patches (Hanski 1999). The intrapatch dynamics occur on a much faster time scale than the interpatch dynamics, such that effectively only the occupancy, not the patch density, needs to be modeled, an example of which is the incidence function model (Hanski 1999). Here, we restrict ourselves to this type of metapopulation.

Increasing patch sizes and reducing separation distances of patches are both desirable for reducing the extinction probability of a metapopulation, but metapopulation theory, in the absence of a decision theory tool, gives us no way to easily choose among those options. Westphal et al. (2003) used stochastic dynamic programming to determine the optimal sequence of management actions for a real metapopulation, such as enlarging patches or building corridors, and found that the best strategy is highly dependent on the occupancy pattern of the metapopulation and that the complex interplay of strategies makes the rendering down of simple rules of thumb quite difficult.

Etienne and Heesterbeek (2001) determined three rules of thumb for metapopulations, 1.) if focusing on extinction, one should decrease the extinction probability of the patch with the lowest extinction probability, 2.) if focusing on recolonization, one should increase the recolonization probability between the patches with the lowest extinction probability, and 3.) decreasing the extinction probability has a greater effect than increasing the recolonization probability by the same amount.

(Etienne 2002) simulates many hypothetical metapopulations and tempers those original conclusions, but recommends that enlarging the largest patch and reducing the effective distance between the largest patches are the best strategies for metapopulation management. Those recommendations are based on percentage changes in extinction and recolonization probabilities. He qualified that former rule by saying that when absolute changes in patch area are compared, enlarging the smallest patch is preferred. The problem with looking at percentage changes is that amount of area needed to reduce the extinction probability of the largest patch by  $n$  % is obviously much greater than the amount of habitat needed to bring about the same reduction in the extinction probability for the smallest patch. In the case of the allocation of habitat for restoration (or the parallel exploration of where habitat loss would be the least deleterious), it is only the absolute change in extinction probability that matters.

Etienne (2002) explores changes in extinction and recolonization separately, but these are confounding factors that cannot be disentangled. If the patches are enlarged then most likely the interpatch distances are reduced, leading to increased recolonization probabilities. The main interest for managers is given some fixed budget (e.g. total amount of area available), how should those resources be distributed to maximize

viability. In this paper, we simulate various hypothetical metapopulations and use an iterative heuristic optimization algorithm to explore solutions to the problem of how to most efficaciously allocate habitat to maximize the time to extinction.

## METHODS

### *Measures of metapopulation viability*

There are many ways of determining metapopulation viability. Monte Carlo simulations of the extinction and recolonization dynamics can be used to approximate the extinction time. One can set up a stochastic Markov chain metapopulation model (Day and Possingham 1995, Etienne 2002, Westphal et al. 2003), in which case the subdominant eigenvalue of the state (pattern of occupancy) transition matrix,  $\lambda_2$  is a measure of the expected time to extinction of the metapopulation (Halley and Iwasa 1998):

$$T_m = \frac{1}{1 - \lambda_2} \quad (1)$$

Metapopulation capacity (Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001) gives a measure of the ability of metapopulation to persist in a landscape, but incorporates no dynamics. Frank and Wissel (1998, Frank 2003) have developed a formula for the mean lifetime of the metapopulation ( $T_m^a$ ) based on a continuous time

Markov chain model, where each patch  $i$  of  $M$  total patches has an extinction rate  $v_i$ , while  $c_{ij}$  is the rate that it will recolonize an empty patch  $j$ :

$$T_m^a = \frac{1}{v_a} \frac{(M-1)!}{M(M-1)^{M-1}} \left( e^{\frac{M}{k}} k^{M-1} \right) \quad (2)$$

where,

$$k = \prod_{i=1}^M \max(\sqrt{2}, z_i)^{\frac{1}{M}}$$

$$v_a = \frac{1}{\left( \frac{1}{M} \sum_{i=1}^M \frac{1}{v_i} \right)} \quad (3)$$

and

$$z_i = \frac{1}{v_i} \sqrt{\left( \frac{1}{2} \left[ \left( \sum_{j \neq i} c_{ji} \right)^{-2} + \left( \sum_{j \neq i} c_{ij} \right)^{-2} \right] \right)^{-1}}. \quad (4)$$

The submodel for extinction has the familiar functional form:

$$v_i = \varepsilon A_i^{-\zeta} \quad (5)$$

where  $A_i$  is the area of patch  $i$ ,  $\zeta$  is a parameter that gives the strength of environmental stochasticity and  $\varepsilon$  scales the area term to rate of extinction.

Likewise, the rate of recolonization of patch  $i$  is:

$$c_{ij} = \delta A_i e^{-\alpha d_{ij}} \quad (6)$$

where  $d_{ij}$  is the interpatch distance,  $\delta$  is a species-specific emigration rate per unit area, and  $\alpha^{-1}$  is a species-specific mean dispersal distance.

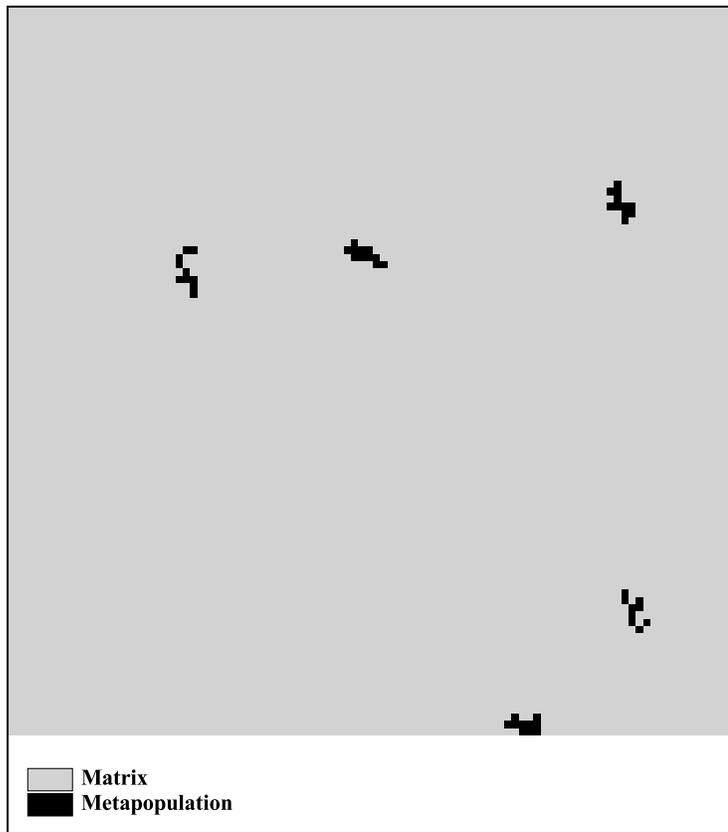
### *Simulation of metapopulations*

We simulated hypothetical 5-patch metapopulations on a 100 x 100 grid, using a simple algorithm following (Etienne 2002). We first randomly place one patch on the grid. The second patch is placed on the landscape according to a Gaussian probability distribution with the mean  $x$  ( $y$ ) coordinate being the  $x$  ( $y$ ) coordinate of the first patch and a standard deviation  $\sigma$ . Each subsequent patch is placed on the grid, with its mean  $x$  ( $y$ ) being the average of those already on the landscape. Next the area is distributed among the patches randomly. We used both a lognormal distribution and a normal distribution to add area to patches in two different scenarios, both with a mean value of 10 grid cells. Once area is assigned to each patch, it is randomly allocated as long as two patches do not combine, such that the patch shape varies from being highly compact to sinuous. If two cells are connected only by their vertices, they are considered part of the same patch. Table 1 lists the combinations of extinction, recolonization, patch creation and distribution parameters, and Figure 1 shows one sample metapopulation. The ranges of the extinction, recolonization, patch distribution and area allocation parameters are meant to simulate the whole array of configurations in nature. We could have used a more complex (i.e. fractal) algorithm for generating random landscapes;

however, this is unnecessary as we are considering only a binary landscape with the standard area-distance patch occupancy model. For each combination, we created 50 replicate landscapes for total of 2700 metapopulation simulations.

	Patch distribution ( $\sigma$ )	Area allocation	Extinction ( $\xi$ )	Recolonization ( $\alpha^{-1}$ )
1	10	Normal (10, 1)	1.00 ( $A_i = 10, v_i = 0.1$ )	10
2	25	10*Lognormal(0, 1)	0.30 ( $A_i = 10, v_i = 0.5$ )	25
3	$\infty$		0.12 ( $A_i = 10, v_i = 0.75$ )	50

**Table 1.** The parameter values used in the simulations.



**Figure 1.** A sample simulated metapopulation (Normal area allocation,  $\sigma = 25$ ,  $\xi = 0.30$ ,  $\alpha^{-1} = 25$ ).

### *Optimization algorithm*

For each hypothetical metapopulation, the goal is to maximize the mean time to extinction, given that we can allocate 50% more of the total metapopulation area and that existing grid cells prior to restoration are fixed. The initial creation of metapopulations explained in the previous section can be thought of as simulating the variety of metapopulations that would occur in nature; given that we have an existing metapopulation, the objective is now to add habitat in order to maximize the lifetime of the metapopulation. The 10,000 grid cell landscape can be represented as a vector,  $\mathbf{s}$ , where each element,  $s_i \in \{0, 1, 2\}$ . If a grid cell is part of the initial, existing metapopulation, then  $s_i = 2$ , while if a grid cell is restored habitat, then,  $s_i = 1$ . Finally, if the grid cell is matrix, non-habitat, then  $s_i = 0$ . Though during the initial creation of the metapopulation we fixed the number of patches to 5, during the optimal restoration, we do not constrain the number of patches. Let  $A_R$  be the total area of the metapopulation after restoration, and  $A_{i_0}$  is the initial area of  $i$ -th patch. Thus, our objective function is:

$$\begin{aligned} & \max T_m^a(\mathbf{s}), \\ & \text{given that } A_R = \sum_{i \in M} A_{i_0} + \left( 0.5 \sum_{i \in M} A_{i_0} \right). \end{aligned} \tag{7}$$

We used a simulated annealing (Metropolis et al. 1953, Kirkpatrick et al. 1983) algorithm to find near-optimal solutions. The concept of simulated annealing is derived from metallurgy, where a substance is heated and then cooled to obtain a desired crystalline structure. If the reduction in temperature is too rapid, then the metal will not be in the lowest energy state. The fundamental idea behind simulated annealing is that

initially in the search across solution space, which is accomplished by small neighborhood moves, all negative changes in the objective function are accepted. Over time the control parameter, the *temperature*, decreases in value and the algorithm becomes choosier, such that only positive changes are accepted. This provides a mechanism to avoid being trapped in a local optimum. Like other heuristic optimization algorithms, simulated annealing is “blind”, that is, it is not cognizant of when it reaches an optimal or near optimal solution, and consequently must be told to terminate, at which point, there is no guarantee that a global maximum is reached. However, under certain conditions, it will asymptotically approach the global optimum (Sait 1999). The algorithm is as follows:

- I. Set the temperature,  $C$ , which is the acceptance parameter (see below for cooling schedule methodology).
- II. Generate a random restored landscape,  $\mathbf{s}_1$ , and calculate  $T_m^a(\mathbf{s}_1)$ . That is, randomly select matrix grid cells ( $s_i = 0$ ) that abut already existing metapopulation grid cells until the budget ( $A_R$ ) is met and calculate the time to extinction.
- III. Randomly delete a restored grid cell ( $s_i = 1$ ) and then randomly add a non-habitat, matrix grid cell ( $s_i = 0$ ) that is adjoining an existing metapopulation cell. Calculate  $T_m^a(\mathbf{s}_2)$ . Evaluate,  $\Delta T = T_m^a(\mathbf{s}_2) - T_m^a(\mathbf{s}_1)$ : if  $e^{\frac{\Delta T}{C}} >$  uniform random number  $[0,1]$ , then accept change,  $\mathbf{s}_1 \leftarrow \mathbf{s}_2$ . The exponential term is a *Boltzmann* probability term.

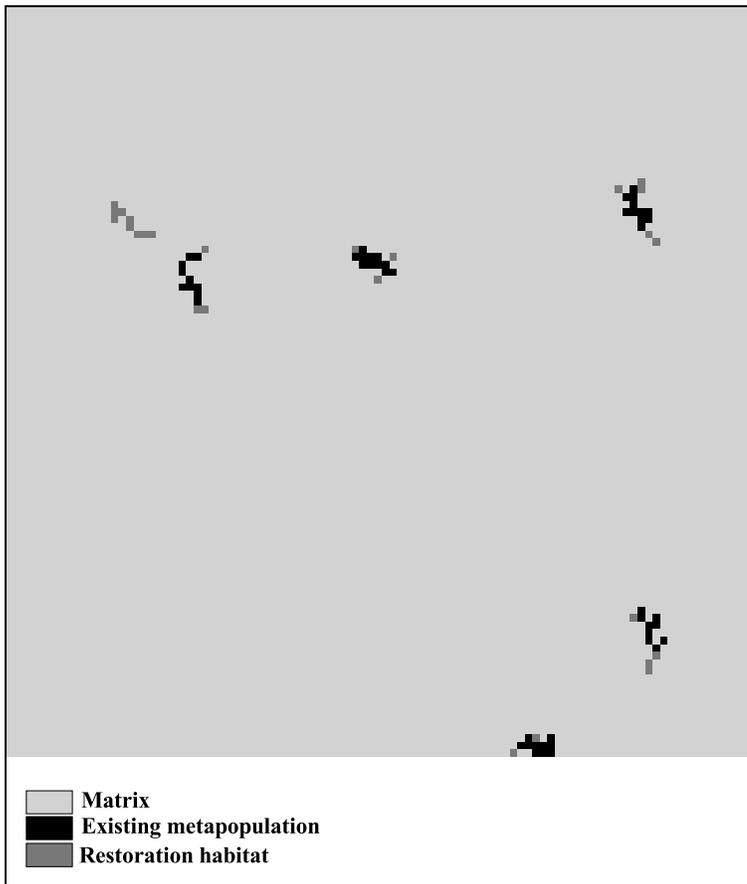
- IV. If the temperature,  $C$ , has not been lowered for  $q$  iterations, reduce the temperature. Otherwise, the temperature remains unchanged.
- V. Go to step III for the maximum number of iterations (10,000) or until  $T_m^a(\mathbf{s}_1)$  has not changed for  $q$  iterations.

We used an adaptive cooling schedule modified from (Huang et al. 1986), where the temperature decrements according to:

$$C_{l+1} = C_l \left[ \max \left( 0.5, e^{\frac{-0.7C_l}{\sigma_c}} \right) \right] \quad (8)$$

where  $\sigma_k$  is the standard deviation of the objective values ( $T_m^a(\mathbf{s}_2)$ ) at temperature  $C_l$ ,  $l$  is the current iteration and  $l + 1$  is the next iteration of the algorithm. The initial temperature,  $C_0$ , equals  $100\sigma_0$ , calculated from 50 initial random restoration landscapes. The number of time spent at each temperature,  $q$ , is set to 50. The cooling schedule parameters were determined after extensive trial-and-error. The fact that the final objective function value was always within a couple percent of the best objective value reached during the course of the iterations indicates that the parameters are giving fairly good (near optimal) solutions. Each simulated annealing run took on the order of several minutes on a Pentium IV processor. Figure 2 shows the optimal restoration of the sample metapopulation in Figure 1 after the implementation of the simulated annealing algorithm. We have constrained the selection of grid cells for restoration to those adjoining existing metapopulation cells, because the addition of many, widely separated patches to the metapopulation results quickly in the diminution of the time to extinction to zero, a trough in solution space from which it is difficult to escape. This makes sense

from a biological point of view if one assumes that patches compete for dispersers from neighboring patches, effectively reducing the mean per-patch recolonization rate. New patches can still be created via step III of the algorithm.



**Figure 2.** The resulting restoration landscape of the sample metapopulation in Figure 1 after the implementation (one run) of the simulated annealing algorithm. In this case, a new patch is created.

Our algorithm allows two patches to become connected by corridors. Whether a corridor results simply in an attenuation of  $\alpha$  or one larger coalesced patch is function of the corridor width and the species natural history. Here we assumed the latter. Our goal is to investigate whether certain rules emerge as to which patch, for example the smallest,

largest, least or most connected, is enlarged to greatest extent and which patches are most likely to be connected by corridors. In terms of reducing extinction, the marginal value of adding area to the smallest patch is greater than that of any other patch. However, our goal is to explore to what extent this is altered by landscape geometry. Frank (2003) concludes that when environmental noise is weak (large  $\xi$ ), the optimal allocation of habitat is uniform, while when environmental noise is high (small  $\xi$ ), allocating habitat according to the degree of connectedness is optimal. However, the conclusions were based on *ex nihilo*, ideal area allocation to metapopulations, not adding to existing metapopulations. Our second goal is to see how closely three restoration regimes approximate the near-optimal solution: maximizing the uniformity of patch size, adding area according to the degree of connectivity (highest immigration rate), or adding area according to the degree of isolation (lowest immigration rate), while maintaining the original patch number ( $M = 5$ ) (Table 2).

Heuristic	Final ideal area of patch $i$	Order of area allocation
Uniform	$A_{if} = \left( \frac{A_R}{M} \right)$	Smallest $A_{io}$ to largest
Most Connected	$A_{if} = \left( \frac{\sum_{j \in M} c_{jio}}{\sum_{i \in M} \sum_{j \in M} c_{jio}} \right) A_R$	Lowest $\sum_{j \in M} c_{jio}$ to highest
Least Connected	$A_{if} = \left( \frac{\frac{1}{\sum_{j \in M} c_{jio}}}{\sum_{i \in M} \left( \frac{1}{\sum_{j \in M} c_{jio}} \right)} \right) A_R$	Lowest $\sum_{j \in M} c_{jio}$ to highest

**Table 2.** The other heuristics whose resulting time to extinction is compared to that of the simulated annealing algorithm. Due to the constraints of the existing size of patches prior to restoration and the limited budget size, the final areas are not always reached. The subscripts  $o$  and  $f$  refer to before and after habitat restoration, respectively, while  $A_R$  is the total metapopulation area after restoration (initial summed area plus the restoration area).

## RESULTS

Tables 3-5 show the comparison of the simulated annealing runs with the other restoration heuristics and the proportion of time that simple rules are fulfilled. None of the simple rules are very robust, but adding more of the new restoration area to the smallest patch or the most connected patch in comparison to the other patches, or reducing the distance between the two largest patches perform the best. Over all runs, the other restoration heuristics poorly approximate the time to extinction of the near-optimal

simulated annealing result. These heuristics are constrained in that they preserve the original patch number, while the simulated annealing algorithm is able to create linkages between patches to form large aggregates. Some patterns emerge, nonetheless. The higher the value of  $\xi$ , the better the heuristic in approximating the near-optimal time to extinction, but with a very high extinction rate, the differential between any strategy will be reduced. Under all parameter combinations, adding a new patch is poor strategy compared to augmenting the size of existing patches, because of the high extinction rate at small patch areas. The lower the extinction rate, the less likely that corridors will be constructed between patches

Parameters	Uniform heuristic	Least connected heuristic	Most connected heuristic	Number of patches	Corridor present	New patch	Smallest patch area
All	0.69	0.65	0.69	4.40	0.46	0.07	0.55
$\xi_1$	0.48	0.40	0.48	5.01	0.15	0.15	0.57
$\xi_2$	0.73	0.70	0.73	4.11	0.62	0.03	0.52
$\xi_3$	0.87	0.86	0.87	4.10	0.62	0.04	0.56
$\alpha^{-1}_1$	0.65	0.61	0.67	4.36	0.49	0.08	0.52
$\alpha^{-1}_2$	0.69	0.64	0.70	4.44	0.45	0.07	0.57
$\alpha^{-1}_3$	0.73	0.70	0.71	4.44	0.45	0.07	0.57
$\sigma_1$	0.59	0.58	0.57	3.74	0.75	0.05	0.63
$\sigma_2$	0.71	0.66	0.71	4.56	0.44	0.08	0.52
$\sigma_3$	0.78	0.72	0.79	4.93	0.20	0.09	0.50
Normal	0.72	0.68	0.73	4.28	0.47	0.01	0.54
Lognormal	0.67	0.62	0.66	4.54	0.46	0.13	0.57

**Table 3.** The results of the simulated annealing runs and comparison with other heuristics. The values for the heuristics indicate the proportion of the time to extinction value of the (near) optimal solution. The number of patches is the average number of patches after the simulated annealing algorithm is implemented. The other entries refer to the proportion of time that that patch had the largest addition, in absolute terms, to its area, any corridor was formed, or a new patch was created. The results are indicated across all runs and for each parameter value separately.

Parameters	Largest patch area	Most connected area	Least connected area	Corridor two smallest patches	Corridor two largest patches	Corridor smallest patch	Corridor largest patch
All	0.08	0.44	0.08	0.20	0.12	0.33	0.24
$\xi_1$	0.09	0.38	0.11	0.05	0.01	0.11	0.04
$\xi_2$	0.07	0.48	0.05	0.26	0.14	0.44	0.31
$\xi_3$	0.07	0.45	0.07	0.29	0.21	0.46	0.37
$\alpha^{-1}_1$	0.08	0.45	0.09	0.21	0.14	0.36	0.28
$\alpha^{-1}_2$	0.08	0.41	0.08	0.21	0.11	0.33	0.24
$\alpha^{-1}_3$	0.06	0.45	0.07	0.19	0.10	0.31	0.21
$\sigma_1$	0.05	0.42	0.09	0.24	0.14	0.55	0.40
$\sigma_2$	0.06	0.44	0.05	0.18	0.10	0.26	0.18
$\sigma_3$	0.11	0.46	0.10	0.12	0.07	0.13	0.09
Normal	0.13	0.34	0.12	0.23	0.19	0.34	0.29
Lognormal	0.02	0.54	0.04	0.18	0.05	0.32	0.19

**Table 4.** The results of the simulated annealing runs. The other entries refer to the proportion of time that that patch had the largest addition, in absolute terms, to its area, a corridor linked two patches, or a new patch was created. The results are indicated across all runs and for each parameter value separately. Only those times when a corridor is possible (connection distance less than available budget) are included.

Parameters	Corridor least connected patch	Corridor most connected patch	Corridor two most connected patches	Corridor two least connected patches	Corridor two closest patches	Two largest patches distance reduced
All	0.14	0.42	0.26	0.02	0.39	0.47
$\zeta_1$	0.03	0.11	0.05	0.01	0.11	0.49
$\zeta_2$	0.18	0.56	0.33	0.03	0.52	0.47
$\zeta_3$	0.20	0.58	0.39	0.04	0.56	0.44
$\alpha^{-1}_1$	0.15	0.45	0.30	0.03	0.42	0.48
$\alpha^{-1}_2$	0.13	0.40	0.24	0.02	0.39	0.47
$\alpha^{-1}_3$	0.14	0.40	0.24	0.02	0.37	0.45
$\sigma_1$	0.23	0.66	0.32	0.03	0.59	0.45
$\sigma_2$	0.06	0.37	0.24	0.01	0.38	0.50
$\sigma_3$	0.02	0.21	0.20	0.02	0.20	0.45
Normal	0.14	0.44	0.29	0.03	0.41	0.57
Lognormal	0.14	0.39	0.22	0.02	0.37	0.37

**Table 5.** The results of the simulated runs. The entries refer to the proportion of time that corridors (patch coalescence) were present. Only those times when a corridor is possible (connection distance less than available budget) are included. For the reduction in distance between the two largest patches, the reduction includes both the presence of a corridor or when the interpatch distance is reduced more in percentage terms than the average interpatch distance of all patches. The results are indicated across all runs and for each parameter value separately.

## DISCUSSION

The results do not make one rather confident about the distillation of simple, robust for rules for allocating restoration habitat to metapopulations. Unlike Etienne (2002), we have not artificially disentangled extinction and recolonization, and we have made restoration area our fundamental currency. Moreover, we have used optimization techniques, which have seldom been used in metapopulation ecology (Westphal et al. 2003). Based on the simple extinction submodel, one would conclude that adding the more of restoration area to the smallest path than other patches would be the most beneficial, because the marginal value is the greatest. However, superimposed on this is the complexity of space, the geometry of patch configuration, and our results have show

that this muddles the situation. Perhaps, the pursuit of simple rules-of-thumb is misplaced in ecology. However, we have shown how one can formulate habitat restoration for metapopulations in a decision theory framework. Simulated annealing algorithms could be applied to real metapopulations, and additional factors could be added, such as the grid cells, or sites, having varying costs, whose total cannot exceed some budget.

Though Frank and Wissel (1998) give a formula for the approximate time to extinction with the inclusion of extinction correlation, we have ignored it here. It is unlikely the inclusion of it would make any rules more robust. In most cases, if extinction correlation (e.g. catastrophes, such fire) exists in metapopulation, its scale is expected to be greater than the scale of the metapopulation. With high extinction correlation, there would be the countervailing tendency to optimally produce more patches and spread the risk, instead of the tendency toward simple patch aggregations as we have found here. We have also not varied the dispersal kernel, though there are good theoretical and empirical reasons to expect it to be a negative exponential function in many cases (Hanski 1999). Moreover, it would be interesting to see how varying our assumption about patch corridors (coalescence) would change the results. Often times the patches that we have simulated were quite sinuous and, for some species, edge effects could manifest themselves in a higher patch extinction rate. However, the traditional patch occupancy models (Hanski 1999) do not include measures of patch shape in the extinction submodel.

Most fundamentally, the metapopulation paradigm is only relevant for a small subset of species that view the landscape in a binary sense, such as some butterflies (e.g.

Glanville fritillary - Hanski 1994, Hanski et al. 1994, Hanski and Thomas 1994, Hanski et al. 1995, Hanski et al. 1996, Hanski 1999), frogs (Sjogren and Ray 1996, Vos and Stumpel 1996), American pika (Moilanen et al. 1998), and a very few birds (Westphal et al. 2003). Even if a species exists as “classical metapopulation”, the area-dispersal distance model may not be correct; other factors, such as habitat quality, may be more important (Fleishman et al. 2002).

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# Chapter 4

## Effects of landscape pattern on bird species distribution in the Mt. Lofty Ranges, South Australia

**Michael I. Westphal,<sup>\* +</sup> S. A. Field,<sup>+¶</sup> A. J. Tyre<sup>+</sup>, D. Paton<sup>&</sup>,  
and H. P. Possingham<sup>+§</sup>**

<sup>\*</sup>Department of Environmental Science, Policy, & Management, University of California, Berkeley, CA 94720, U.S.A.

<sup>+</sup>The Ecology Centre, Department of Zoology & Entomology, the University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>§</sup> Department of Mathematics, University of Queensland, Australia

<sup>¶</sup>Department of Applied and Molecular Ecology, University of Adelaide, Australia

<sup>&</sup> Department of Environmental Biology, University of Adelaide, Australia

*. . . we have to remember that what we observe is not nature in itself but nature exposed to our method of questioning.*

- Werner Heisenberg

## **ABSTRACT**

We assessed how well landscape metrics at 2, 5, and 10 km. scales could explain the distribution of woodland bird species in the Mount Lofty Ranges, South Australia. We considered 31 species that have isolated or partially isolated populations in the region and used the Akaike Information Criterion to select a set of candidate logistic regression models. The 2 km. distance was the most appropriate scale for a plurality of the species. While the total amount of area of native vegetation around a site was the most important determining factor, the effect of landscape configuration was also important for many species. Most species responded positively to area-independent fragmentation, but the responses to mean patch isolation and mean patch shape were more variable. Considering a set of candidate models for which there is reasonable support (Akaike weights  $> 0.10$ ), 12 species responded negatively to landscapes with highly linear and isolated patches. No clear patterns emerged in terms of taxonomy or functional group as to how species respond to landscape configuration. Most of the species had models with relatively good discrimination (12 species had ROC values  $> 0.70$ ), indicating that landscape pattern alone can explain their distributions reasonably well. For six species there were no models that had strong weight of evidence, based on the AIC and ROC

criteria. This analysis shows the utility of the Akaike Information Criterion approach to model selection in landscape ecology. Our results indicate that landscape planners in the Mount Lofty Ranges must consider the spatial configuration of vegetation.

## INTRODUCTION

With the advent of the landscape paradigm in ecology, there has been great attention paid to how landscape configuration affects species distribution and population dynamics (Turner et al. 2001). However, the impacts of the fraction of suitable habitat in the landscape as opposed to landscape configuration, which includes such properties of landscape pattern as patch shape, isolation and fragmentation, are often difficult to disentangle, and this has important implications for how we manage habitat loss and/or reconstruction. In a simulation study Fahrig (1997, 1998) found that when the percentage of habitat in a landscape exceeds 20%, then species persistence was virtually assured, regardless of the spatial configuration of the habitat. A review of birds and mammals by Andr n (1994) also suggests that habitat patch isolation only becomes important in terms of species richness or abundance when the percentage of habitat decreases below a 20-30% threshold.

Empirical studies of birds, for instance, vary widely in terms of the importance of the spatial pattern of habitat even when they have analyzed landscapes with large ranges of percent habitat cover. McGarigal and McComb (1995) found in a study of birds in Oregon that forest cover explained more variance in species abundance than landscape structure, and most of the significant effects of fragmentation on abundance were positive. Meyer and Irwin (1998) found that the main influences of landscape structure on spotted owls were due to the amount of habitat, not configuration. Trzcinski et al. (1999) compared the effects of forest cover and area-independent fragmentation (using the residuals of the correlation between habitat area and a measure of fragmentation) on

breeding bird distributions of 31 species in forested landscapes in Ontario. They found that all species responded positively to forest cover, while the response to fragmentation was weak and variable. However, in another study in eastern Ontario with similar forest types and range of percent cover, Villard et al. (1999) determined that more than half of the species had measures of landscape configuration as significant explanatory variables in models of species occupancy. Unlike Trzcinski et al. (1999), they used a smaller landscape scale and included a measure of patch isolation. Even within a species the effect of fragmentation has been shown to vary across regions with different proportions of habitat cover. The Scarlet Tanager showed its strongest response to fragmentation in the more deforested Midwest and Atlantic regions of its range in North America (Rosenberg et al. 1999). Fahrig (2002) asserts that fragmentation effects are as likely to be positive as negative based on the limited empirical studies to date. Indeed, there is a discordance between the predictions of models and the rather equivocal results of empirical studies.

The main goal of this study was to look at how well landscape variables measured at various spatial scales (2, 5, 10 km.) explain the distribution of woodland bird species in the Mount Lofty Ranges (MLR) region of South Australia. At the time of World War II, about half of the region was covered by native vegetation, and since then, there has been precipitous clearing for agriculture, particularly in the southern part of the peninsula (Bryan 2000). Garnett and Crowley (2000) list eight species that have already gone extinct in the MLR. Because of the relatively recent land clearance, there may exist an *extinction debt*, with more species doomed before a relaxation to a new level of species richness (Possingham and Field 2001). In order to develop plans for habitat

reconstruction in the region, it is necessary to understand the landscape determinants of species distributions.

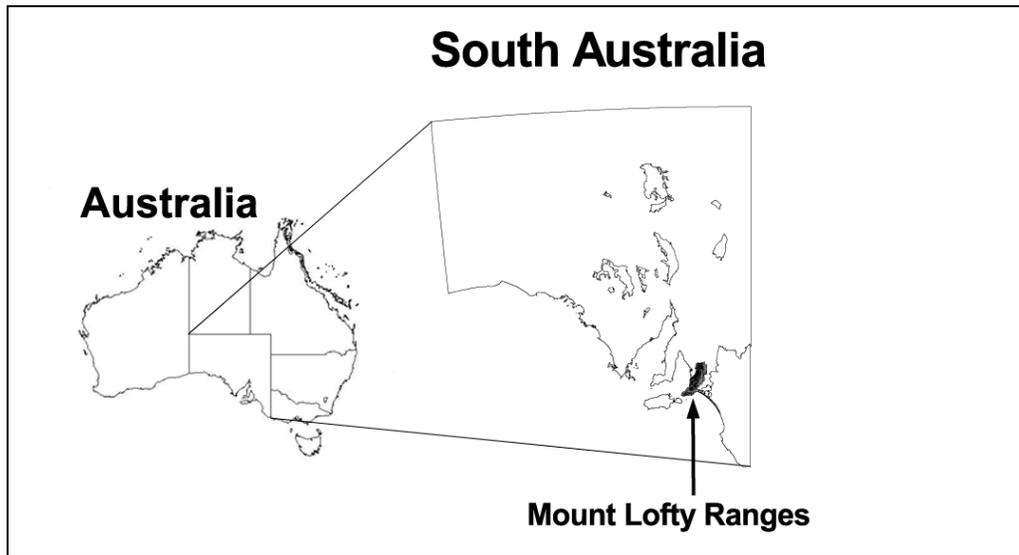
Unlike previous studies, we have used the techniques of Akaike Information Criterion (AIC) and the Receiving Operator Characteristic (ROC) for model selection and discrimination, respectively. Because of the large spatial scale over which the bird survey data were collected, the analysis was not amenable to the inclusion of patch-level variables; that is, the survey data were from searched areas larger than one patch. Our first goal was to determine if they landscape variables alone could explain the species distributions adequately. Secondly, we sought to determine the relative importance of area measures versus landscape configuration variables in determining the species occupancy.

## **METHODS**

### *Study Site*

The Mount Lofty Ranges (MLR) of South Australia is a relatively high rainfall (400 mm/yr – 1100mm/yr) region, amidst semi-arid land (Figure 1). Of a total 500,000 ha., only about 16% is covered by native vegetation with an understory, primarily eucalypt woodland (particularly *Eucalyptus baxteri*, *Eucalyptus fasciculosa*, *Eucalyptus leucoxylon*, *Eucalyptus obliqua*, *Eucalyptus riminalis*) in a matrix of mixed agricultural land, including pasture, cropland, vineyards, and orchards (Bryan 2000). There are a total of about 4,000 native woodland patches (mean =13.1 ha, standard deviation of 26.5

ha.) in the MLR. The region is a ‘biological island’, and using atlas data, we have defined 37 woodland bird species as having populations that are isolated or partially isolated from their nearest populations outside the MLR (Paton et al. 1994).



**Figure 1.** The study site in Australia.

### *Bird distribution data*

In 1984-85, the South Australian Ornithological Association conducted an intensive survey of birds in Adelaide region of South Australia, including the MLR (Paton et al. 1994). The basic survey method involved overlaying the region with a grid having squares of 10,000 yrd x 10,000 yrd, in agreement with a previous Royal Australasian Ornithologists Union atlas undertaken in 1974-75, and surveying at least one point in each grid cell. In all, the Adelaide region bird atlas included of 268 grid squares, over 1700 survey points, 6000 individual surveys, and 100,000 observations. In some

cases, the survey points noted represented a center point of perhaps an area of 5-6 km. x 5-6 km that was searched, and in other cases, they reflect a much more localized area. Though variation was evident in the number of surveys per point and in the effective survey area for each point, there is assumed to be no systematic variation across the region. The accuracy of the coordinates is probably within 1-2 minutes of latitude and longitude (D. Paton, pers. comm.). The observers recorded all species that were seen or heard during the census. Using the boundaries of the MLR as defined hydrologically by Bryan (2000), we selected only those survey points having native vegetation within a distance of 2 km. in order to keep the sample size constant among all models at the three scales. There are 499 survey points for the MLR region (Figure 2). We considered a species present at a survey point if it was recorded there during at least one survey over the two years of the bird atlas study. We employed a Geographic Information System (GIS) of the vegetation in the region, which was compiled by the South Australia Department of Environment and Heritage in 1986 using aerial photographs and ground surveys.

# Mount Lofty Ranges

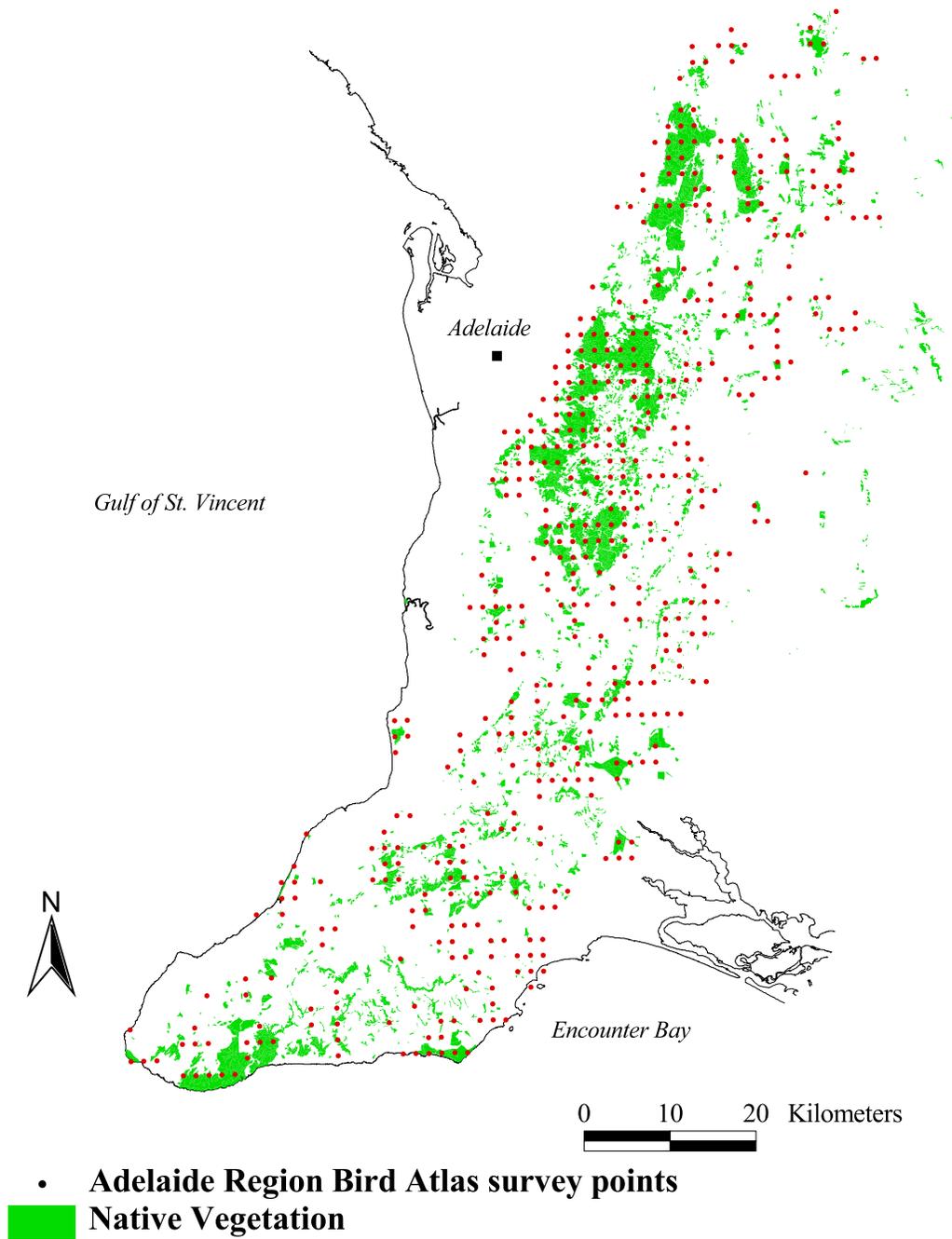


Figure 2. The Mount Lofty Ranges native vegetation and location of bird atlas survey points.

## *Landscape Metrics*

We created buffered areas with radii of 2, 5, and 10 km. around each survey point and intersected those areas with the native vegetation coverage, using the Avenue scripting language in ArcView 3.2a (ESRI Inc. 2000). That is, we selected “minilandscapes” around each survey point at various scales for later characterization with the landscape metrics. We considered a binary landscape (either native vegetation or not) and did not more finely delineate the various native vegetation types. We used Patch Analyst, an extension in ArcView 3.x (Elkie et al. 1999), to calculate some standard FRAGSTATS metrics (McGarigal and McComb 1995) for the buffered areas around each point: total landscape area of native vegetation (TLA), mean perimeter area ratio of patches (MPAR), mean nearest neighbor distance (edge to edge) of patches (MNN), and landscape shape index (LSI), which is a measure of the total native vegetation-matrix edge in the landscape. LSI is the amount of edge in the landscape divided by the square root of area and adjusted for the vector form of the coverage. It equals 1.0 when the landscape consists of just one circular patch. It increases without bound as the landscape shape becomes more irregular or as the number of patches increases (McGarigal and McComb 1995). The scale of the survey area was larger than a single patch, so we ignored the patch-specific measures and included only the landscape metrics, which are measures of mean values in the buffered landscapes. We did not have much confidence in the mapping of broad vegetation community classes, and we did not have data on fine-scale vegetation features that may be important (e.g. vegetation structure, nectar sources, disturbance history, amount of non-native weeds, etc.) (Neave

et al. 1996). Over this spatial scale, climatic variables would probably be poor explanatory variables. In a study in open eucalypt forest in southeastern Australia over a much larger spatial scale, Neave et al. (1996) found that out of seven species modeled, only one species had distribution best explained by climatic variables.

In order to remove correlations between the metrics, we performed simple linear regression (S-Plus 4.5, MathSoft Inc., 1998) (Trzcinski et al. 1999). Though LSI is adjusted for the total landscape area, we nonetheless regressed it by TLA and used the residuals as the adjusted measure of LSI (fragmentation). We then regressed MPAR and MNN separately by TLA and the adjusted LSI and used the residuals as adjusted measures of MPAR and MNN. We also tried regressing instead MAPR by the three other variables and taking the residuals as a measure of MPAR (and such removing the tiny correlation between MPAR and MNN –  $r < 0.4$  for all three distance classes), but this did not qualitatively change the results. Thus, our four explanatory variables (TLA, LSI, MPAR, MNN) are completely uncorrelated with each other.

### *Logistic Regression Models and AIC*

We used the landscape metrics as explanatory variables in logistic regression analyses of bird species occupancy for the survey points in the MLR. We considered only species that are isolated or partially isolated in the MLR (based on Paton et al. (1994) and expert opinion of HP as to whether there is significant dispersal between the populations within and outside the MLR) and present in at least 5% of the sites. This gives a total of 31 species (Table 2).

Species	Presences (out of 499)
Striated Thornbill, <i>Acanthiza lineata</i>	250
Brown Thornbill, <i>Acanthiza pusilla</i>	151
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	112
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	165
Little Wattlebird, <i>Anthochaera chrysoptera</i>	64
Sulfur-crested Cockatoo, <i>Cacatua galerita</i>	86
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	119
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	130
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	30
Brown Treecreeper, <i>Climacteris picumnus</i>	27
White-winged Chough, <i>Corcorax melanorhamphos</i>	34
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	200
Laughing Kookaburra, <i>Dacelo novaeguineae</i>	237
Crested Shrike-tit, <i>Falcunculus frontatus</i>	69
Musk Lorikeet, <i>Glossopsitta concinna</i>	101
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	228
Superb Fairy-wren, <i>Malurus cyaneus</i>	183
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	161
Red-browed Finch, <i>Neochmia temporalis</i>	130
Golden Whistler, <i>Pachycephala pectoralis</i>	199
Spotted Pardalote, <i>Pardalotus punctatus</i>	55
Scarlet Robin, <i>Petroica multicolor</i>	192
Brush Bronzewing, <i>Phaps elegans</i>	25
New Holland Honeyeater, <i>Phylidonyris novaehollandiae</i>	160
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	207
Adelaide Rosella, <i>Platycercus elegans</i>	215
Eastern Rosella, <i>Platycercus eximius</i>	35
Grey Fantail, <i>Rhipidura fuliginosa</i>	238
White-browed Scrubwren, <i>Sericornis frontalis</i>	135
Grey Currawong, <i>Strepera versicolor</i>	210
Rainbow Lorikeet, <i>Trichoglossus haematodus</i>	158

**Table 2.** Isolated or partially isolated bird species in the Mount Lofty Ranges with presences  $\geq$  5% of survey points

Some other species with isolated or partially isolated populations, such as the Beautiful Firetail (*Stagonopleura bella*), Chestnut-rumped Hylacola (*Sericornis pyrrhopygii*), Tawny-crowned Honeyeater (*Phylidonyris melanops*), Black-chinned Honeyeater (*Melithreptus gularis*), Bassian thrush (*Zoothera lunulata*), and Diamond Firetail (*Stagonopleura guttata*) were simply recorded at too few points. Though a model with

so few presences may actually discriminate well between species presences and absences, the small data set may not be representative of the species as a whole.

We evaluated all possible combinations of the four explanatory variables in the logistic regression, modeling the three distance scales separately. This gives a total of 45 models for each species (15 models for each distance scale). We did not consider interactions among the variables. We fitted the generalized linear models (GLM) using S-Plus 4.5 (MathSoft Inc., 1998).

We evaluated the spatial autocorrelation of both the independent and dependent variables with Mantel tests (Fortin and Gurevitch 1993, Legendre 1993, Koenig and Knops 1998, Koenig 1999). Mantel tests evaluate the similarity between a matrix of ecological distance (1 – similarity in some ecological variable) and the matrix of geometric distance. If spatial autocorrelation exists, then the closer points are in geometric space, the more similar should the values be of some ecological variable. The ecological distance for the response variable (species presence and absence) was calculated using the Jaccard similarity index, which measures the similarity in species assemblages among survey sites (Legendre and Legendre 1983). Likewise, for all the independent variables (the landscape metrics) combined, we calculated the Gower similarity index between all pairs of sites (Legendre and Legendre 1983). In both cases, we found spatial autocorrelation, which is not surprising, given that the neighborhoods around nearby survey points overlap in some cases. In the original bird atlas, the extent of this has not been documented very well. This is an often intractable problem when historical data is appropriated for a later uses. However, spatial autocorrelation does not affect the relative influence of the explanatory variables (Trzcinski et al. 1999). In this

case, spatial autocorrelation simply inflates the sample size. Here we are not using traditional significance tests of the Fisherian/inferential statistics paradigm to evaluate models, but AIC values, which do not depend on sample size. Since the survey points are rather evenly distributed across the landscape, the spatial autocorrelation does not bias the contribution of certain survey points. If some of the survey points were clumped, then spatial autocorrelation would be problematic, and the weightings of those points would have to be altered in the regression.

We employed the Akaike Information Criterion (AIC) to select the best models. The AIC has its roots in Kullback-Leibler (KL) information and statistical maximum likelihood (Burnham and Anderson 1998, Anderson et al. 2000, Burnham and Anderson 2001). The value for AIC is,

$$\text{AIC} = -2 \ln(\ell(\hat{\theta} | data)) + 2k \quad (1)$$

where  $\ln(\ell(\hat{\theta} | data))$  is the value of the maximized log-likelihood over the unknown parameters ( $\theta$ ), given the data and the model, and  $k$  is the number of model parameters. It is insufficient to simply select the model with the lowest AIC value. Other models may have AIC values very close to that of the best model, and the model selection uncertainty cannot be ignored. The evidence for each alternative model can be determined by evaluating the difference between model AIC and the minimum AIC,

$$\Delta_i = \text{AIC}_i - \text{minAIC} \quad (2)$$

The larger the  $\Delta_i$ , the smaller the likelihood of that model being the best model in the set of candidate models considered. Models having  $\Delta_i \leq 2$  can be considered as having

substantial support as candidate models (Burnham and Anderson 1998, Anderson et al. 2000, Burnham and Anderson 2001).

Alternatively, one can use Akaike weights,  $w_i$ , as indicators of the strength of evidence for the  $i$  model,

$$w_i = \frac{\exp\left(\frac{-\Delta_i}{2}\right)}{\sum_{r=1}^R \exp\left(\frac{-\Delta_r}{2}\right)} \quad (3)$$

The  $w_i$  can be interpreted approximately as the probability that model  $i$  is the best K-L model in the set of  $R$  models being considered (Burnham and Anderson 1998, Anderson et al. 2000, Burnham and Anderson 2001). We determined a set of plausible candidate models for each species by including only those with  $w_i \geq 0.1$ , which is comparable to the  $\Delta_i$  criterion above. Using AIC has many advantages over traditional inferential statistics, most notably its ability to address model selection uncertainty. Inferential statistics can only compare two models at a time, while AIC methods allow one to simultaneously evaluate a whole suite of candidate models. Like Bayesian statistics, it is rooted in the more intellectually robust and practically relevant idea of multiple working hypotheses, instead of a single null vs. alternative hypothesis. This paradigm of multiple working hypotheses is more easily amenable to the communication with the public and thus is more useful in applied ecology and environmental science. Anderson et al. (2000) give an exegesis of the problems related to  $p$ -values and hypothesis testing of traditional inferential statistics, including: the misinterpretation of the meaning of a  $p$ -value, the  $\alpha$ -level is without theoretical basis, the creation of “strawman” null hypotheses, and the fact that a  $p$ -value is explicitly conditional on the null hypothesis and is dependent on the

sample size. For logistic regression, traditional likelihood ratio tests can only compare nested models, while AIC does not have this limitation (Burnham and Anderson 1998, Anderson et al. 2000, Burnham and Anderson 2001).

### *Model Validation*

There are two different aspects of model validation. Discrimination refers to the ability of the model to distinguish between occupied and unoccupied sites, while calibration describes the agreement between the model predictions and actual observations (Pearce and Ferrier 2000). A model could predict the probabilities well in a relative sense (discrimination) but not in an absolute sense (calibration). Here we are concerned with the ability of the model to differentiate between presences and absences, so we only consider model discrimination.

Traditional measures of model discrimination capacity depend on an arbitrary cutoff for translating the predicted probabilities into presence or absence, often 0.5 (Pearce and Ferrier 2000). The choice of the cutoff depends on whether one wants to minimize the number of false positives or false negatives. For instance, using logistic regression to select reintroduction sites for an endangered species requires a high threshold probability in order to minimize the failure of reintroduction and reduce the number of false positives, the sites erroneously predicted to be suitable habitat. However, using logistic regression to model habitat selection in an area proposed for development requires a low threshold probability to be precautionary about a species occurrence across the landscape and minimize the number of false negatives. Moreover, typical measures

of model performance using specificity (proportion of predicted negatives to true negatives) and sensitivity (proportion of predicted positives to true positives) may be misleading if the species occurs at almost all or none of the sites, as the accuracy measure is sensitive to the frequency of the species occurrence in the test sample (Pearce and Ferrier 2000)

One threshold independent discrimination method is the Receiver Operating Characteristic (ROC) curve, which involves plotting each pair of true positive and false positive proportions for every possible decision threshold between 0 and 1 (Fielding 1997, Elith 2000, Pearce and Ferrier 2000). The area under the ROC curve can be roughly interpreted as the probability that a model will correctly distinguish a true presence and a true absence drawn at random (Pearce and Ferrier 2000). A value of 0.5 indicates that the model is no better than random. We computed the ROC value for every candidate model for each species, using the jackknifed original data (S-Plus 4.5, MathSoft Inc., 1998).

## **RESULTS**

Tables 3 and 4 show the results of the logistic regression analyses for 25 species which had models with Akaike weights greater than 0.1 and ROC values greater than 0.60. This latter value is arbitrary and we could apply a more stringent criterion for model discrimination, but our goal is primarily inference as opposed to model development for prediction. Species consistently responded positively to the total area of native vegetation, while the responses to the other configuration measures were quite

variable. Based only on the model with the highest Akaike weight for each species, 22 species responded positively to landscape area, while only three responded negatively. If one includes the candidate models for each species with Akaike weights greater than 0.1, then 17 and 8 species responded positively and negatively, respectively, to fragmentation. The converse is true for mean patch shape and mean patch isolation. Considering all candidate models, then 16 and 18 species responded negatively to landscape with highly linear patch shapes and high isolation, respectively, while 9 and 5 responded positively to landscapes with those characteristics. More species responded better to landscape metrics at the 2 km. scale than the larger distance scales, as is evidenced by which models have the highest Akaike weights.

The distribution of the Crested Shrike-tit showed no landscape effects, and the best model was derived by fitting simply a random explanatory variable. No models for the Sulphur-crested Cockatoo, Laughing Kookaburra, Little Wattlebird, Rainbow Lorikeet, and Superb Fairy-wren had ROC values greater 0.60, indicating that landscape metrics alone for these species are insufficient to explain their distributions.

Species	km.	Candidate Models	$\Delta AIC$	$w$	ROC
Striated Thornbill	2	<b>TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.45</b>	<b>0.67</b>
	2	TLA+LSI	1.63	0.20	0.67
	2	TLA+LSI+MNN-MPAR	1.79	0.19	0.67
Brown Thornbill	2	<b>TLA+LSI-MNN-MPAR</b>	<b>0.00</b>	<b>0.66</b>	<b>0.67</b>
	2	TLA-MNN-MPAR	2.35	0.20	0.67
Buff-rumped Thornbill	2	<b>TLA</b>	<b>0.00</b>	<b>0.22</b>	<b>0.65</b>
	2	TLA-MPAR	0.31	0.19	0.64
	2	TLA-LSI	1.02	0.13	0.62
	2	TLA-LSI-MPAR	1.37	0.11	0.63
Eastern Spinebill	2	<b>TLA+LSI-MNN-MPAR</b>	<b>0.00</b>	<b>0.48</b>	<b>0.68</b>
	2	TLA+LSI-MPAR	0.29	0.42	0.68
Fan-tailed Cuckoo	5	<b>TLA+MNN</b>	<b>0.00</b>	<b>0.17</b>	<b>0.70</b>
	2	TLA+LSI-MPAR	0.15	0.15	0.72
	2	TLA-MPAR	0.54	0.13	0.73
	5	TLA+MNN-MPAR	0.97	0.10	0.70
Y.t. Black-Cockatoo	5	<b>TLA+LSI</b>	<b>0.00</b>	<b>0.35</b>	<b>0.70</b>
	5	TLA+LSI+MNN	1.46	0.17	0.70
	5	TLA+LSI-MPAR	2.00	0.13	0.69
Sh. Bronze-Cuckoo	5	<b>TLA+LSI</b>	<b>0.00</b>	<b>0.35</b>	<b>0.68</b>
	5	TLA+LSI-MNN	1.88	0.14	0.68
	5	TLA+LSI+MPAR	1.96	0.13	0.67
Brown Treecreeper	2	<b>TLA-LSI</b>	<b>0.00</b>	<b>0.37</b>	<b>0.75</b>
	2	TLA-LSI-MPAR	0.54	0.28	0.74
	2	TLA-LSI+MNN	2.00	0.14	0.73
	2	TLA-LSI+MNN-MPAR	2.54	0.10	0.73
W.w. Chough	5	<b>TLA-MNN-MPAR</b>	<b>0.00</b>	<b>0.25</b>	<b>0.74</b>
	10	-LSI	0.83	0.16	0.72
W.t. Treecreeper	5	<b>TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.32</b>	<b>0.78</b>
	5	TLA-LSI+MPAR	0.48	0.26	0.78
	2	TLA+LSI-MNN-MPAR	1.36	0.16	0.78
	2	TLA+LSI-MNN-MPAR	1.91	0.13	0.78
Musk Lorikeet	5	<b>-LSI+MPAR</b>	<b>0.00</b>	<b>0.49</b>	<b>0.67</b>
	5	-TLA-LSI+MPAR	1.64	0.21	0.66
	5	-LSI+MNN+MPAR	1.71	0.21	0.67
Y.f. Honeyeater	2	<b>TLA-MNN-MPAR</b>	<b>0.00</b>	<b>0.31</b>	<b>0.71</b>
	2	TLA-MNN	1.13	0.17	0.71
	2	TLA+LSI-MNN-MPAR	1.55	0.14	0.70

\*Only models with Akaike weights greater than 0.1 and ROCs higher than 0.6 are shown. The bold type indicates the model with the highest Akaike weight. The sign refers to how the species responds to that landscape characteristic.

**Table 3.** Results of the logistic regression analyses of bird species

Species	km.	Candidate Models	$\Delta AIC$	$w$	ROC
W.n. Honeyeater	<b>10</b>	<b>TLA+LSI</b>	<b>0.00</b>	<b>0.19</b>	<b>0.68</b>
	10	TLA	0.49	0.14	0.68
	10	TLA+LSI-MNN	1.10	0.11	0.68
Red-browed Finch	<b>5</b>	<b>TLA+MNN</b>	<b>0.00</b>	<b>0.41</b>	<b>0.62</b>
	5	TLA+MNN+MPAR	1.71	0.18	0.61
	5	TLA-LSI+MNN	1.98	0.15	0.61
Golden Whistler	<b>2</b>	<b>TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.66</b>	<b>0.71</b>
	2	TLA+LSI-MNN-MPAR	1.99	0.24	0.71
Spotted Pardalote	<b>10</b>	<b>TLA-LSI</b>	<b>0.00</b>	<b>0.19</b>	<b>0.72</b>
	5	TLA-LSI	0.30	0.16	0.72
	10	TLA-LSI-MNN	0.32	0.16	0.71
	10	TLA-LSI+MPAR	0.50	0.15	0.71
	10	TLA-LSI-MNN+MPAR	0.81	0.13	0.70
Scarlet Robin	<b>2</b>	<b>TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.62</b>	<b>0.76</b>
	2	TLA+LSI-MNN-MPAR	1.53	0.29	0.75
Brush Bronzewing	<b>2</b>	<b>TLA-LSI-MNN-MPAR</b>	<b>0.00</b>	<b>0.44</b>	<b>0.79</b>
	2	TLA-LSI-MPAR	0.95	0.27	0.79
	2	TLA-MNN-MPAR	1.73	0.18	0.76
N.h. Honeyeater	<b>10</b>	<b>-TLA+LSI</b>	<b>0.00</b>	<b>0.31</b>	<b>0.60</b>
	10	-TLA+LSI+MNN	1.21	0.17	0.61
	10	-TLA	1.26	0.16	0.60
Crescent Honeyeater	<b>2</b>	<b>TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.56</b>	<b>0.77</b>
	2	TLA+LSI-MNN-MPAR	0.62	0.41	0.77
Adelaide Rosella	<b>10</b>	<b>-TLA+LSI-MPAR</b>	<b>0.00</b>	<b>0.48</b>	<b>0.64</b>
	10	-TLA+LSI+MNN-MPAR	1.40	0.24	0.64
	10	-TLA+LSI	1.95	0.18	0.63
Eastern Rosella	<b>10</b>	<b>TLA-MNN+MPAR</b>	<b>0.00</b>	<b>0.26</b>	<b>0.72</b>
	10	TLA-MNN	0.25	0.23	0.72
	10	TLA-LSI-MNN+MPAR	1.27	0.14	0.69
	10	TLA-LSI-MNN	1.61	0.12	0.68
Grey Fantail	<b>10</b>	<b>TLA+LSI</b>	<b>0.00</b>	<b>0.46</b>	<b>0.70</b>
	10	TLA+LSI+MNN	1.12	0.27	0.70
	10	TLA+LSI-MPAR	1.98	0.17	0.70
W.b. Scrubwren	<b>2</b>	<b>TLA+LSI-MNN</b>	<b>0.00</b>	<b>0.53</b>	<b>0.79</b>
	2	TLA+LSI-MNN-MPAR	0.36	0.45	0.79
Grey Currawong	<b>2</b>	<b>TLA+LSI-MNN-MPAR</b>	<b>0.00</b>	<b>0.54</b>	<b>0.76</b>
	2	TLA+LSI-MPAR	1.15	0.31	0.77
*Only models with Akaike weights greater than 0.1 and ROCs higher than 0.6 are shown. The bold type indicates the model with the highest Akaike weight. The sign refers to how the species responds to that landscape characteristic.					

**Table 3 cont.**

Species	AREA	FRAG	PISOLATE	PSHAPE
Striated Thornbill, <i>Acanthiza lineata</i>	++	++	+	--
Brown Thornbill, <i>Acanthiza pusilla</i>	++	++	--	--
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	++	-	-	-
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	++	++	--	--
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	++	+	++	-
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	++	++	+	-
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	++	++	-	+
Brown Treecreeper, <i>Climacteris picumnus</i>	++	--	+	-
White-winged Chough, <i>Corcorax melanorhamphos</i>	++	-	--	--
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	++	++	-	--
Musk Lorikeet, <i>Glossopsitta concinna</i>	-	--	+	++
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	++	+	--	--
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	++	++	-	
Red-browed Finch, <i>Neochmia temporalis</i>	++	-	++	+
Golden Whistler, <i>Pachycephala pectoralis</i>	++	++	-	--
Spotted Pardalote, <i>Pardalotus punctatus</i>	++	--	-	+
Scarlet Robin, <i>Petroica multicolor</i>	++	++	-	--
Brush Bronzewing, <i>Phaps elegans</i>	++	--	--	--
New Holland Honeyeater, <i>Phylidonyris novaehollandiae</i>	--	++	+	
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	++	++	-	--
Adelaide Rosella, <i>Platycercus elegans</i>	--	++	+	-
Eastern Rosella, <i>Platycercus eximius</i>	++	-	--	++
Grey Fantail, <i>Rhipidura fuliginosa</i>	++	++	+	-
White-browed Scrubwren, <i>Sericornis frontalis</i>	++	++	--	-
Grey Currawong, <i>Strepera versicolor</i>	++	++	--	--
*The sign refers to how the probability of occupancy for that species varies with each landscape characteristic. Double marks refer to responses from the best model, while single marks include all candidate models.				

**Table 4.** Summary of the effects of area, fragmentation, patch shape, and patch isolation on the bird species for 25 species having models with sufficient Akaike weights (> 0.1) and discrimination (ROC > 0.6)\*.

## DISCUSSION

The results generally concur with the work of McGarigal and McComb (1995) in finding that area is generally more important than landscape configuration. Of the species that had reasonably discriminating models, all but one had landscape area as an explanatory variable in the candidate model with the highest Akaike weight, while the configuration measures (particularly MPAR and MNN) were not always part of the best candidate model (Tables 3,4). Only three species responded negatively to the area of native vegetation around survey points: the Musk Lorikeet, Adelaide Rosella and the New Holland Honeyeater. Both make extensive use of matrix habitat. The Musk Lorikeet utilizes fruit orchards in the region, and the Adelaide Rosella and New Holland Honeyeater are common in suburban parks and gardens and occur throughout the metropolitan area of Adelaide (Paton et al. 1994).

Most of the species responses positively to area-independent fragmentation. Many of the woodland birds in the MLR are found in small fragments, so this may be indicative of an insensitivity by many species to small patch size and a greater importance on the number of patches in the landscape. Species that responded positively to fragmentation had inconsistent responses to mean patch shape and isolation. The effect of the landscape configurations is a function of the degree of matrix utilization by a species. The type of matrix habitat can mitigate the negative aspects of the configuration of the native vegetation, and our ignoring of the matrix is a limitation of this study. The results illustrate the importance of disentangling the confounding components of what is commonly referred to as fragmentation. The reduction of habitat area often results

simultaneously in more irregular shaped patches, greater patch number and higher patch isolation.

The focus for the Mount Lofty Ranges region should be first to mitigate the effects of habitat loss, but as in Villard et al. (1999), the landscape configuration is quite important for many species. Out of 25 species with sufficient models, 12 species had candidate models suggesting that they may adversely affected by landscapes with high patch isolation and highly linear patches. This is not surprising with native vegetation comprising less than 20% of the region and with a significant proportion of the clearance coming in the last 50 years (Bryan 2000). However, the responses to landscape configuration were quite complex, and it is very difficult to distill any patterns based on taxonomy or natural history.

Some the results may be spurious; underlying habitat variables not measured in this study but which are correlated with the observed landscape metrics may be truly driving the distribution patterns. It is important to be mindful of the fact that habitat clearance in the region has not been a random process. For example, the White-browed Scrubwren prefers dense riparian habitat, and its occurrence in more fragmented areas may reflect the underlying distribution of riparian areas. Moreover, the White-Naped honeyeater, Striated Thornbill, and Spotted Pardalote are often associated with manna gums (*E. viminalis*). It is not surprising that no model explained occupancy patterns for the Sulfur-crested Cockatoo, Crested Shrike Tit, Rainbow Lorikeet and Laughing Kookaburra. These are wide ranging species and probably respond to the landscape at a much greater scale. The presence of riparian areas (with e.g *Eucalyptus camaldensis*) would be the main determinant of the distribution of the Crested Shrike Tit. The tree

density of riparian woodlands seems to be important for Crested-Shrike Tits (Jansen and Robertson 2001). The Superb Fairy wren is rather ubiquitous in eucalypt woodlands and is probably inured to changes in landscape configuration. It probably is most sensitive to microhabitat vegetation variables, such as the presence of shrub cover (Nias 1984, Nias 1986, Neave et al. 1996).

The results illustrate the importance of considering a different landscape scale depending on the species in question. Though a plurality species responded better to landscape metrics at the 2 km. scale (based on which models had the highest AIC and ROC values), many had candidate models at the 5 km. and 10 km. scale, and this may be indicative of the dispersal range of the species. That the 10 km scale had greater explanatory power for the Yellow-tailed Black Cockatoo and the rosellas, is not unexpected since they are large-bodied, vagile species. Cockatoos wander over tens of kilometers during the non-breeding season (Saunders 1977). The New Holland Honeyeater and the White-Naped Honeyeater had candidate models at the 10 km scale as well. Being nectarivorous species, they may track the phenology of their nectar sources (Franklin and Noske 1999). The Crescent and Yellow-faced Honeyeaters may forage over smaller scales, as they responded best at the 2 km. scale.

These results do not indicate the relative importance of landscape variables compared to patch-level variables. Patch-level variables of vegetation type and structure as well as biophysical variables may be quite important explanatory variables. In a review of 61 studies over a wide array of taxa comparing patch-level variables to landscape variables, Mazerolle and Villard (1999) noted that in over 90% studies, patch-level variables were significant predictors of species abundance or presence or

abundance, but that in about 60% of the studies landscape variables were significant predictors. Studies with birds have been rather equivocal. Several have found patch-level variables more important determining factors of species occupancy or abundance (e.g. Berry and Bock 1998, Estades 1999, Mortberg and Wallentinus 2000, Bajema and Lima 2001) while other studies have found landscape variables to be the primary explanatory factors (e.g. Jansson and Agelstam 1999, Saab 1999, Howell et al. 2000, Loyn et al. 2001). In addition, there are interspecific factors. The presence of aggressive honeyeaters, particularly the Noisy Miner (*Manorina melanocephala*) has been shown to be a significant determinant of the bird community in southeastern Australia (Grey et al. 1997, Grey et al. 1998, Ford et al. 2001). Changing landscape structure can alter species interactions (Schmiegelow and Monkkonen 2002), which could affect species distributions. Fragmentation and the changing heterogeneity of the landscape may have synergistic effects on physical, chemical and biotic fluxes that can impinge on species distributions in complex ways (Hobbs 2001). The high model selection uncertainty for many species is probably indicative of the absence of important explanatory variables.

It must be emphasized that response of a species to a landscape with certain mean patch characteristics does not necessarily imply anything about their responses to patch-level variables. Indeed, the classification of species as forest or forest edge species by Howe (1984) is not very informative when making predictions about landscape-level responses. For instance, Howe (1984) classifies the Striated Thornbill, Eastern Spinebill, Brown Treecreeper, White-winged Chough, Red-browed Finch, Scarlet Robin, Adelaide Rosella and Grey Fantail as forest edge species; yet, they have do not respond

concordantly to the landscape-level metrics. This paper is a cautionary note on extrapolating landscape-level responses from assumed patch-specific responses.

Nevertheless, the results do show that landscape variables alone perform reasonably well in explaining the occupancy patterns of many birds in this region, which was the main thesis of this research. In some cases, patch-level variables can be ignored when building models of species distributions. Many species (15 of 25) have models with ROC values greater than 0.7, which indicates good discrimination. Though it would be ideal to test these models with independent data, they simply do not exist for the region. If one were applying these logistic regression models for predictions in landscape planning, then perhaps it would be necessary to only apply with confidence those models with quite high discrimination. Finally, like all logistic regression analyses, there is the implicit assumption that wherever a species occurs it is suitable breeding and not sink habitat (Pulliam 1988, Pulliam 1996). If there is a long relaxation time after habitat loss, for instance, the population dynamics may be nonequilibrium and the distribution may not be static. Spatial autocorrelation exists in the data, which may have confounding effects. The observability among different species varies, and we have not taken into account false negative survey errors (Tyre et al., *in review*).

We have shown how the Akaike Information Criterion can be quite useful in statistical inference. Unlike typical inferential techniques, the AIC approach allows one to select a suite of candidate models for which there is good support from the data. By simply selecting the model with lowest AIC (or using likelihood ratio tests in the Fisherian/inferential paradigm), model selection uncertainty is ignored. Indeed for the Mount Lofty Ranges birds one would come up with different conclusions for some

species if one only selected the best model. In practice, one could be more or less conservative in selecting a set of candidate models, but here we have chosen to err on the side of caution (model probability  $\geq 10\%$ ) in exploring the effects of landscape configuration on species distribution. Both AIC and ROC can be important techniques in the toolkits of landscape ecologists.

In 1991, the Native Vegetation Act of South Australia was passed, which effectively outlawed the further clearance of native vegetation. There is now a great interest in restoring habitat across the region. Since the species' needs in terms of the spatial configuration of habitat are often quite variable, habitat reconstruction in a strictly qualitative or ad hoc manner is generally not biologically effective nor cost efficient. We are in the process of applying these logistic regression functions of the effect of spatial context on species distributions in simulated annealing algorithms (Metropolis et al. 1953, Kirkpatrick et al. 1983, Possingham et al. 2000, McDonnell et al. 2002) to derive optimal landscape reconstruction scenarios for the avifauna in the Mount Lofty Ranges.

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# Chapter 5

## **Optimizing landscape configuration: a case study of woodland birds in the Mount Lofty Ranges, South Australia**

**Michael I. Westphal<sup>§+</sup> and Hugh P. Possingham<sup>+\*</sup>**

<sup>§</sup>Department of Environmental Science, Policy and Management, University of  
California, Berkeley, CA 94720, U.S.A.

<sup>+</sup>The Ecology Centre, University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>\*</sup>Department of Mathematics, University of Queensland, Australia

*Mathematics without natural history is sterile, but natural history without mathematics is muddled.*

- John Maynard Smith

## **ABSTRACT**

We formulate the optimal landscape restoration problem for 22 birds in the Mount Lofty Ranges, South Australia and use simulated annealing and an iterative improvement heuristic algorithm to find the efficient solutions for a variety of objective functions and budget sizes. Our analyses provide guidelines on priority sites for revegetation and aspects of landscape configuration for the revegetated patches. This paper represents the first use of decision-theory tools for multi-species, optimal habitat restoration on a real landscape.

## INTRODUCTION

The area of landscape planning and design is increasingly becoming an important topic in conservation biology (Lambeck 1997), as we shift from conservation within parks to that in highly human-modified, multi-use landscapes. One aspect of this is habitat reconstruction or restoration, which besides being important for maximizing biodiversity in its own right can also have ancillary benefits. In Australia, for example, the “ghosts of vegetation clearance past”, such as dryland salinity, affects almost 2.5 million ha and is responsible for an annual cost of \$A 270 million (CSIRO Land and Water 2003). Thus, it is essential that strategic habitat reconstruction be enacted that is both cost effective and efficacious in terms of promoting species conservation.

One way to reconstruct landscapes is to determine the habitat content and context for several key species and restore the landscape according to their needs. Habitat suitability models can be used to glean requirements of minimum patch size, habitat type, and aspects of the landscape configuration (McGarigal and Marks 1995, McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999, Westphal 2003). Traditional population viability analyses (PVAs) can then determine the relative impact of altering the spatial configuration of habitat for each species (Beissinger and Westphal 1998); however with rather large landscapes, the number of permutations is immense. Moreover, it is not very tractable to gather the detailed demographic and dispersal data needed to build PVAs for a whole community of species. For most species, static

distribution data are the best data available. Another approach is to design a landscape for a whole community of species with regard to surrogate landscape measures.

However, a study in a forested region of southeastern Australia has found no general applicability for this approach for large sets of species, due either to the inappropriateness of the measure or the incorrect scale (Lindemayer et al. 2002a). Various bird species in the same study site responded differently to the landscape mosaic, underscoring the need to examine the effects of landscape configuration separately for each species (Lindemayer et al. 2002a). The focal species approach has been promoted for landscape reconstruction, where habitat is created that satisfies the ecological requirements of the most area-limited, resource-limited, dispersal-limited, and process-limited (e.g. fire) species (Lambeck 1997, Watson et al. 2001). However, the underlying theoretical basis for the focal species approach is questionable, and the data needed to adequately select focal species are often lacking (Lindemayer et al. 2002b).

Most fundamentally, the focal species approach and the static measures of landscape configuration have no way of adjudicating among the possible conflicting needs of different species and explicitly including financial costs. This is the utility of a decision-theoretic framework. Decision theory tools, including linear programming, mixed integer programming, and heuristics, have been used to solve spatial problems in natural resource management, most notably for multi-species reserves design (Csuti et al. 1997, Pressey et al. 1997a, Pressey et al. 1997b, McDonnell et al. 2002) and harvest scheduling problems in forestry (Boston 1999, Clark 1999, Hof 2000, Hoganson 2000, Richards 2000, Boston 2001, Kurttila 2001). Some authors have looked at optimal habitat

reservation under hypothetical scenarios with timber harvesting (Haight 1995, Bevers 1999, Loehle 2000), spatial environmental correlation (Hof 1996), or with the incorporation of multi-species population dynamics (Rothley 2002). Forest harvesting decisions in space and time that maximize population size have been explored with a genetic algorithm (Moore 2000).

There have been some studies of single-species habitat reservation on real landscapes. Van Langevelde et al. (2000, van Langevelde 2002) developed models to address the allocation of habitat for the nuthatch, both in terms of enlarging existing sites and adding ‘stepping stones’ between reserves, where there is a competing land use, agriculture. Haight et al. (2001) considered the optimal allocation of resources for the purchase of additional habitat in order to minimize the risk of extinction for the San Joaquin kit fox. Westphal et al. (2003) showed how stochastic dynamic programming can be combined with a Markov chain metapopulation model to explore optimal habitat reconstruction dynamically. However, due to the computation constraints (“curse of dimensionality” - Bellman 1957), this technique is limited by the size of the state space and is only useful for a metapopulation with a relatively small number of patches. Moreover, the underlying population dynamics model is based on the “classical” metapopulation paradigm, where the intrapatch dynamics occur on a much faster time scale than the interpatch recolonization dynamics, and frequent extinction and recolonization events makes the system amenable to patch occupancy population models. This is appropriate for only a small subset of species and is inherently a single-species approach.

In this paper, we provide the first investigation of multi-species optimal habitat reconstruction for a real landscape. Following Possingham and Shea (1999, Possingham et al. 2001), we set up the optimal habitat reconstruction problem in a decision theory framework and show how heuristic algorithms can be used to solve the problem. The steps for the formulation of any decision theory problem are: the description of the system and available management options, the statement of the objective function and constraints, and the selection and execution of the algorithm used to solve the problem. We are focusing on the spatial aspect of the optimal habitat reconstruction problem, and we realize that the site-level problem of facilitating the development of a certain vegetation community composition and structure is the more arduous task.

## **METHODS**

### *Study Site and Species Distribution Models*

The Mount Lofty Ranges (MLR) of South Australia is a relatively high rainfall (400 mm/yr – 1100mm/yr) region of Australia, embedded in a semi-arid region (Figure 1). For the purposes of this study, we use the boundary of the region as defined hydrologically (Bryan 2000). Of a total 500,000 ha, only about 16% is covered by native vegetation. The native vegetation is primarily eucalypt woodland (particularly *Eucalyptus baxteri*, *Eucalyptus fasciculosa*, *Eucalyptus leucoxylon*, *Eucalyptus obliqua*, and *Eucalyptus viminalis*) in a matrix of mixed agricultural land, including pasture, crops,

vineyards, and orchards. The region is a 'biological island', and using atlas data, we defined 37 woodland bird species as having populations that are isolated or largely isolated from their nearest populations outside the MLR (Paton et al. 1994).

# Mount Lofty Ranges Native Vegetation

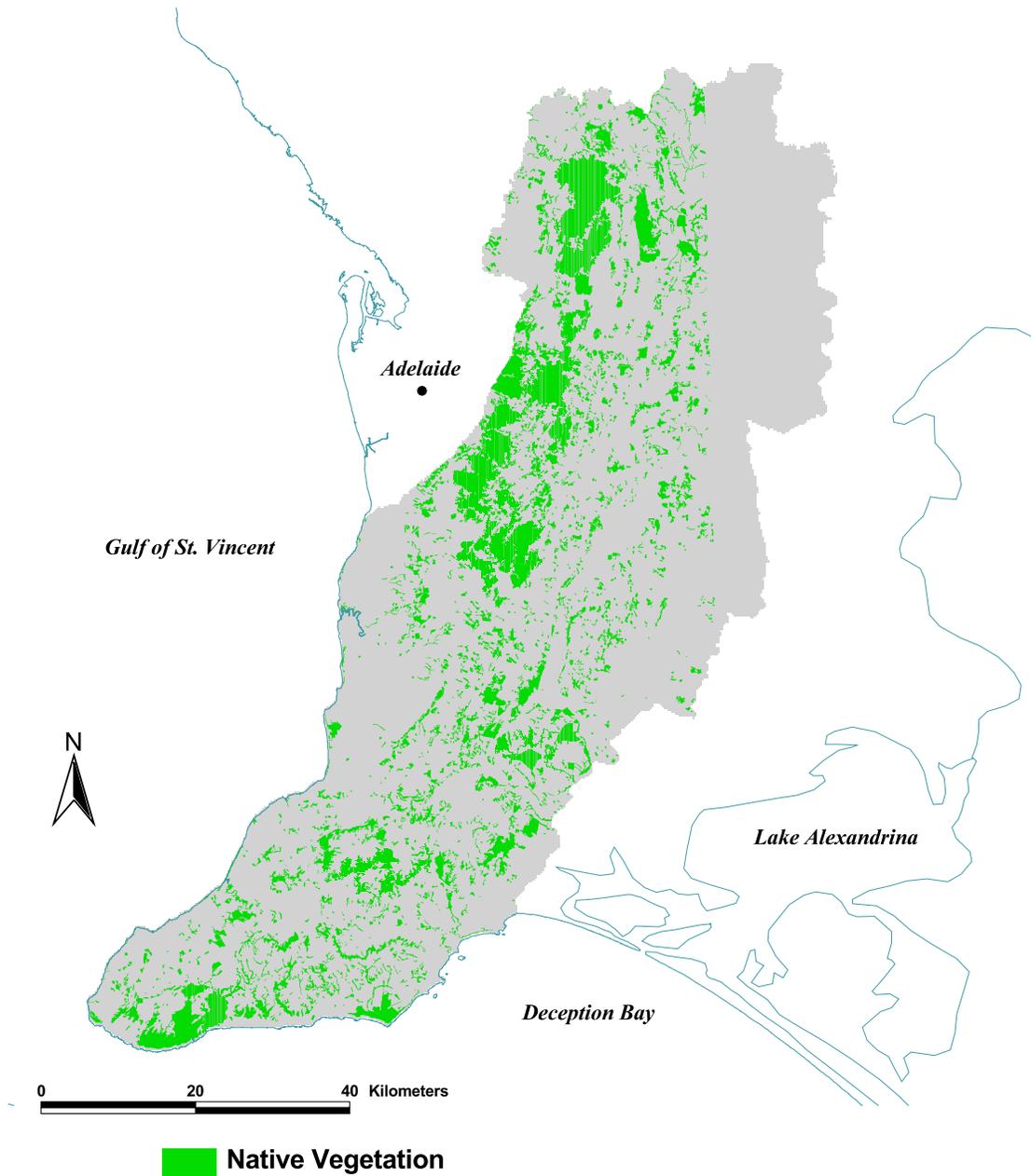


Figure 1. The Mount Lofty Ranges study area.

In 1984-85, the South Australian Ornithological Association conducted an intensive survey of birds in Adelaide region of South Australia, including the MLR (Paton et al. 1994). Using survey data from 499 points in the region, we previously conducted logistic regression analyses on the effects of landscape configuration on the species distributions (Westphal et al. 2003). At scales of 2, 5, 10 km. around the survey points, we used FRAGSTATS metrics as the explanatory variables of presence-absence for each species: total landscape area (TLA), number of patches (NumP), mean patch size (MPS), the size of the largest patch (Lrg), mean nearest neighbor distance (edge to edge) of patches (MNN), and landscape shape index (LSI), which a measure of the total edge in the landscape. Here we refitted the logistic regression models on the raster landscape of the region with a grain cell size of 6.25 ha, the minimum planning unit of interest (Table 1). Two grid cells are assumed to be separate patches if they are connected only by their vertices, but do not share edges. We considered only the 2 km neighborhood scale for computational efficiency. This is the appropriate landscape scale for most species considered (Westphal et al. 2003). We assumed a binary landscape, that is, the vegetation is classified simply as native vegetation or matrix (e.g. pasture, vineyards, orchards, urban areas).

Species	Regression Equation	ROC
Striated Thornbill, <i>Acanthiza lineata</i>	$-1.54 + 0.00205*MPS + 0.531*LSI + 0.00112*Lrg$	0.67
Brown Thornbill, <i>Acanthiza pusilla</i>	$-1.72 - 0.000218*MNN + 0.00303*MPS + 0.356*LSI$	0.65
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	$-1.32 - 0.000218*MNN + 0.00307*MPS$	0.64
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	$-2.97 + 0.00151*TLA - 0.144*NumP + 1.11*LSI$	0.67
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	$-2.54 + 0.00242*TLA + 0.290*LSI$	0.70
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	$-2.17 + 0.140*NumP + 0.00173*Lrg$	0.67
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	$-4.07 + 0.00353*TLA + 0.0906*NumP - 0.00559*MPS$	0.70
Brown Treecreeper, <i>Climacteris picumnus</i>	$-3.48 - 0.0189*TLA + 0.178*NumP + 0.0215*Lrg$	0.73
White-winged Chough, <i>Corcorax melanorhamphos</i>	$-1.53 - 0.00189*TLA - 0.121*NumP - 0.000765*MNN + 0.00525*MPS$	0.64
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	$-2.81 + 0.00942*TLA - 0.138*NumP + 0.845*LSI - 0.00649*Lrg$	0.79
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	$-0.958 + 0.00423*TLA - 0.00306*MPS$	0.71
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	$-2.33 - 0.00161*MPS + 0.516*LSI + 0.00257*Lrg$	0.66
Red-browed Finch, <i>Neochmia temporalis</i>	$-1.80 + 0.00149*TLA + 0.000172*MNN + 0.286*LSI$	0.62
Golden Whistler, <i>Pachycephala pectoralis</i>	$-2.39 + 0.00238*TLA + 0.000157*MNN + 0.535*LSI$	0.70
Spotted Pardalote, <i>Pardalotus punctatus</i>	$-1.66 + 0.00764*TLA - 0.550*LSI - 0.00627*Lrg$	0.67
Scarlet Robin, <i>Petroica multicolor</i>	$-2.87 + 0.783*LSI + 0.00230*Lrg$	0.75
Brush Bronzewing, <i>Phaps elegans</i>	$-3.27 + 0.00257*TLA - 0.119*NumP$	0.77
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	$-2.403 + 0.00297*TLA + 0.565*LSI$	0.76
Adelaide Rosella, <i>Platycercus elegans</i>	$-1.12 - 0.00142*TLA - 0.293*NumP + 1.16*LSI$	0.61
Grey Fantail, <i>Rhipidura fuliginosa</i>	$-2.77 - 0.145*NumP + 0.000223*MNN - 0.00323*MPS + 1.29*LSI + 0.00283*Lrg$	0.64
White-browed Scrubwren, <i>Sericornis frontalis</i>	$-4.69 - 0.117*NumP + 1.49*LSI + 0.00329*Lrg$	0.78
Grey Currawong, <i>Strepera versicolor</i>	$-2.83 + 0.00418*TLA - 0.1948*NumP - 0.00260*MPS + 1.16*LSI$	0.77

**Table 1.** Species included in the optimization and their logistic regression functions.

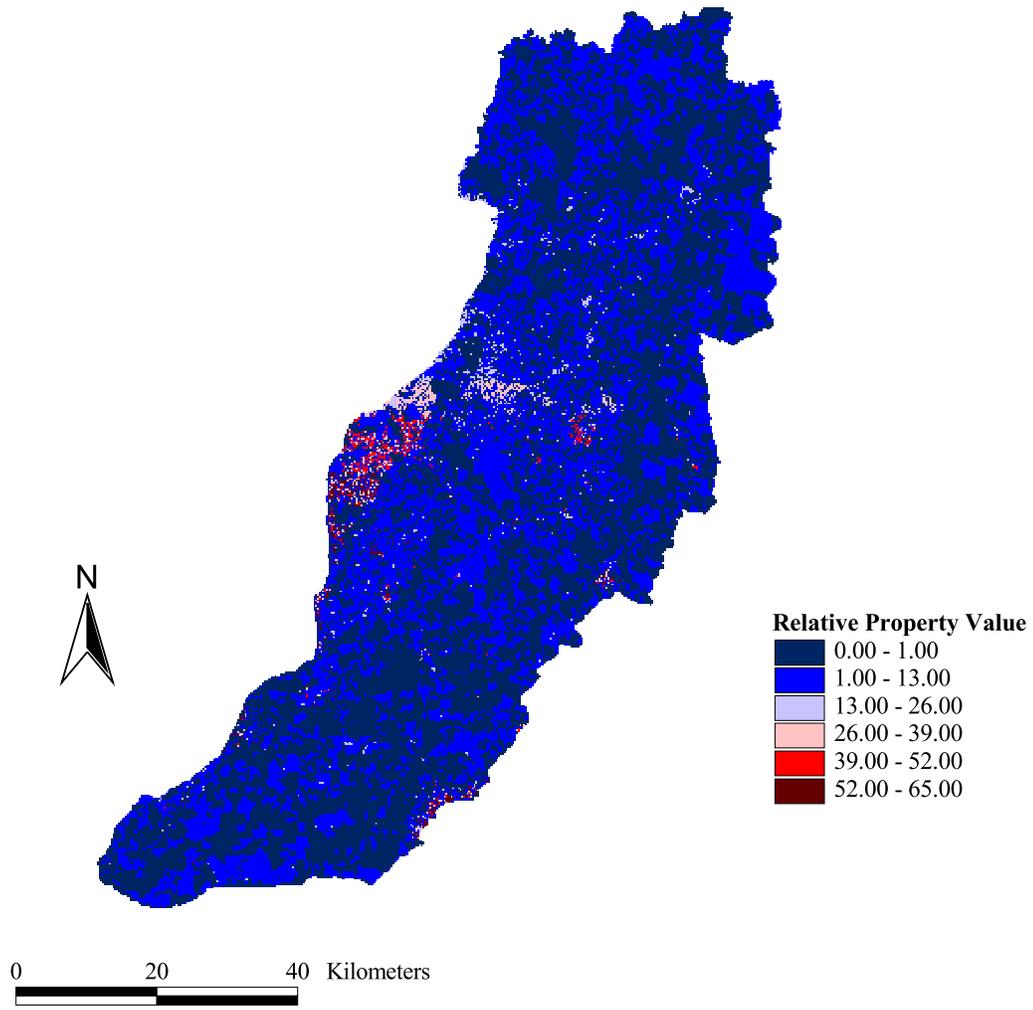
We included a species in our optimization algorithms if its distribution model had a ROC (Receiver Operating Characteristic) area under the curve value exceeding 0.6. ROC is a measure of a model's discrimination, and the area under the curve value is equivalent to the probability that the model can discriminate between a true positive and a true negative value (Hanley and McNeil 1982, Fielding and Bell 1997, Elith 2000, Pearce and Ferrier 2000). A value exceeding 0.6 implies that the model is at least 20% better than random. Since there are no independent data on which to evaluate the models, we have jackknifed the original data. A total of 22 species out of 37 have models with adequate discrimination (Table 1).

The South Australian Department of Environment Heritage and Aboriginal Affairs compiled the vegetation GIS coverage used for the logistic regression analyses in 1986, based on aerial photographs interpretation (1:40000 maps) and extrapolation from point-based sampling. The vegetation remnant comprised about 10% of the study area, according to the original coverage. We used an updated vegetation coverage for the optimization program, based primarily on aerial photographs (1:4000) taken in 2000. Due to a finer minimum mapping unit (1 ha) and more detailed mapping in general, the proportion of native vegetation in the landscape is now calculated to be about 16% of the region, though this may include sites with degraded understories.

We explore both scenarios with equal site costs and variable site costs, and for the latter, the cost of revegetation is assumed to be a linear function of property values. The South Australian Department of Environment and Heritage extrapolated the property value coverage from values assigned by the South Australia Valuer General.

There are a total of 193,239 parcels, with a mean area of 2.92 ha ( $\sigma = 14.92$  ha) (Bagg, *pers. comm.*). We used a vector coverage of land use, compiled by the South Australian Department of Transport, Urban Planning and the Arts in 1991, to exclude sites in our optimization program that are urban areas, reservoirs and quarries. We converted both these vector coverages to rasters (grids) with a 6.25 ha grain size, in accord with the vegetation data. About 10% of the approximately 83,000 sites in the region did not have property value data, so we simply interpolated based on the average of the values within a one-cell neighborhood (Figure 2). The sites with missing property value data are well distributed in the region and are not disproportionately biased to any land use type.

# Mount Lofty Ranges Property Value



**Figure 2.** The relative property value for Mount Lofty Ranges. The value is standardized by dividing the raw value (\$/ha) by the median value.

Given some budget size (either total amount of revegetation area or financial costs), we set our objective to maximize the summed probability of occurrence over all bird species and all revegetated sites in the region, given some budget  $q$ . Let  $\mathbf{y}$  be the original landscape with no revegetation, where each element,  $y_i \in [0, 1]$ . We are considering a binary landscape, where each site is either native vegetation or not. If the site is vegetated, then  $y_i = 1$ , otherwise  $y_i = 0$ . Likewise,  $\mathbf{x}$  is the landscape vector with revegetation added, where each element,  $x_i \in [0, 1]$ . Let  $n$  be the number of species under consideration, and  $m$  the number of sites (grid cells) in the landscape. Our control variable is which sites to select for revegetation. The objective function is:

$$\text{Maximize } V(\mathbf{x}) = \left[ \sum_{j=1}^n \sum_{i=1}^m (x_i - y_i) p_{ij}(\mathbf{x}) \right] - \beta \sum_{i=1}^m (x_i - y_i) B_i \quad (1)$$

$$\text{Subject To: } C(\mathbf{x}) = \sum_{i=1}^m c_i (x_i - y_i) \leq q,$$

where  $p_{ij}(\mathbf{x})$  is the probability that species  $j$  would occur if site  $i$  was revegetated, which is a function of the vector of vegetation sites,  $\mathbf{x}$ ,  $B_i$  is the total edge for site  $i$  (amount of perimeter forming boundary with non-native vegetation),  $\beta$  is a Boundary Length Multiplier, and  $c_i$  is the cost of acquisition and/or revegetation for site  $i$ . The second boundary length term in the maximization can be thought of as a penalty term. The probabilities of occurrence are the fitted probabilities from the logistic regression models (with the range in probabilities standardized from 0.0 to 1.0) and so are calculated from the landscape metrics of the 2 km. neighborhood around and including site  $i$ . We have

chose to weight all species equally. This is our “baseline” scenario.

In the second “threshold” scenario, we have modified the probabilities of occurrence, such that if  $p_{ij}(\mathbf{x}) < 0.3$ ,  $p_{ij}(\mathbf{x}) = 0$ , because low probabilities of occurrence are unlikely to represent high quality habitat. We have considered three budget sizes for both scenarios: 1000, 5000, and 10000 ha. All sites are assumed to have equal costs. For the third and fourth scenarios, we have converted the probabilities to population numbers, with the number of individuals per site the probability of occurrence multiplied by the average density per 2 ha per species found during 2000 field surveys of the MLR (Table 2). It may be more realistic to have the population density modify the objective function in non-linear fashion. In the third “saturating” scenario, we have fitted the Michaelis-Menten function of chemical kinetics to population numbers, assuming the goal is to create habitat for 1000 individuals per species and the half-saturation constant to be 500. Though it will obviously vary from species to species, without any specific information on viability and population densities in the rest of the landscape, 1000 individuals in the revegetated sites is a reasonable goal. The objective function is:

$$\text{Maximize } V(\mathbf{x}) = \left[ \sum_{j=1}^n \left( \frac{\sum_{i=1}^m (x_i - y_i) p_{ij}(\mathbf{x}) d_{ij}}{k_s + \sum_{i=1}^m (x_i - y_i) p_{ij}(\mathbf{x}) d_{ij}} \right) \right] - \beta \sum_{i=1}^m (x_i - y_i) B_i \quad (2)$$

$$\text{Subject To: } C(\mathbf{x}) = \sum_{i=1}^m c_i (x_i - y_i) \leq q,$$

where  $d_{ij}$  is the average density for species  $j$  in site  $i$  (adjusted for the 6.25 ha grain size), and  $k_s$  is the half-saturation constant, which is 500.

Species	Density (Individuals/ 2 ha)
Striated Thornbill, <i>Acanthiza lineata</i>	4.71
Brown Thornbill, <i>Acanthiza pusilla</i>	3.01
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	3.45
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	1.78
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	1.05
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	2.48
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	1.04
Brown Treecreeper, <i>Climacteris picumnus</i>	2.25
White-winged Chough, <i>Corcorax melanorhamphos</i>	4.63
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	1.52
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	2.55
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	2.57
Red-browed Finch, <i>Neochmia temporalis</i>	3.21
Golden Whistler, <i>Pachycephala pectoralis</i>	1.39
Spotted Pardalote, <i>Pardalotus punctatus</i>	1.70
Scarlet Robin, <i>Petroica multicolor</i>	1.35
Brush Bronzewing, <i>Phaps elegans</i>	1.14
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	2.21
Adelaide Rosella, <i>Platycercus elegans</i>	3.68
Grey Fantail, <i>Rhipidura fuliginosa</i>	2.09
White-browed Scrubwren, <i>Sericornis frontalis</i>	3.08
Grey Currawong, <i>Strepera versicolor</i>	1.48

**Table 2.** Average densities for each species from 2000 surveys in the Mount Lofty Ranges.

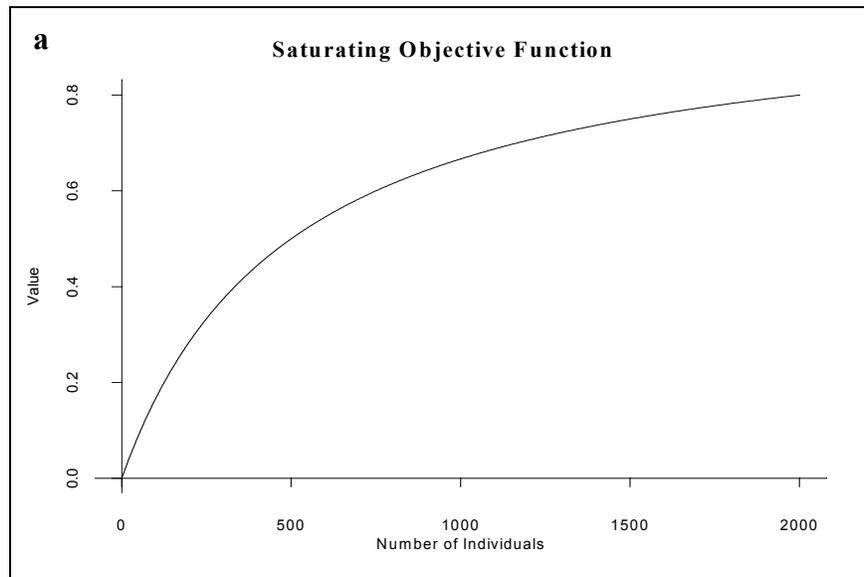
About 103 patches were surveyed using 2 ha area counts. Each sites was visited three times with 3 back-to-back 20-minute counts.

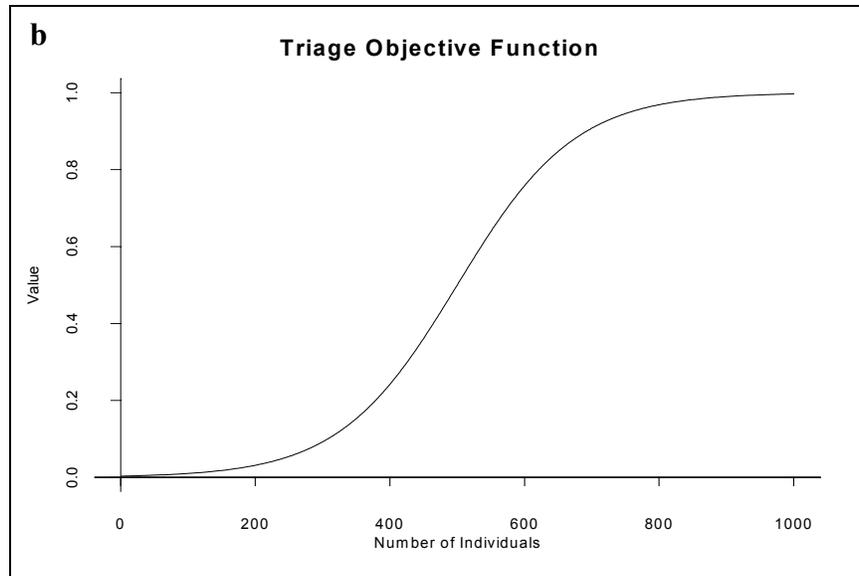
For the fourth, “triage”, scenario we have fitted a sigmoidal curve to the population numbers per species, assuming that our goal is again to achieve 1000 individuals per species and assuming that the utility of the revegetated sites is 0 below 50 individuals. The objective function is:

$$\text{Maximize } V(\mathbf{x}) = \sum_{j=1}^n \left( \frac{1}{1 + \exp \left( a \left( \left( \sum_{i=1}^m (x_i - y_i) p_{ij}(\mathbf{x}) d_{ij} \right) - b \right) \right) \right) - \beta \sum_{i=1}^m (x_i - y_i) B_i \quad (3)$$

$$\text{Subject To: } C(\mathbf{x}) = \sum_{i=1}^m c_i (x_i - y_i) \leq q,$$

where  $a = -1.14 \times 10^{-2}$  and  $b = 500$ . For the two non-linear objective functions, we have only considered the 1000 ha budget size and have assumed that all sites have equal costs (Figure 3).





**Figure 3.** Curves showing the translation of population numbers to value for each species under the a.) saturating (Michaelis-Menten) objective function scenario, and b.) the triage (sigmoidal) objective function scenario.

Lastly, we repeated the 1000 ha “baseline” scenario using property value data. Now the cost of site  $i$ ,  $c_i$ , is the property value (\$/ha), normalized by dividing by the median site value. Property values are an imperfect measure of true revegetation costs, with the true costs of habitat restoration lying somewhere between the equal site cost scenario and the inclusion of property values. Moreover, errors necessarily arise when spatial vector data is converted to raster coverage and there is discordance between the scale of the properties (average size = 2.92 ha.) and the scale of the planning unit used in the optimization (6.25 ha). Thus, we have only used property values as site costs in one scenario, with an “effective” budget size of 1000 ha. The “effective” area of a site is the site area (6.25 ha) multiplied by the site property value, divided by the median property

value.

This optimal landscape restoration problem is akin to the reserve site selection problem, where probabilities of occurrence are used instead of the simple binary presence or absence data (Araujo 2000, Haight 2000, Polasky 2000, Williams 2000, Araujo 2002, Williams 2002). However, here we are interested in strategically adding more habitat to the landscape, instead of preserving existing areas. Moreover, we have the additional complication of the probabilities of occurrence for each species being functions of what neighboring sites are restored, which changes with each iterative alteration of the landscape.

### *The Optimization Algorithm*

This number of combinations for this type of optimization problem (without property values) is:

$$\binom{L}{M} = \frac{L!}{(L-M)!M!} \quad (4)$$

where  $L$  is the number of locations, and  $M$  is the number of elements. The number of available locations,  $L$ , for the MLR is about 70,000. If the budget size is 10000 ha ( $L = 1600$  sites for the equal cost scenario), for example, then the problem is massive:  $\binom{L}{M} = \binom{70000}{1600} \approx 2.74 \times 10^{3310}$ . It is unlikely that a good solution would be found by a simple,

“memory-less” random sampling of the solution space. Moreover, since the probabilities of occurrence of species in any site are dependent upon the sites around it in a highly nonlinear fashion, linear programming techniques (e.g. branch and bound) (Winston 1995) are incapable of finding an optimal solution. Because it is combinatorial optimization problem with integer variables, nonlinear programming (NLP) methods are infeasible (Loehle 2000). The problem is *computationally hard* (a so-called *NP-hard problem*), and as such there are no known *efficient (polynomial time)* algorithms that can solve this problem exactly (Cormen et al. 1990). That is, there are no known algorithms whose solving time is a polynomial function of the problem size. The time to solve these problems is believed to increase exponentially with the problem size (Cormen et al. 1990).

Heuristic algorithms are often used to find near optimal solutions for computationally hard problems. Under certain conditions, it can be shown that they asymptotically approach the global optimum (Sait and Youssef 1999). The heuristic algorithm we have employed is simulated annealing (Metropolis et al. 1953, Kirkpatrick et al. 1983), which has been used quite effectively in reserve design problems (Ball 1999, Possingham et al. 2000, Andelman 2002, McDonnell et al. 2002, Noss 2002) and forest management (Liu 2000, Meilby 2001, Baskent 2002, Ohmann 2002, Von B. W. Chen 2002). It has a “valley jumping” property (Sait and Youssef 1999), meaning that it incorporates a means of occasionally accepting neighboring solutions in the state space that decrease the objective function in order to prevent being trapped in a local optimum. Moreover, it is “blind”, that is, it is not cognizant of when it reaches an optimal or near

optimal solution, and consequently must be told to terminate, at which point, there is no guarantee that a global maximum is reached. The concept of simulated annealing is derived from metallurgy, where a substance is heated and then cooled to obtain a desired crystalline structure. If the reduction in temperature is too rapid, then the metal will not be in the lowest energy state.

To implement this algorithm for our landscape restoration problem, we first select a random restored landscape, and then the algorithm iteratively explores neighboring solutions by randomly adding or deleting sites to the system. Initially, any change is accepted, and as the *temperature* is lowered, the algorithm becomes choosier, rejecting changes that decrease the value of the objective function too much. By the end of the iterations, when the system is “cold”, the algorithm only accepts positive changes. The simulated annealing algorithm for the MLR habitat reconstruction problem is structured as follows:

- I. Set the temperature,  $T$ , which is the acceptance parameter.
- II. Generate a random restoration landscape, excluding those sites that are urban areas, reservoirs or quarries. For every revegetated site, the program searches a neighborhood of 2 km. around it, calculates the landscape metrics, and then determines the probability of occurrence for every species. Summed across all sites, this gives the objective function,  $V(\mathbf{x}_1)$ .
- III. Randomly choose a site to delete from and then add to the landscape. Continue adding random sites, until the cost  $C(\mathbf{x}_2) \geq q$ . Delete sites, until  $C(\mathbf{x}_2) \leq q$ . Evaluate the change in the objective function,  $\Delta V = V(\mathbf{x}_2) - V(\mathbf{x}_1)$ :

- if  $e^{\frac{\Delta V}{T}} >$  uniform random number  $[0, 1]$ , then accept change,  $\mathbf{x}_1 \leftarrow \mathbf{x}_2$
- IV. If the temperature,  $T$ , has not been lowered for  $y$  iterations, reduce the temperature. Otherwise, the temperature remains unchanged.
- V. Go to step III for the set number of iterations or until the  $V(\mathbf{x}_1)$  is not replaced after  $z$  times.

The most critical aspect of the simulated annealing algorithm is the cooling schedule. After initial exploration, we settled on an adaptive cooling schedule modified from Huang et al. (1986). The goal of adaptive annealing is to control the temperature such that the objective function value function increases in a uniform manner. The difference in the average value of two consecutive configurations,  $\bar{V}(T_{k+1}) - \bar{V}(T_k)$ , must be less than the standard deviation of the value at temperature  $T_k$ ,  $\lambda\sigma(T_k)$ , where  $\lambda \leq 1$ . From the annealing curve, the average value versus the logarithm of temperature, Huang et al. (1986) derived the following decrement rule:

$$T_{k+1} = T_k \exp\left(-\frac{T_k \lambda}{\sigma}\right). \quad (5)$$

We set  $\lambda$  to 0.7. The initial temperature,  $T_0$ , equals  $20\sigma$ , calculated from 100 initial random revegetation configurations. This exponential function allows more time to be spent at lower temperatures. To prevent squelching (cooling too quickly and becoming trapped in very suboptimal region of solution space) at high temperatures,  $T_{k+1}$  is never allowed to be lower than  $0.5T_k$ . The number of times spent at each temperature,  $y$ , is set

to 10. Finally, the algorithm terminates if a change is not accepted after 30 iterations ( $z$ ).

We augmented the simulated annealing algorithm with a *deterministic clustering algorithm (iterative improvement)* when it is still “warm”, that is, when the number of accepted moves divided by the total number of moves is 0.8. To reiterate, the ratio of the number of accepted moves to total moves in the early stages of the algorithm is unity. The clustering algorithm randomly selects a revegetated site and, if available, revegetates one of its neighbors and deletes a random site elsewhere if it improves the objective function. It continues the process with the other seven neighbors and then repeats the process with the other original revegetated sites, randomly chosen. The rationale behind this clustering algorithm is that for many species, large contiguous patches are preferred. The clustering algorithm effectively reduces the number of simulated annealing iterations needed. After the clustering algorithm finishes, the simulated annealing algorithm continues until the above termination criterion is satisfied. After the termination of the simulated annealing algorithm, the operation of the clustering algorithm is repeated. This time the algorithm continues to repeat the clustering operation as long as the new objective function is at least 5% better than the original objective function before the clustering. It ignores “tabu” sites evaluated in previous iterations of the clustering algorithm.

To determine a suitable Boundary Length Multiplier,  $\beta$ , we have varied it from zero to the value under each scenario where the boundary length penalty term is double the maximum value of the summed probabilities of occurrence (or population densities) over all species. Since the simulated annealing algorithm is non-deterministic, each run

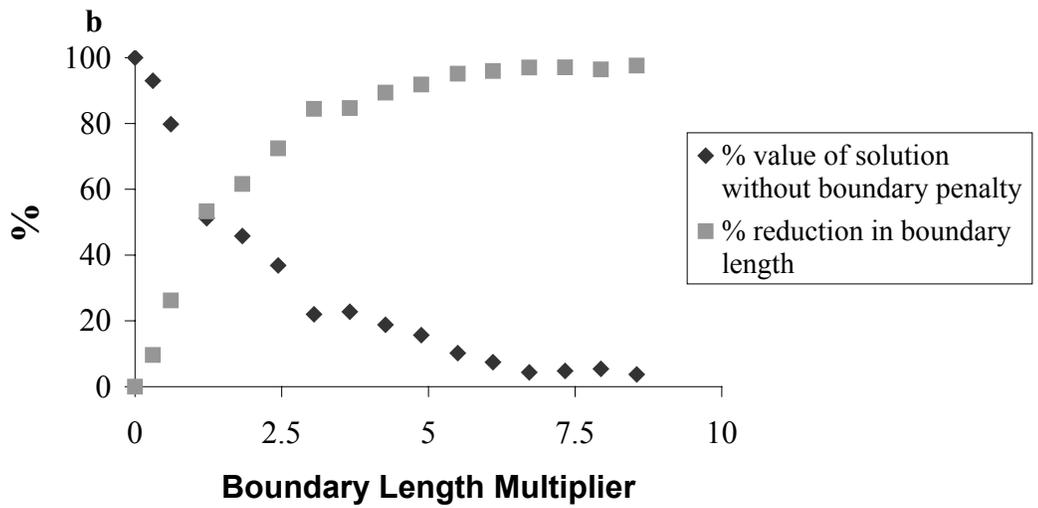
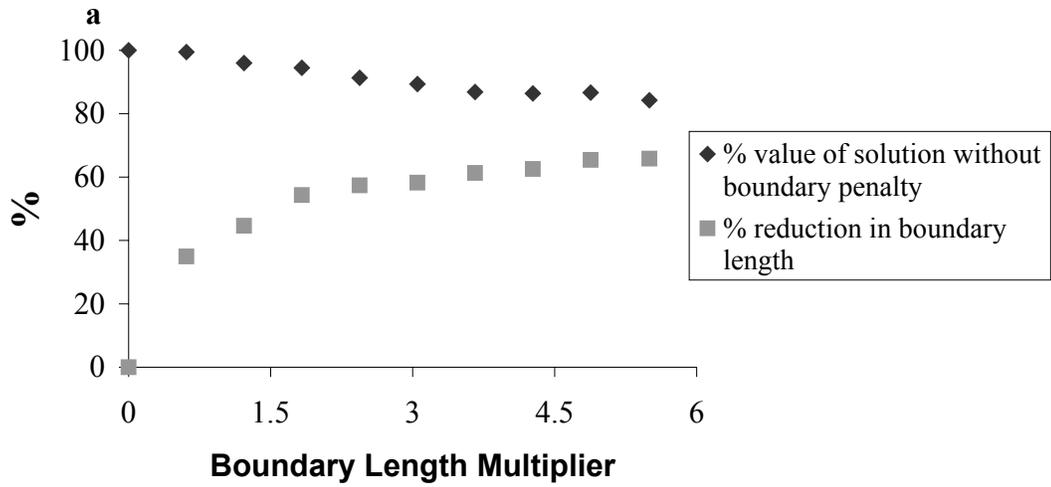
will generate a different solution. For each scenario and budget size, we ran the algorithm 50 times. All aspects of the optimization program, including the calculation of the landscape metrics, the simulated annealing algorithm and the deterministic clustering algorithm, are written in the C programming language. On a Intel Pentium IV processor, the average time to complete each run of the algorithm was 60, 120 and 300 minutes for budget sizes of 1000 ha, 5000 ha and 10000 ha, respectively.

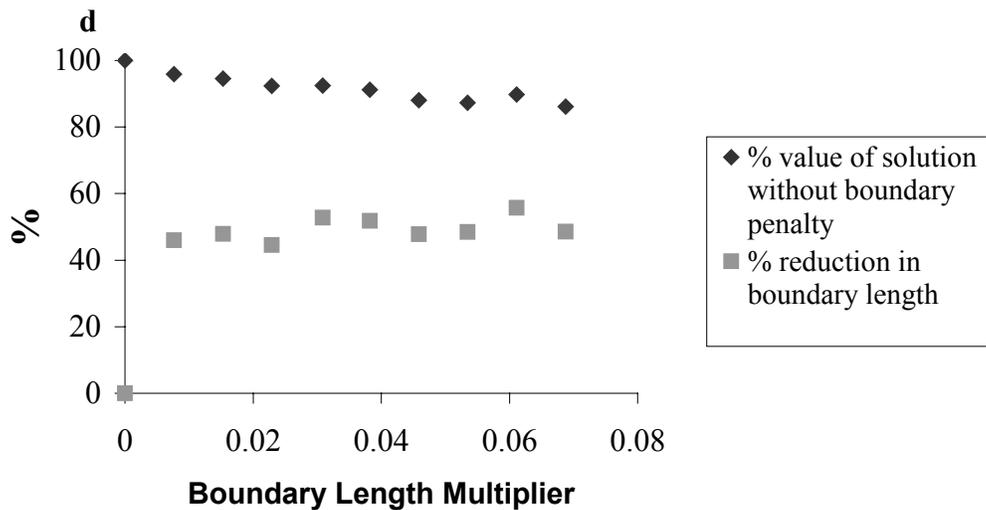
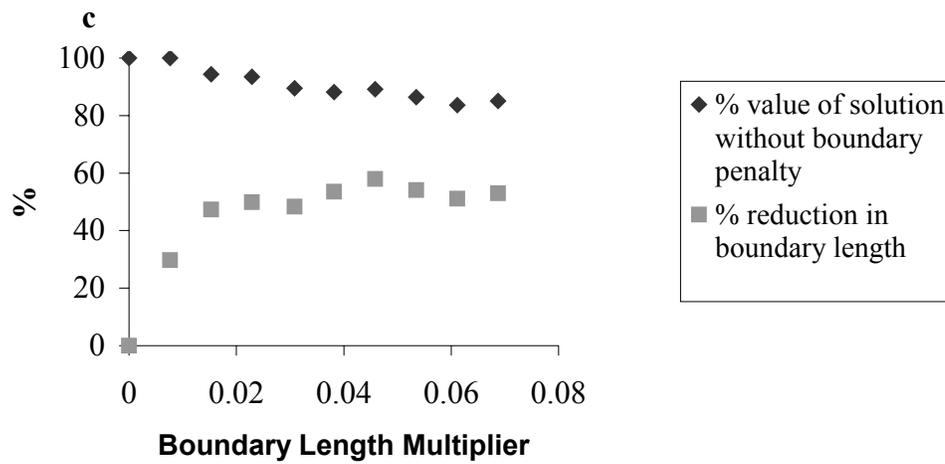
## RESULTS

### *Boundary Length Multiplier*

The tradeoffs between minimizing boundary length and maximizing the value for the four different objective functions are illustrated in Fig. 4. It is desirable to have revegetated sites clustered closer together to reduce management costs. Most species in the MLR respond positively to landscapes with large patch sizes and high connectivity, and these are explicitly incorporated into the species probability of occurrence functions. Thus, the Boundary Length Multiplier is just an augmenting factor, because most species respond positively to revegetated landscapes with small boundary lengths. In all cases, the value of the objective function in the absence of the boundary penalty is a convex, saturating curve as a function of the boundary length penalty multiplier  $\beta$ . For the three equal-cost scenarios, the objective function values declines relatively linearly with increasing Boundary Length Multiplier over the range of values considered, while with

property values included, the objective function value declines almost exponentially. The latter is due to the fact that a large Boundary Length Multiplier results in fewer sites being incorporated into the solution. For the further analyses presented in this paper, we have selected the Boundary Length Multiplier,  $\beta$ , that gives an objective function value that is 90% of the optimal, while also reducing the total boundary length of the revegetated sites by about 50%. The exception to this is under the property value scenario, because the objective function drops off very steeply with an increasing Boundary Length Multiplier. Concomitantly, there is only a very small diminution in boundary length (Table 3). Of course, the exact choice of the Boundary Length Multiplier is the domain of policy and for our purposes fairly arbitrary. It depends on the relative prioritization of maximizing the biodiversity value of the revegetated landscapes versus costs associated with management. We have sought to apply a reasonable rationale.





**Figure 4.** Curves showing the tradeoff between maximizing the objective function and minimizing boundary length for a.) the baseline objective function (10 runs, 5000 ha budget), b.) the baseline objective function with property values (10 runs, 1000 ha effective budget), c.) the triage objective function (10 runs each, 1000 ha), and d.) saturating objective function (10 runs, 1000 ha). The curve for the threshold objective function is the same as Figure 4.a.

Objective Function	Boundary Length Multiplier
Linear	2.44
Threshold	2.44
Linear, property values	0.0
Triage	0.02292
Saturating	0.03820

Table 3. Boundary Length Multipliers used in subsequent analyses for each objective function.

### *Summed Irreplaceability*

One way to distill information on solutions obtained using stochastic algorithms is to show the *summed irreplaceability*, that is, over all runs, how many times a site is selected. Though the probability that any site  $i$  is selected in each run is given by a binomial distribution, according to the *Central Limit Theorem*, the number of selections for each site  $i$  over all  $n$  runs approaches a normal distribution. The *summed irreplaceability* of site  $i$  is:

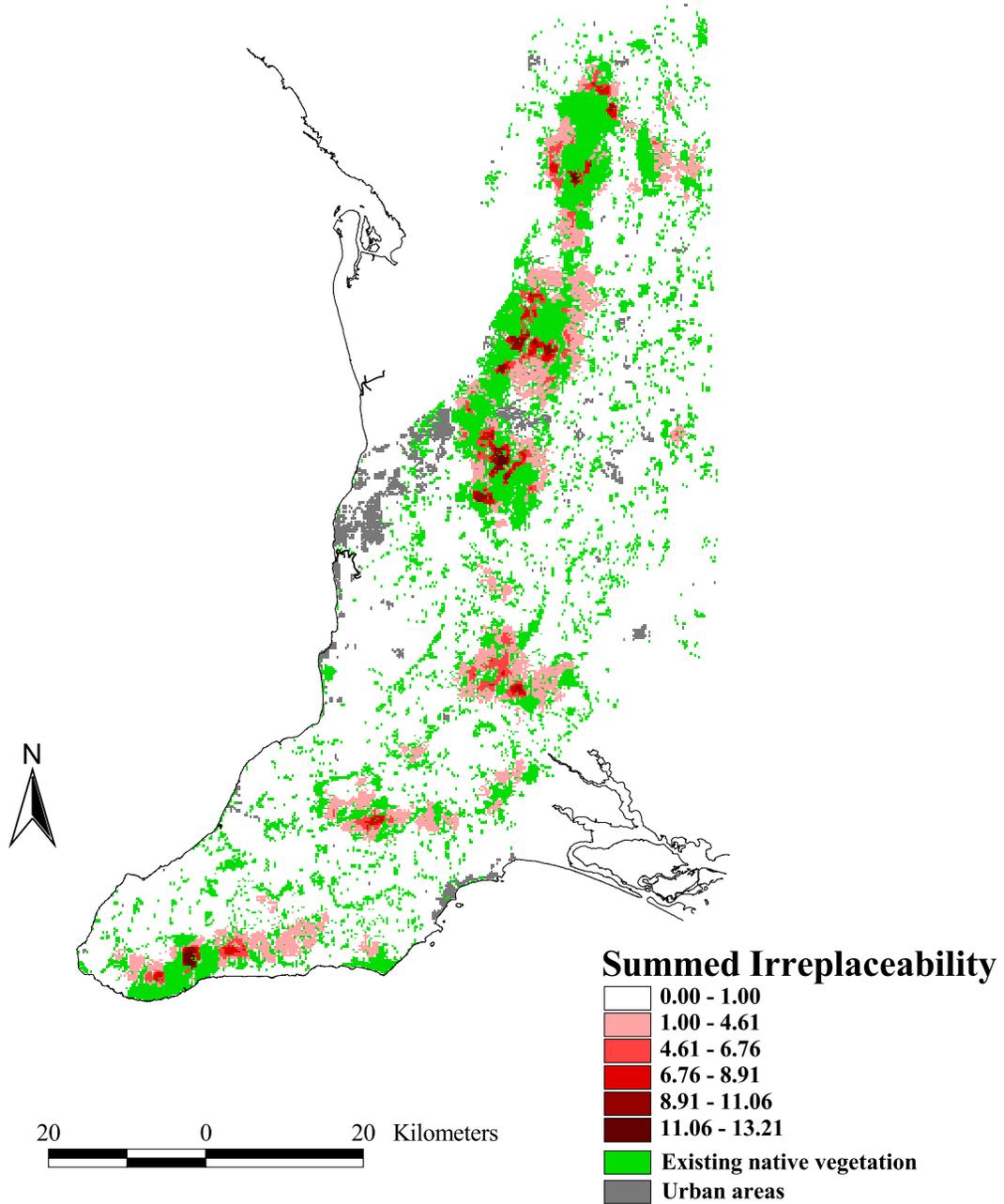
$$I_i^{qn} = \frac{\sum_{i=1}^n S_i}{p_i^{qn}} \quad (6)$$

The summation term in the numerator is the number of times that site  $i$  is selected over  $n$  runs of the algorithm, where  $s_i \in [0,1]$ . The  $p_i^{qn}$  is the 95% confidence interval value for the probability that site  $i$  would be selected at random, given a budget size,  $q$ , and the  $n$  replicates, assuming a normal distribution, with the mean and variance determined by 50

Monte Carlo trials where all available sites are chosen with equal probability. Hence, an  $I_i$  of greater than 1.0 indicates a site is selected on average more frequently than random, with a significance level,  $\alpha = 0.05$ . The sites with high summed irreplaceability are priority sites for revegetation.

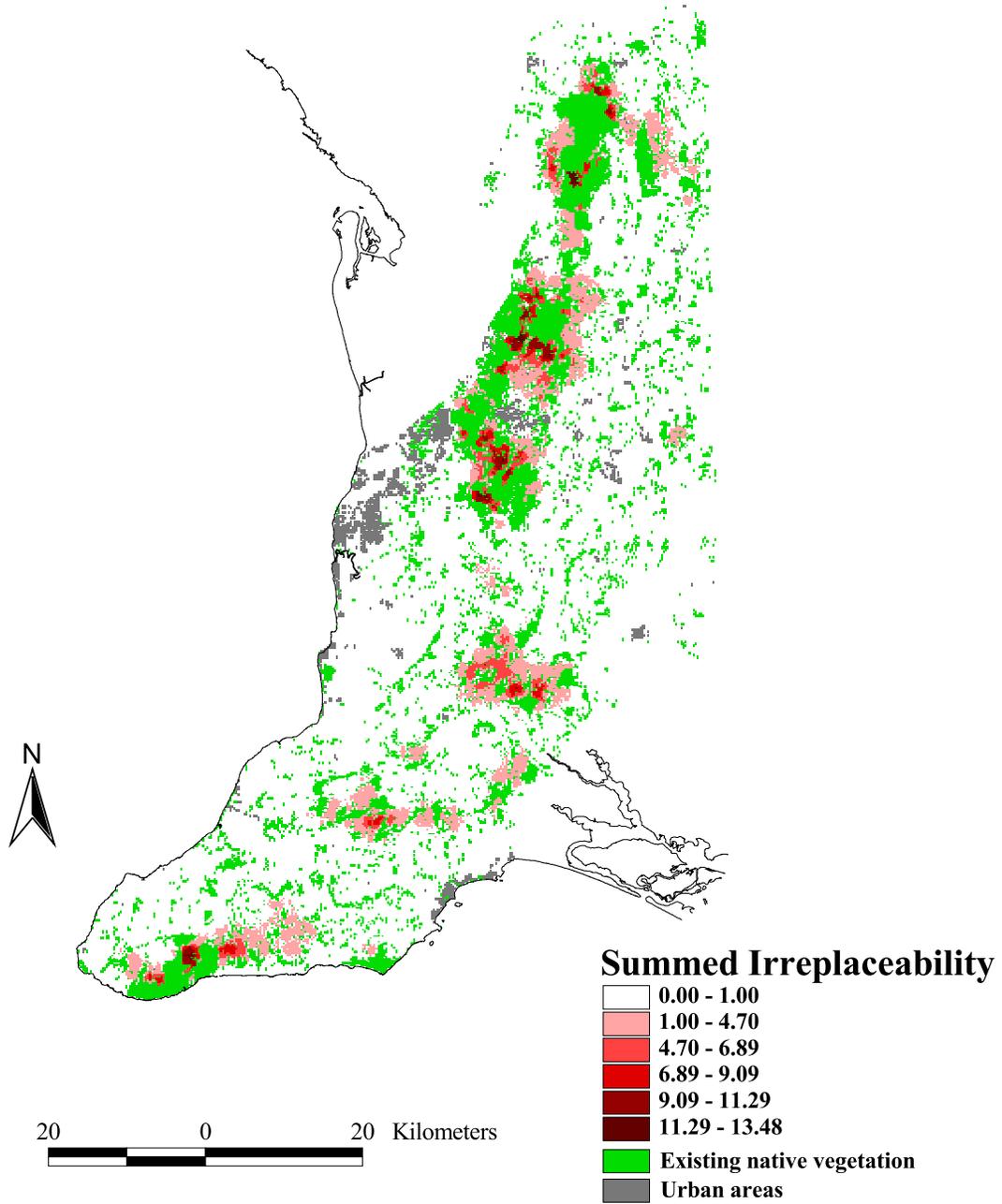
Figures, 5-9, show the summed irreplaceability maps for the region. For the equal cost scenarios, the sites with the highest summed irreplaceabilities are concentrated not surprisingly in areas with large blocks of contiguous vegetation, and there is a great deal of congruence between the summed irreplaceabilities for the scenarios. The summed irreplaceability map for the property value scenario differs markedly, highlighting how variable economic costs can significantly change the optimal solution. Few highly irreplaceable sites are located near the main spine of the MLR and the city of Adelaide, with more being concentrated in the east and south of the region, areas of lower property values. For the property value scenario there is the interplay of maximizing the number of inexpensive sites but also assuring a high degree of spatial contagion. Table 4 shows a matrix of the Gower's similarity index for pairwise comparisons of the summed irreplaceability maps of the various objective functions and budget sizes (Legendre and Legendre 1983). In each pairwise comparison, we included only sites that had a summed irreplaceability value of greater than 1.0 for one of the maps. A Gower's similarity index of 1.0 indicates perfect concordance. For comparisons between the equal cost scenarios, the Gower's similarity indices are around 0.90, indicating a high degree of similarity between the maps. However, there is much less similarity between the equal cost and variable cost scenarios, with Gower's similarity indices ranging from 0.74 – 0.84.

## MLR Optimal Habitat Reconstruction -1000 ha (Baseline scenario)



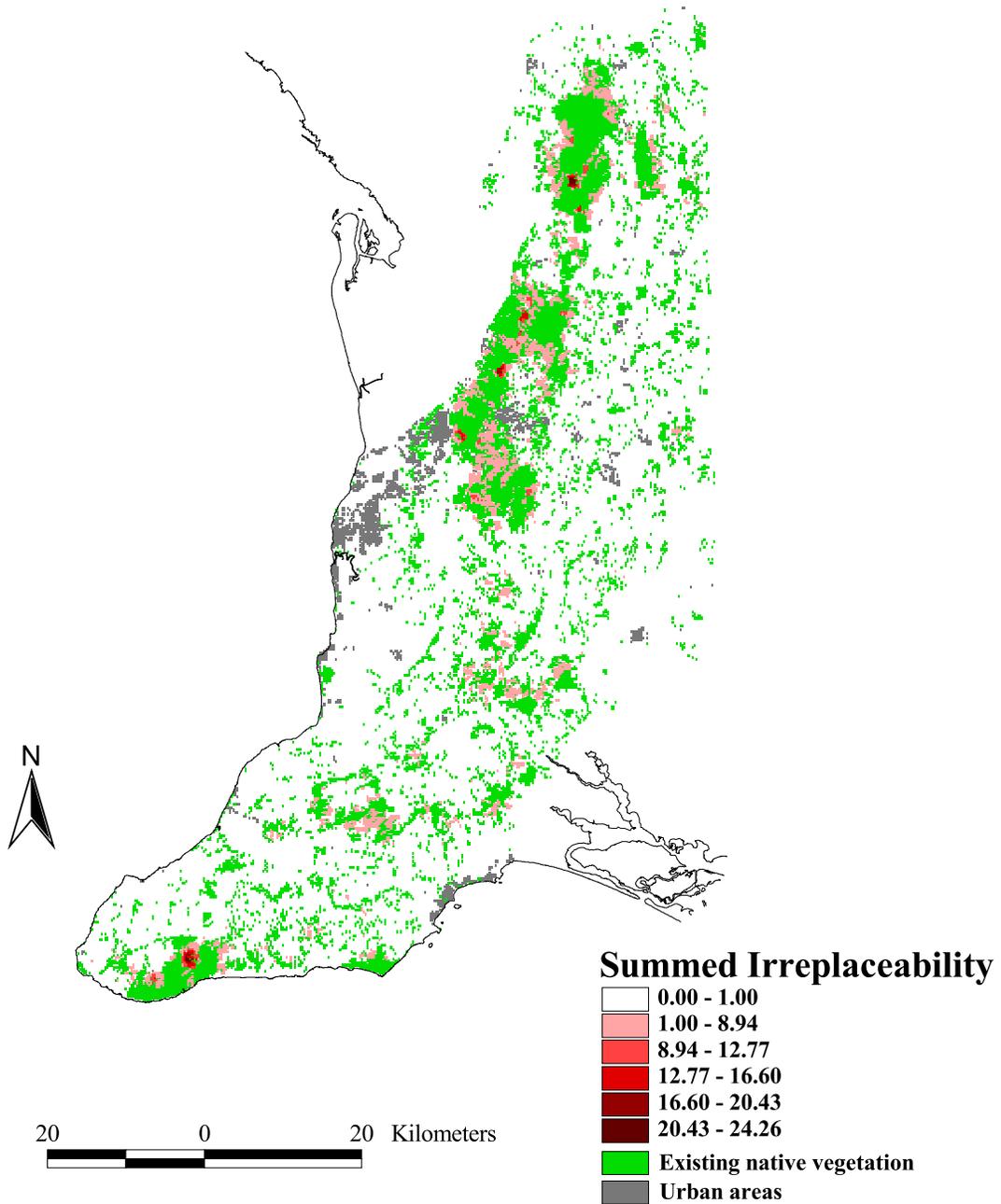
**Figure 5.** Summed irreplaceability for the baseline objective function scenario with a budget size of 10000 ha (50 runs).

# MLR Optimal Habitat Reconstruction -1000 ha (Threshold scenario)



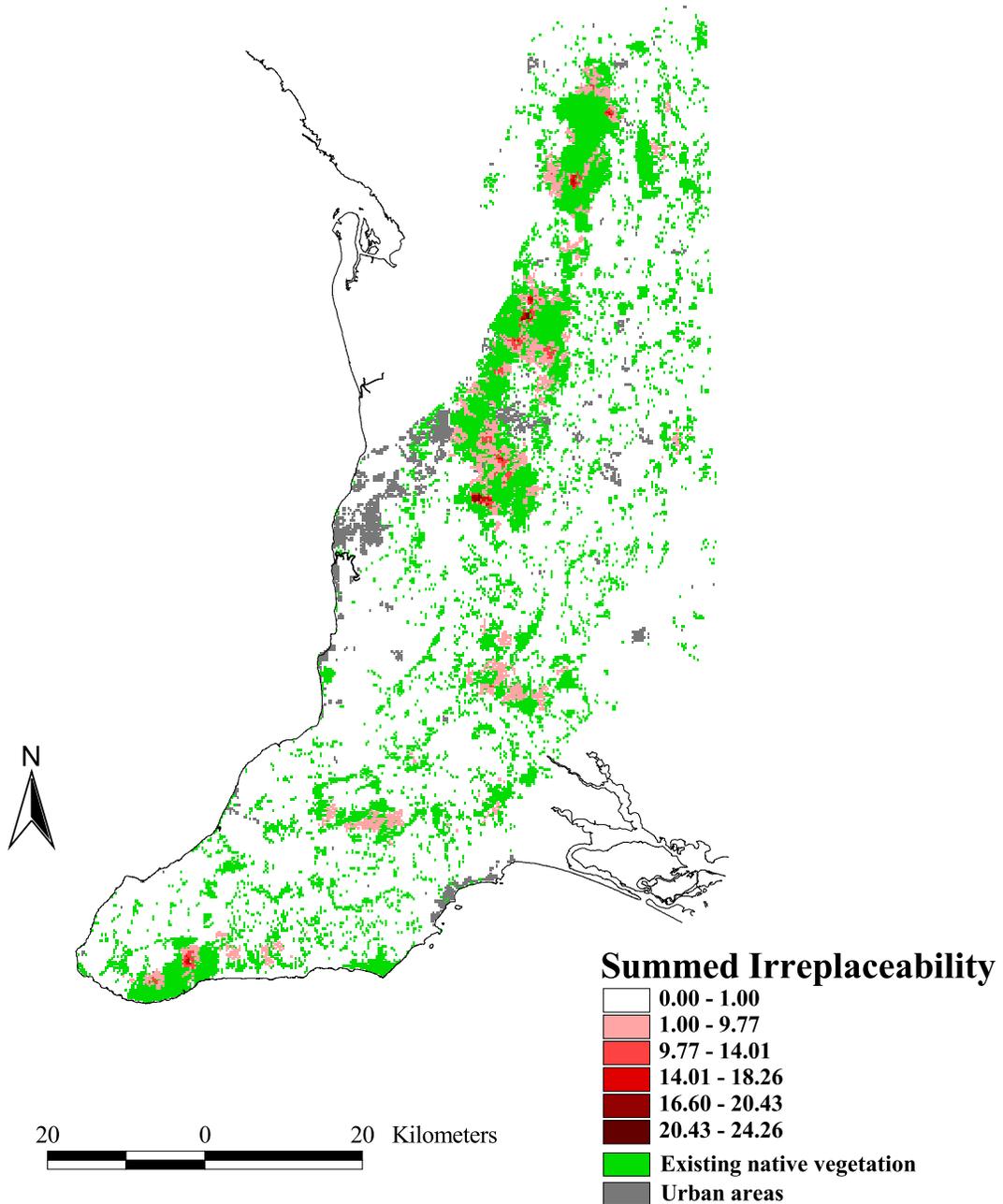
**Figure 6.** Summed irreplaceability for the threshold objective function scenario with a budget size of 10000 ha (50 runs).

# MLR Optimal Habitat Reconstruction -1000 ha (Saturating scenario)



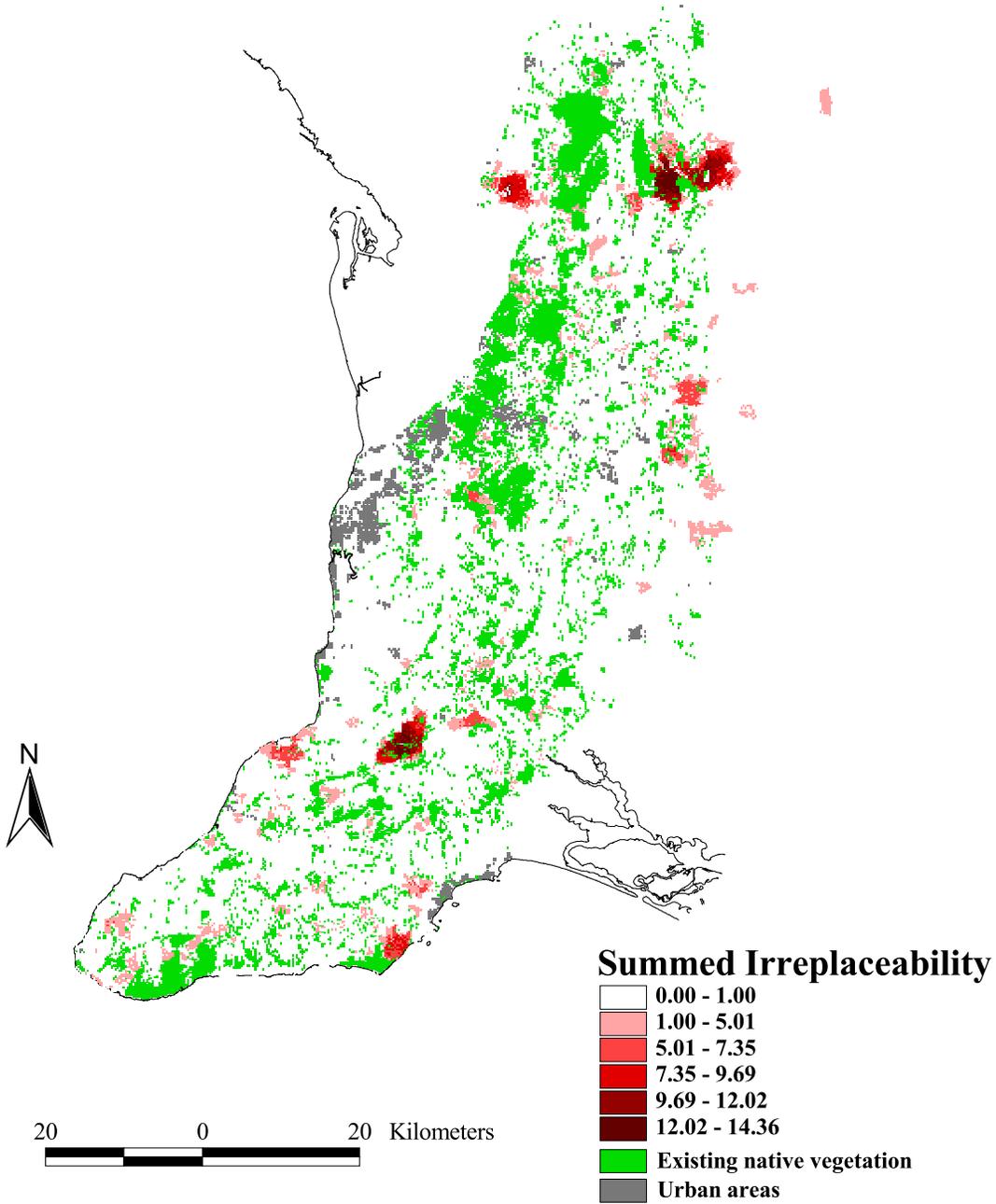
**Figure 7.** Summed irreplaceability for the saturating objective function scenario with a budget size of 1000 ha (50 runs).

## MLR Optimal Habitat Reconstruction -1000 ha (Triage scenario)



**Figure 8.** Summed irreplaceability for the triage objective function scenario with a budget size of 1000 ha (50 runs).

# MLR Optimal Habitat Reconstruction -1000 ha (Property value scenario)



**Figure 9.** Summed irreplaceability for the baseline objective function with property values included for a budget size of 1000 ha (50 runs).

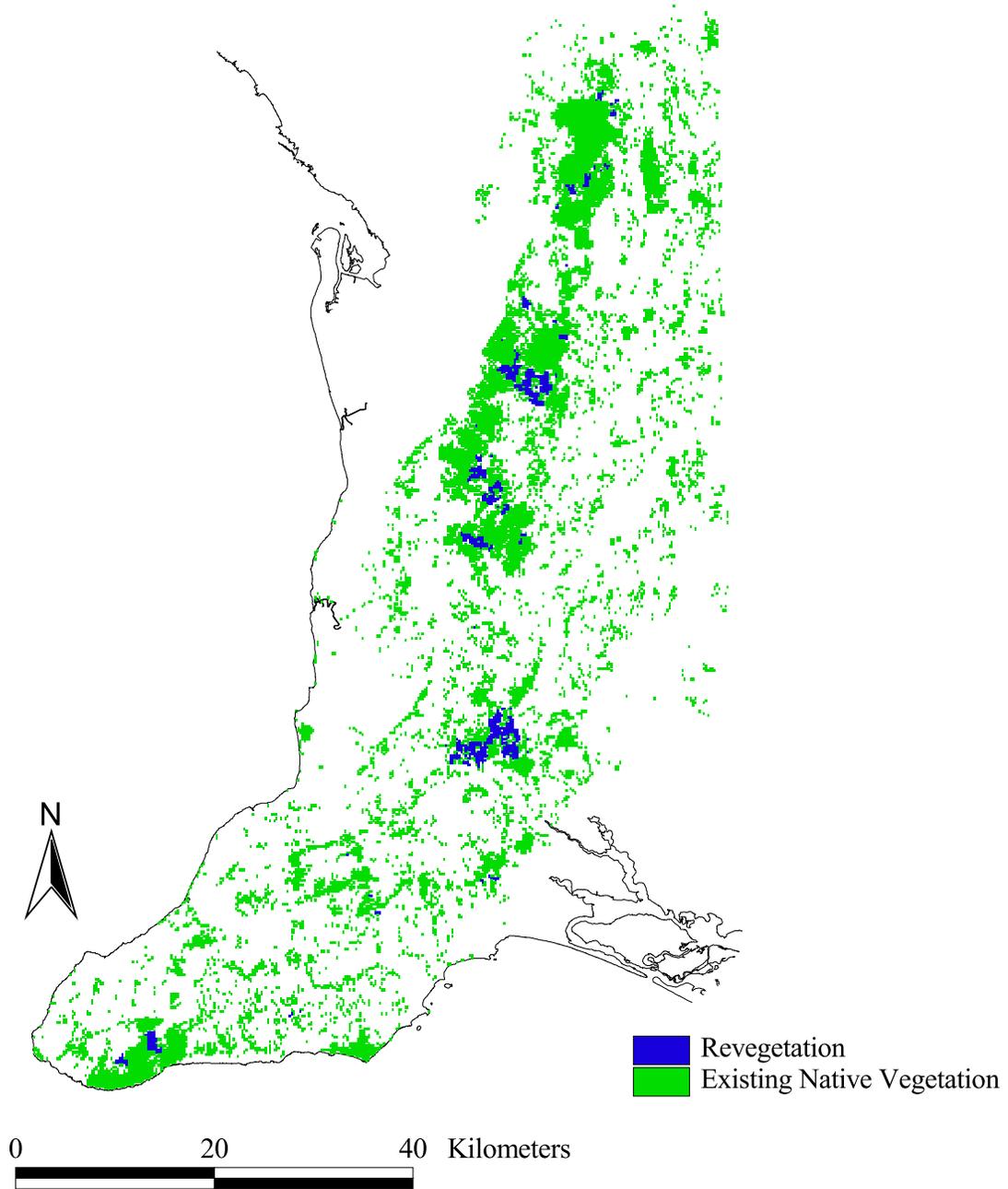
	<b>Base (1000)</b>	<b>Base (5000)</b>	<b>Base (10000)</b>	<b>Thresh (1000)</b>	<b>Thresh (5000)</b>	<b>Thresh (10000)</b>	<b>PV (1000)</b>	<b>Sat (1000)</b>	<b>Triage (1000)</b>
<b>Base (1000)</b>	----- -	0.90	0.90	0.91	0.90	0.90	0.83	0.91	0.92
<b>Base (5000)</b>	0.90	----- -	0.92	0.90	0.93	0.92	0.74	0.90	0.91
<b>Base (10000)</b>	0.90	0.92	-----	0.88	0.92	0.93	0.74	0.90	0.91
<b>Thres (1000)</b>	0.91	0.90	0.88	-----	0.87	0.88	0.78	0.91	0.92
<b>Thresh (5000)</b>	0.90	0.93	0.92	0.87	-----	0.92	0.75	0.90	0.91
<b>Thresh (10000)</b>	0.90	0.92	0.93	0.88	0.92	-----	0.74	0.90	0.91
<b>PV (1000)</b>	0.83	0.74	0.74	0.78	0.75	0.74	-----	0.84	0.84
<b>Sat (1000)</b>	0.91	0.90	0.90	0.91	0.90	0.90	0.84	----- -	0.92
<b>Triage (1000)</b>	0.92	0.91	0.91	0.92	0.91	0.91	0.84	0.92	-----

**Table 4.** Matrix of the Gower's Similarity Index for pairwise comparisons of the summed irreplaceability maps of the various objective functions and budget sizes. The value in parentheses is the budget size in hectares (Base = Baseline objective function, Thresh = Threshold objective function, Sat = Saturating objective function, PV = Property value scenario).

### *Nested Subset Analysis*

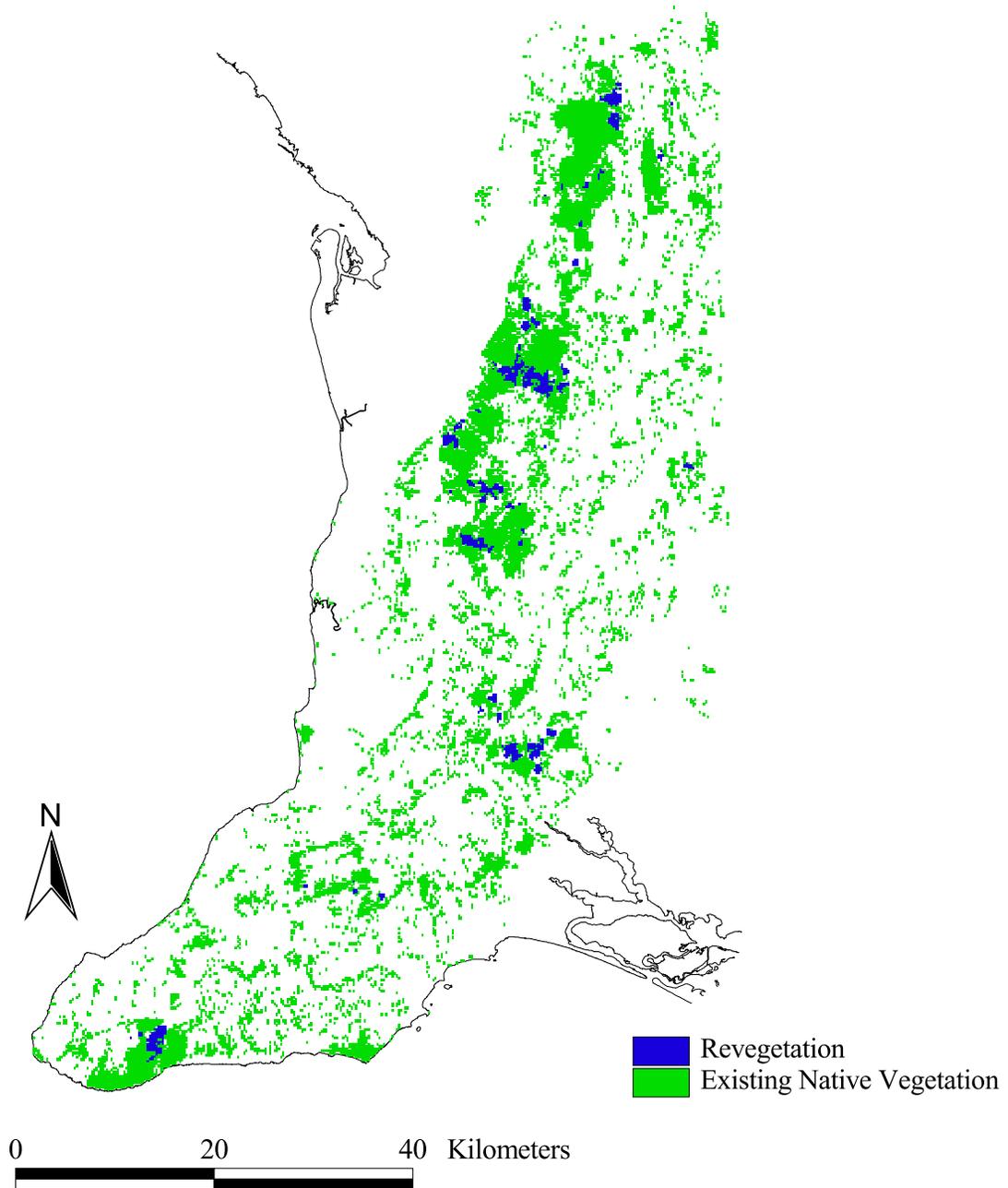
Our optimization problem as we have formulated it, does not include the population and landscape dynamics of the system. Restoration may occur at a small budget size, though ultimately, the conservation goal may be to restore a much larger portion of the landscape. To incorporate future revegetation processes when more money may become available, it is essential that one chooses a solution at a smaller budget, from which it is still possible to traverse solution space to reach a good solution at a larger budget size. This can be determined by finding the solution(s) that are the best nested subsets for the solutions at the larger budget sizes. Figures 10 and 11 show the best subsets at 5000 ha of the 10000 ha solutions for the baseline and threshold objective function scenarios. The standard deviations for both cases are 7.12% and 7.05%, respectively, of the best nested subset values, indicating that solutions at the smaller budget sizes are all fairly good subsets of the larger solution.

## Best Subset - 5000 ha (Baseline scenario)



**Figure 10.** Best subset solution at 5000 ha for the solution at 10000 ha under the baseline objective function scenario (50 runs).

## Best Subset - 5000 ha (Threshold scenario)



**Figure 11.** Best subset solution at 5000 ha for the solution at 10000 ha under the threshold objective function (50 runs).

## *Landscape Characterization*

Another way to condense information on the revegetated landscapes is to characterize their configuration, including the number of existing and new revegetated patches and patch connectivity, which is displayed in Table 5. The mean patch sizes for the optimization scenarios refer only to patches that have some portion that is new revegetated area. Likewise, the connectivity measure only includes revegetated patches. For the equal cost scenarios, the percent of the total revegetated area in new patches is less than a few percent in all cases. Accreting area to existing large patches is a more beneficial tack. The average size of revegetated patches ranges from 1768 – 3174 ha, compared to the average patch size of 35 ha in the present, unvegetated landscape. The reduction in mean nearest neighbor (MNN) ranges from 57 – 87%.

However, when property values are incorporated, a much higher percentage (15 %) of the revegetated area is in the form of new patches. Overall, while connectivity is not significantly different from the existing, the overall mean patch size of the revegetated patches (332 ha) is still ten times greater than in the unvegetated, existing landscape. The former is due to less expensive sites being selected, which are further from areas where existing vegetation is highly concentrated. The total revegetation area is on average 8810 ha for an effective budget size of 1000 ha. Variable sites costs results in many more sites being selected than under the equal cost scenarios.

For all scenarios, randomly allocating revegetated area within the constraint of the budget, both in terms of the average probability of occurrence per species and the average

number of individuals in the triage and saturating objective function scenarios, poorly approximates the near-optimal solution. The average probability of occurrence in the revegetated sites is 20 – 40% greater than the average value in the present landscape. These results provide benchmarks on the desired average patch size and connectivity that revegetation in the MLR should attempt to achieve.

<b>Objective Function*</b>	<b>Budget size (ha)</b>	<b>Revegetation Area (ha)</b>	<b>MPS total (ha)</b>	<b>MPS new (ha)</b>	<b>MPS existing (ha)</b>	<b>% New Patch</b>	<b>MNN (m)</b>
Baseline	1000	-----	2684 (493)	5 (5)	2894 (599)	1 (1)	25 (22)
	5000	-----	2012 (397)	8 (3)	2511 (526)	1 (0)	57 (23)
	10000	-----	1768 (320)	8 (2)	2461 (488)	1 (0)	74 (34)
Baseline, Property Values	1000	8810 (1409)	332 (55)	18 (7)	887 (149)	15 (6)	159 (61)
Threshold	1000	-----	2824 (1017)	6 (9)	3061 (1023)	1 (1)	27 (24)
	5000	-----	1941 (416)	8 (3)	2453 (523)	1 (1)	58 (28)
	10000	-----	1905 (460)	8 (2)	2693 (607)	1 (0)	78 (24)
Triage	1000	-----	3174 (1461)	7 (5)	3897 (1512)	2 (2)	34 (36)
Saturating	1000	-----	2060 (523)	10 (10)	2405 (569)	2 (2)	48 (27)

<b>Objective Function*</b>	<b>Avg. % Occurrence</b>	<b>Avg. % Occurrence (Random*)</b>	<b>Avg. Random* Revegetation Area (ha.)</b>	<b>Avg. Number Individuals</b>	<b>Avg. Individuals (Random*)</b>
Baseline	70 (2)	28 (1)	-----	-----	-----
	72 (1)	31 (0)	-----	-----	-----
	74 (1)	34 (0)	-----	-----	-----
Baseline, Property Values	62 (2)	28 (2)	442 (133)	-----	-----
Threshold	71 (2)	23 (1)	-----	-----	-----
	73 (1)	25 (1)	-----	-----	
	74 (1)	28 (0)	-----	-----	
Triage	75 (3)	-----	-----	842 (41)	348 (14)
Saturating	70 (2)	-----		789 (25)	348 (14)
	<b>Area (ha)</b>	<b>MPS (ha)</b>	<b>MNN (m)</b>	<b>Avg. % Occurrence</b>	
Present, unvegetated landscape	78369	35	194	51	
* 50 replicates					

**Table 5.** Summary of the landscape characteristics for the five scenarios. Standard deviations are in parentheses.

## DISCUSSION

### *Limitations of Habitat Suitability Models*

The foundation of our optimization program is the probability functions of species occurrence in the landscape, and they implicitly assume that where a species is present there is suitable habitat and that its distribution is static. The species may be in a declining non-equilibrium state, confined to relict areas that are not particularly good habitat. Not all presences are equivalent, but without information on source-sink dynamics (Pulliam 1988, 1996) or population density, we have no way of surmounting this problem. Likewise, metapopulation theory tells us that suitable habitat may be unoccupied. It would be preferable to include population dynamics, where our objective function would be population viability over some time horizon. However, for most species there is a dearth of the requisite data for spatially-explicit population dynamic models, particularly dispersal information (Beissinger and Westphal 1998). For most landscape-level, multi-species approaches to habitat reconstruction, distribution data will be used *faute de mieux*. Some studies have shown that short-term persistence at least can be predicted from distribution data (Gates 2000, Araujo 2002). Furthermore, this framework is the “if you build it they will come” approach. It is assumed that once the most optimal spatial configuration of vegetation is created, then the species will be able spread into those newly restored areas. Impermeable habitat types may preclude

population diffusion. Though we have used results from logistic regression analyses of bird distribution data, simple rules based on expert opinion, indicating the minimum patch sizes or level of connectivity can be substituted where there are lacunae in distribution data.

### *Biodiversity Surrogates*

Our goal has been to derive optimal habitat reconstruction strategies for birds in the Mount Lofty Ranges, though other species could easily be added if the data exist. We have chosen species that are well representative of the avian community, and most of those species with isolated or partially isolated populations were included. Extrapolation of our results to other taxa would most likely be amiss. Surrogate schemes have proved rather inadequate in conserving other taxa. There is evidence that because invertebrates respond to much smaller spatial scales, the conservation of vertebrate groups, such as birds, may not represent invertebrates well (Murphy and Wilcox 1986, Oliver et al. 1998). For instance, while the White-backed Woodpecker serves as an adequate umbrella species for woodland beetles (Martikainen et al. 1998), the California Gnatcatcher was found to be a poor umbrella species for lepidoptera in coastal sage scrub in California (Rubinoff 2001). In a thorough review Andelman and Fagan (2000) examined the efficiency of umbrella species, flagship species and other taxon-based surrogate schemes in various regions of the United States and concluded that none of them performed better than random in terms of capturing other species or protecting

habitat.

*Optimization and strategic habitat restoration*

We have shown how the problem of habitat reconstruction can be formalized as a mathematical optimization problem, and in a sense it can be viewed as the quantification of the focal species approach (Lambeck 1997), where constraints are explicitly incorporated. Quantitative assessment methods such as this can provide what has been referred to as the “highest form of rationality” (Hollick 1981); yet, they are not oracles but decision-support tools that exist alongside other political and societal criteria that impinge on any conservation problem. It must be emphasized that the optimization algorithm itself is not a model, but a solution method. Though the simulated annealing parameters need to be fine-tuned by experimentation, generally the limitation and uncertainty is due to the underlying models of species distribution or dynamics.

There has been some criticism of iterative heuristics in reserve design in favor of the use of integer linear programming (Rodrigues 2000, 2002); however, it must be reiterated that with any interesting landscape design problem, such as revegetation in this paper, non-linearities in the response variable effectively preclude the use of these integer linear programming. The explicit mathematical formulation of conservation planning problems at the start, including the objectives, constraints, and costs, leads to greater accountability, objectivity, and transparency in the solutions (Rodrigues 2000). It is axiomatic in conservation biology that species require large tracts of well-connected

habitat, but an optimization approach winnows down the vagueness and provides some quantitative rigor. Though we have looked at revegetation, this approach is a subset of the larger problem of landscape design. More sophisticated economics could be integrated into the constraint, including economic productivity of the landscape over a certain time horizon, and the control variable could include a myriad of land uses. It is important that an algorithm is not “shoe-horned” to fit every landscape problem. There are a plethora of heuristics that may be effective depending on the problem, including genetic algorithms, tabu search, stochastic evolution, simulated evolution, great deluge, hybrid approaches and simple greedy algorithms (Sait and Youssef 1999, Bettinger 2002).

The most obvious limitation of this study is the consideration of simply a binary landscape. The addition of habitat heterogeneity results in a more constrained solution space. We are in the process of conducting logistic regression analyses with the inclusion of broad vegetation classes and using a predicted vegetation map to explore strategic revegetation in a heterogeneous landscape.

Using property value as a surrogate for the costs of revegetation is imperfect, since, for instance, owners of high value properties may be willing to restore some of their property to native vegetation for economic reasons (e.g. vineyards with inns). In some cases, devoting a portion of a property to native vegetation may maximize the overall property value (e.g. hobby farms). The actual cost lies somewhere between the extrema of the two cost scenarios presented here.

Our goal in this paper has been primarily to introduce a new methodology for

landscape restoration that is rigorous, repeatable and flexible enough to handle various objectives functions. Nevertheless, our results can serve as benchmarks for revegetation in the Mount Lofty Ranges, providing information on priority sites for revegetation and aspects of landscape configuration. Under scenarios assuming equal costs, our analyses suggest that revegetation in the region should strive to create landscapes with a mean revegetation patch size ranging from 1770 – 3170 ha and with the connectivity of the revegetated patches increased from 60 – 87% over the average connectivity in the present landscape.

Conservation cannot exist in a vacuum, detached of the realities of socioeconomic constraints. Thus, it is important that conservation biology adopt a more optimization approach to landscape planning and design in order to determine the best strategies for biodiversity conservation given scarce resources available.

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# Chapter 6

## Optimal habitat reconstruction for woodland birds in the Mount Lofty Ranges, South Australia

**Michael I. Westphal<sup>§+</sup> and Hugh P. Possingham<sup>+\*</sup>**

<sup>§</sup>Department of Environmental Science, Policy and Management, University of  
California, Berkeley, CA 94720, U.S.A.

<sup>+</sup>The Ecology Centre, University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>\*</sup>Department of Mathematics, University of Queensland, Australia

*Space is the stature of God.*

- Joseph Joubert

## **ABSTRACT**

We formulate the optimal landscape restoration problem for 29 birds in the Mount Lofty Ranges, South Australia and use simulated annealing and an iterative improvement heuristic algorithm to find the efficient solutions for various budget sizes, site cost scenarios and assumptions on the available habitat types for restoration. Our analyses provide guidelines on priority sites for revegetation, which vary depending on whether variable site costs are included or what assumptions are made on the habitat type of the restoration site. Generally, accreting habitat to large patches is preferred. The size of the patches in which the restored sites were imbedded ranged from 122 – 598 ha. This serves as a benchmark for the size of restoration patches. Maximizing the amount stringybark or non-stringybark woodland (as opposed to low woodland, shrubland or open forest) maximizes the probabilities of occurrence of the species considered, but the exact proportion depends on the assumptions of the available habitat type for each site. Other simple rules for landscape restoration performed poorly, with objective function values that ranged from 48 - 73% of that of the near-optimal solutions. This indicates the utility of using a decision-theory framework for landscape restoration. We ran the simulated annealing algorithm for three focal species separately, the Brush Bronzewing (*Phaps elegans*), the Brown Treecreeper (*Climacteris picumnus*) and the Scarlet Robin (*Petroica multicolor*), and then calculated the corresponding multi-species objective function value.

The objective function value for the single-species scenarios ranged from 63 – 91% of that of the multi-species solution objective function value. This highlights the difficulty in assuming that the habitat needs of a focal species represent that of the community. This paper represents one of the first uses of decision-theory tools for multi-species, optimal habitat restoration on a real landscape. Our results should inform conservation policy in the region, and the programs can be elaborated with improved or altered species or vegetation data and different assumptions on species prioritization, site costs and the available vegetation type for each restoration site. The methodology and software that we have presented has applicability for general landscape design outside the Mount Lofty Ranges.

## INTRODUCTION

As conservation biology matures, there will increasingly be a shift from within-park conservation and the simple delineation of nature reserves to landscape design in spatially heterogeneous, highly human-altered regions with competing land uses and the superposition of socioeconomic constraints and interests. One aspect of this is habitat reconstruction or restoration (Lambeck 1997) in highly fragmented landscapes. Even though there may be relatively few recorded extinctions following dramatic habitat loss, the landscape may be in non-equilibrium, and so there may be a long time lag before the extinctions actuate, the so-called “extinction debt” (Tilman et al. 1994). There may be other ancillary benefits to habitat restoration besides arresting species loss. In Australia, for example, dryland salinity affects 630 000 ha of remnant and planted native vegetation (Cramer and Hobbs 2002), which is due to or exacerbated by land clearing. The deleterious effects of dryland salinity is estimated to cost \$A 270 million annually (CSIRO Land and Water 2003). With very limited resources, it is of salient importance that a framework for strategic habitat reconstruction be developed that is both cost efficient and efficacious.

There are two points that must be considered for effective habitat reconstruction. First, there must be a cognizance of the whole landscape context, not just the local, patch-level habitat. The occurrence and viability of species may be contingent on the configuration of habitat in the landscape, particularly as the amount of habitat as a proportion of the total landscape area becomes quite small. In a simulation study, Fahrig (1997) found that below 20% habitat cover, the habitat configuration became important

for species persistence. In a review of 61 studies over a wide array of taxa comparing patch-level variables to landscape-level variables, (Mazerolle and Villard 1999) noted that in about 60% of the studies landscape variables were significant predictors of species presence or absence.

Secondly, strategic habitat reconstruction should explicitly adopt a decision theory framework, where the objective, constraints and costs are clearly defined. The focal species approach has been promoted for landscape reconstruction, where habitat is created that satisfies the ecological requirements of the most area-limited, resource-limited, dispersal-limited, and process-limited (e.g. fire) species (Lambeck 1997, Watson et al. 2001). Lindemayer et al. (2002) have criticized it on theoretical grounds, but most importantly, the focal species approach is incapable of dealing with the possible conflicting needs of species and incorporating financial costs (Westphal and Possingham 2003).

There have been some studies of single-species habitat reservation on real landscapes using optimization methods (van Langevelde et al. 2000, Haight 2001, van Langevelde 2002, Westphal et al. 2003). Westphal and Possingham (*submitted*) looked at optimizing landscape configuration for a woodland bird community in a binary landscape of native vegetation or agricultural area. In this paper, we extend on that work by considering a heterogeneous landscape of various vegetation types.

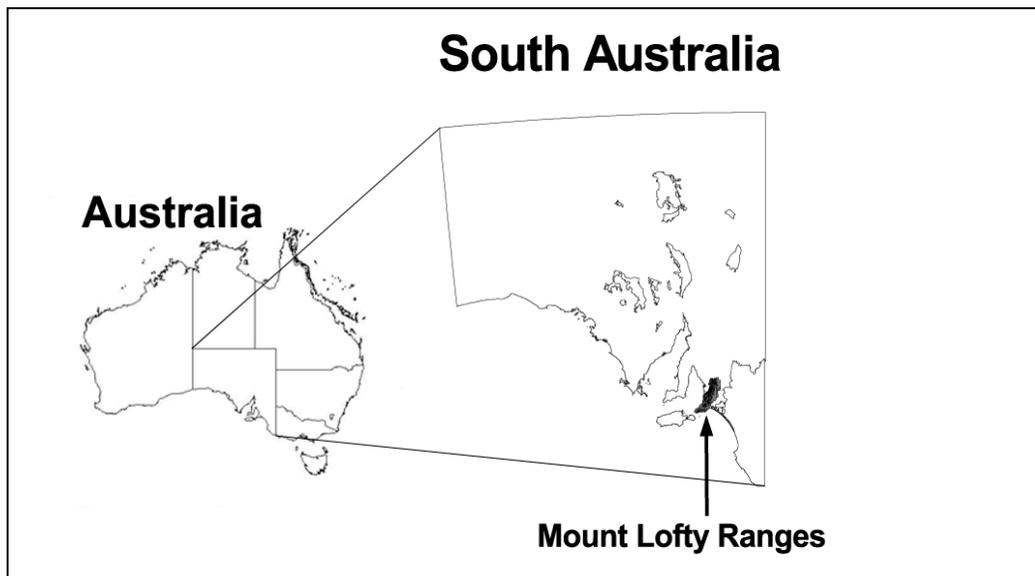
## METHODS

### *Study site*

The Mount Lofty Ranges (MLR) of South Australia is a relatively high rainfall (400 mm/yr – 1100mm/yr) region of Australia, embedded in a semi-arid region (Figures 1, 2). For the purposes of this study, we use the boundary of the region as defined hydrologically (Bryan 2000). Of a total 500,000 ha, only about 16% is covered by native vegetation (Figure 3). The native vegetation is primarily eucalypt woodland (particularly *Eucalyptus baxteri*, *Eucalyptus fasciculosa*, *Eucalyptus leucoxylon*, *Eucalyptus obliqua*, and *Eucalyptus viminalis*) in a matrix of mixed agricultural land, including pasture, crops, vineyards, and orchards. The region is a ‘biological island’, and using atlas data, we defined 37 woodland bird species as having populations that are isolated or largely isolated from their nearest populations outside the MLR (Paton et al. 1994). Though the region is not characterized by a high species diversity nor a large number of endemics, there are many unique subspecies. Moreover, the region represents the western extent of the Eastern Australian bird fauna.

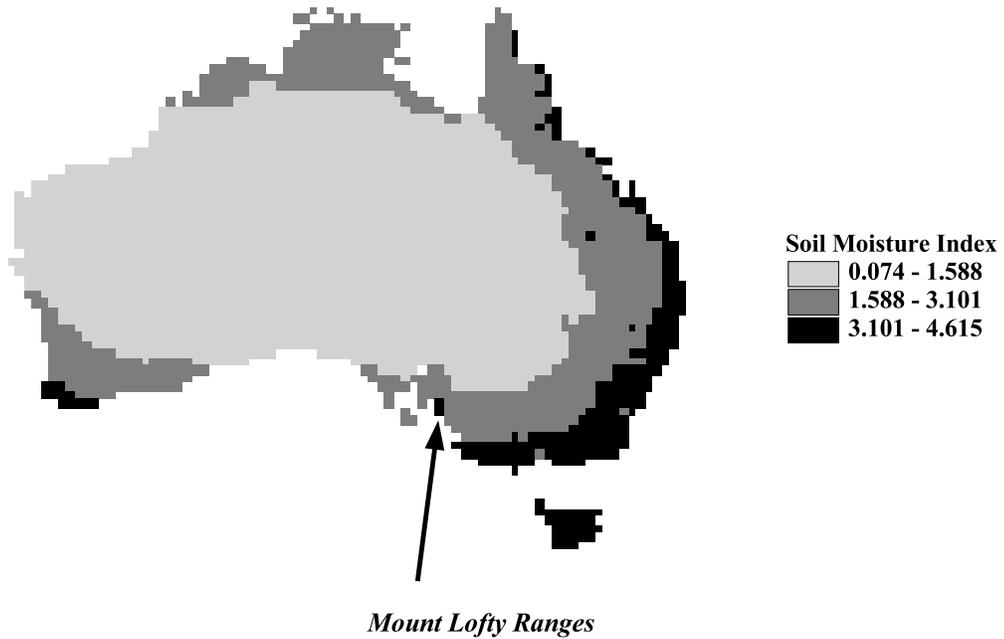
Most of the vegetation clearance in the MLR has taken place since WWII, and question remains as to the degree and time scale of any extinction debt. Ford and Howe (1980) used island biogeography theory to predict that of the original terrestrial bird fauna of 120 species, almost 50 would eventually go extinct before relaxation. Garnett and Crowley (2000) list eight species that have disappeared from the region to date, and

Possingham and Field ( 2001) consider another 16 total species to be almost extinct or “living dead” and likely to be extinct within 200 years.



**Figure 1.** The location of the Mount Lofty Ranges within Australia.

## Soil Moisture %



**Figure 2.** Soil moisture index (annual averages), as a % of 100 mm. A value of 100 indicates that the soil has a constant water capacity of 100 mm. The values are transformed by  $\ln(x + 1)$  (Dingle et al. 2000).

# Mount Lofty Ranges Native Vegetation

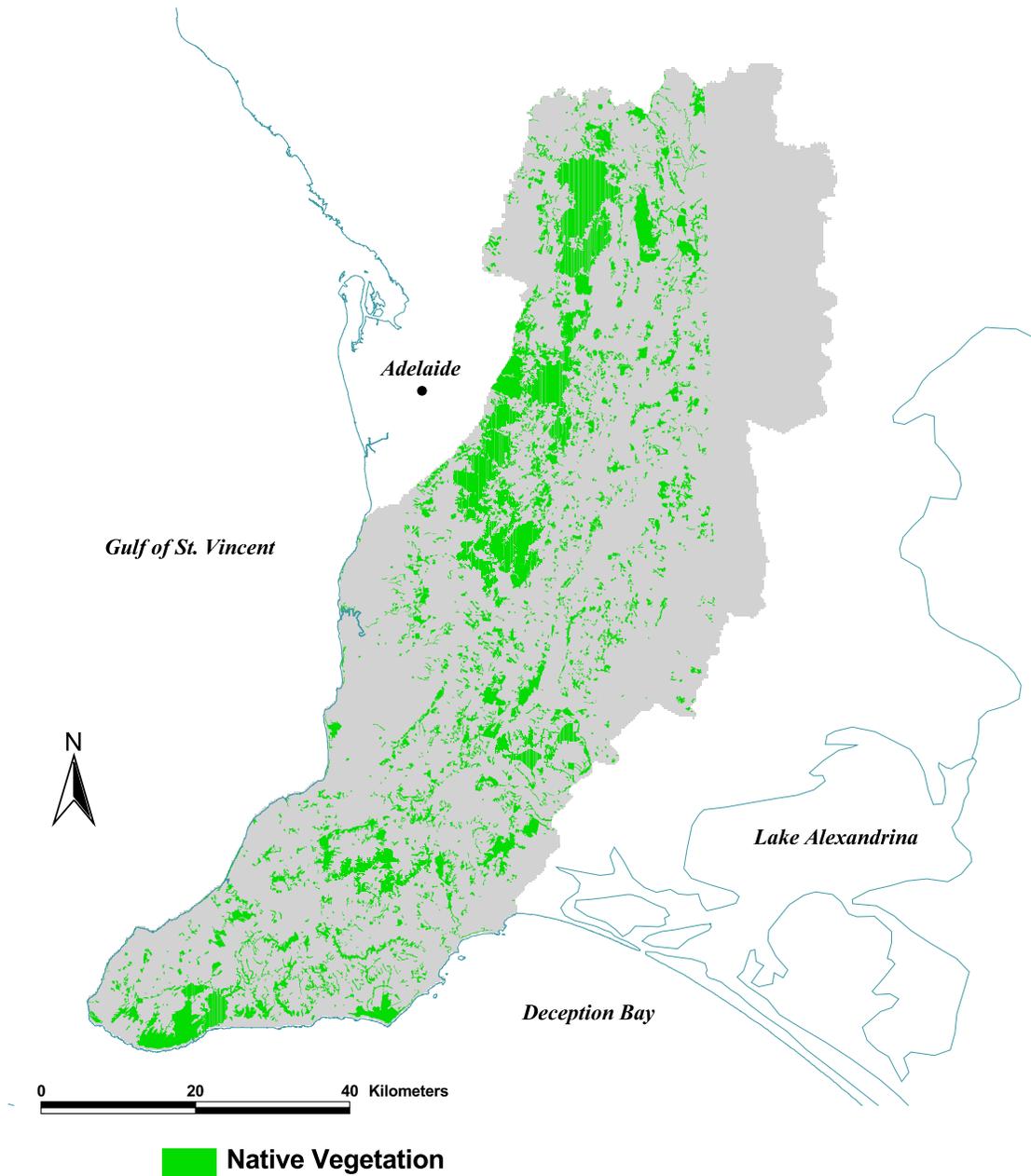


Figure 3. The Mount Lofty Ranges study area.

The main cause of the extinction and population declines appears to be habitat loss. In contrast, the nearby Kangaroo Island, which has a similar avian community, retains about 40% of its original native vegetation and has experienced only one bird extinction. One sobering prediction from metapopulation models is that species close to their viability thresholds have especially long lag times before extinction (Hanski and Ovaskainen 2002). Though empirical studies of extinction debt in large fragmented landscapes is rare, studies from habitat fragments suggest that the time lag for birds, for example, is on the order decades (Brooks et al. 1999). The MLR is a case study for habitat clearance in Australia, and having a settlement history that is older than many regions, the MLR has progressed further down the trajectory of habitat clearance and landscape alteration. Strategic revegetation methodologies in the MLR may serve as templates for revegetation in other areas.

### *Species distribution models*

In 1984-85, the South Australian Ornithological Association conducted an intensive survey of birds in Adelaide region of South Australia, including the MLR (Paton et al. 1994). Using survey data from 499 points in the region, we previously conducted logistic regression analyses on the effects of landscape configuration on the species distributions (Westphal et al. 2003) (Figure 3). At scales of 2, 5, 10 km. around the survey points, we used FRAGSTATS metrics as the explanatory variables of presence-absence for each species: total landscape area (TLA), number of patches (NumP), mean patch size (MPS), the size of the largest patch (Lrg), mean nearest

neighbor distance (edge to edge) of patches (MNN), and landscape shape index (LSI), which a measure of the total edge in the landscape. Here we refitted the logistic regression models on the raster landscape of the region with a grain cell size of 6.25 ha, the minimum planning unit of interest. We included additional explanatory variables: the amount of area of six broad habitat types within the neighborhood around the survey point. The habitat types are divided into four structural classes (open forest, woodland, low woodland, and shrubland/heathland) and whether the dominant overstory tree species are stringybark (*E. baxteri*, *E. obliqua*) or non-stringybark (e.g. gum species) (Table 1). We considered only the 2 km neighborhood scale for computational efficiency, and this is the appropriate landscape scale for most species considered (Westphal 2003) (Table 2).

<b>Structural type</b>	<b>Dominant overstory</b>	<b>Example</b>
open forest	non-stringybark spp.	<i>E. ovata</i> , <i>E. camuldensis</i> , <i>Calitris gracilis</i>
open forest	stringybark spp.	<i>E. baxteri</i> , <i>E. obliqua</i>
woodland	non-stringybark spp.	<i>E. leucoxyton</i> , <i>E. camuldensis</i> , <i>E. fasciculosa</i> , <i>E. viminalis</i>
woodland	stringybark spp.	<i>E. baxteri</i> , <i>E. obliqua</i>
low woodland	non-stringybark spp.	<i>E. fasciculosa</i> , <i>E. cosmophylla</i>
shrubland/heath	non-stringybark spp.	<i>E. incrassata</i> , <i>E. diversifolia</i> , <i>Allocausarina</i> spp., <i>A. longifolia</i>

**Table 1.** The broad habitat types of the Mount Lofty Ranges for the purposes of this study.

Species	Regression Equation	ROC
Striated Thornbill, <i>Acanthiza lineata</i>	$-1.44 - 0.00660*TLA + 0.00234*MPS + 0.435*LSI + 0.00832*str1 + 0.0289*ns1 + 0.00769*str2 + 0.00801*ns2 + 0.00779*str2 + 0.00888*ns3$	0.69
Brown Thornbill, <i>Acanthiza pusilla</i>	$-2.15 + 0.425*LSI - 0.00471*str2 + 0.00379*str2 + 0.00344*ns3$	0.71
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	$-1.77 - 0.0114*TLA + 0.0130*str1 + 0.0131*str2 + 0.0177*ns2 + 0.0127*str2 + 0.0136*ns3$	0.68
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	$-2.95 - 0.134*NumP + 1.13*LSI + 0.00331*ns2 + 0.00214*str2 + 0.00132*ns3 - 0.911*ns4$	0.70
Sulfur-crested Cockatoo, <i>Cacatua galerita</i>	$-1.86 - 0.00887*TLA + 0.000227*MNN + 0.0104*str1 + 0.0150*ns2 + 0.00792*str2 + 0.00753*ns2$	0.65
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	$-2.48 + 0.251*LSI + 0.00288*str1 + 0.0189*ns1 + 0.00445*ns2 + 0.00219*str2 + 0.00195*ns3$	0.71
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	$-1.80 - 0.00137*TLA + 0.0717*NumP + 0.00524*str1 - 0.0104*str2 + 0.00408*ns2 + 0.00496*str2$	0.75
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	$-3.45 + 0.00554*TLA - 0.0105*MPS - 0.0110*str2 - 0.00355*ns2$	0.72
Brown Treecreeper, <i>Climacteris picumnus</i>	$-6.41 - 0.0488*TLA + 0.000349*MNN - 0.00379*MPS + 1.48*LSI + 0.0291*Lrg + 0.0216*str1 + 0.0199*str2 + 0.0330*ns2 + 0.0211*str2$	0.75
White-winged Chough, <i>Corcorax melanorhamphos</i>	$-4.079 - 0.336*NumP - 0.000388*MNN + 1.63*LSI - 0.00754*str1 - 0.943*ns1 - 0.0228*str2 + 0.00330*ns3 - 0.863*ns4$	0.80
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	$-2.82 - 0.194*NumP + 1.01*LSI - 0.00336*Lrg + 0.00890*str1 + 0.0314*ns1 + 0.00721*str2 + 0.00710*ns2 + 0.00874*str2 + 0.00495*ns3$	0.80
Crested Shrike-tit, <i>Falcunculus frontatus</i>	$-1.65 - 0.00242*MPS - 0.00241*str1 - 0.0112*str2 + 0.00648*ns2 - 0.694*ns4$	0.73
Musk Lorikeet, <i>Glossopsitta concinna</i>	$-2.62 - 0.00586*TLA - 0.161*NumP + 0.000350*MNN - 0.00401*MPS + 0.852*LSI + 0.00535*Lrg - 0.0533*ns1 + 0.00927*ns2 - 0.107*ns4$	0.71
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	$-0.909 - 0.00386*MPS + 0.00391*str1 - 0.0209*ns1 + 0.00734*ns2 + 0.004909*str2 + 0.00513*ns3$	0.70
Superb Fairy-wren, <i>Malurus cyaneus</i>	$-1.57 - 0.000976*TLA - 0.264*NumP + 1.04*LSI + 0.0294*ns1 - 0.00841*str2 + 0.00591*str2$	0.69
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	$-2.02 - 0.00639*TLA + 0.340*LSI + 0.00898*str1 + 0.00839*str2 + 0.0133*ns2 + 0.00825*str2 + 0.00609*ns3 - 0.127*ns4$	0.70
Red-browed Finch, <i>Neochmia temporalis</i>	$-0.970 - 0.00527*TLA + 0.00781*str1 + 0.00477*str2 + 0.00819*ns2 + 0.00734*str2 + 0.00643*ns3$	0.62
Golden Whistler, <i>Pachycephala pectoralis</i>	$-2.42 + 0.000168*MNN + 0.532*LSI + 0.00170*str1 + 0.00350*ns2 + 0.00456*str2 + 0.00227*ns3$	0.71
Spotted Pardalote, <i>Pardalotus punctatus</i>	$-2.616 - 0.00265*Lrg - 0.138*ns1 + 0.00100*ns2 + 0.00407*str2 + 0.00353*ns3$	0.73
Scarlet Robin, <i>Petroica multicolor</i>	$-2.42 - 0.00264*TLA + 0.511*LSI + 0.00644*str1 + 0.0190*ns1 + 0.00408*ns2 + 0.00750*str2 + 0.00784*ns3$	0.77
Brush Bronzewing, <i>Phaps elegans</i>	$-2.98 + 0.00460*TLA - 0.519*LSI - 0.00319*str1 + 0.0296*ns1 - 0.00835*ns2 + 0.0159*ns4$	0.80
New Holland Honeyeater, <i>Phylidonyris novaehollandiae</i>	$-1.45 + 0.00383*TLA - 0.153*NumP + 0.840*LSI - 0.0122*str1 - 0.0219*str2 - 0.0101*ns2 - 0.00371*ns3$	0.74

Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	$-2.48 + 0.632*LSI + 0.00183*str1 + 0.00525*ns2 + 0.00348*str2 + 0.00369*ns3 - 0.178*ns4$	0.78
Adelaide Rosella, <i>Platycercus elegans</i>	$-1.00 - 0.331*NumP + 1.21*LSI - 0.00635*str1 - 0.00975*str2 - 0.00460*ns2 + 0.00755*str2 - 0.00292*ns3$	0.69
Eastern Rosella, <i>Platycercus eximius</i>	$-2.61 - 0.00439*TLA - 1.23*ns1 + 0.0149*ns2 - 0.651*ns4$	0.81
Grey Fantail, <i>Rhipidura fuliginosa</i>	$-1.44 - 0.00154*TLA - 0.154*NumP + 0.793*LSI + 0.00690*str1 + 0.00305*ns2 + 0.00454*str2$	0.69
White-browed Scrubwren, <i>Sericornis frontalis</i>	$-4.39 - 0.00490*TLA - 0.121*NumP + 1.35*LSI + 0.00361*Lrg + 0.00627*str1 + 0.0330*ns1 + 0.00378*ns2 + 0.00631*str2 + 0.00535*ns3$	0.80
Grey Currawong, <i>Strepera versicolor</i>	$-2.78 - 0.203*NumP - 0.00254*MPS + 1.18*LSI + 0.00474*str1 + 0.00614*ns2 + 0.00459*str2 + 0.00378*ns3$	0.77
Rainbow Lorikeet, <i>Trichoglossus haematodus</i>	$-1.68 + 0.00181*TLA + 0.000159*MNN + 0.434*LSI - 0.00291*str1 - 0.0180*str2 + 0.00333*ns2 - 0.0107*ns3 - 0.0194*ns4$	0.71
<b>ns = non-stringybark</b> <b>str = stringybark</b> <b>1 = open forest</b> <b>2 = woodland</b> <b>3 = low woodland</b> <b>4 = shrubland/heathland</b>		

**Table 2.** Species included in the optimization and their logistic regression functions.

We included a species in our optimization algorithms if its distribution model had a ROC (Receiver Operating Characteristic) area under the curve value exceeding 0.6. ROC is a measure of a model's discrimination, and the area under the curve value is equivalent to the probability that the model can discriminate between a true positive and a true negative value (Hanley and McNeil 1982, Fielding and Bell 1997, Elith 2000, Pearce and Ferrier 2000). A value exceeding 0.6 implies that the model is at least 20% better than random. Since there are no independent data on which to evaluate the models, we have jackknifed the original data. A total of 29 species out of 37 have models with adequate discrimination (Table 2).

The South Australian Department of Environment Heritage and Aboriginal Affairs compiled the vegetation GIS coverage used for the logistic regression analyses in 1986, based on aerial photographs interpretation (1:40000 maps) and extrapolation from point-based sampling. DEHAA identified a total of 46 remnant vegetation communities and five structural types in terms of overstory dominance, defined as having a proportion of occurrence greater or equal to 40%. The vegetation remnant comprised about 10% of the study area, according to the original coverage. We have used new updated vegetation coverage for the optimization program, based primarily on aerial photographs (1:4000) taken in 2000. The new coverage has been augmented with site data from about 500 more sites, complete with cover information on all species, and complete species presence lists for over 300 sites. There are 51 floristic groups, defined by dominant species and organized into open forest, woodland, mallee, shrubland, coastal shrubland, grassland, sedgeland and fernland. Due to a finer minimum mapping unit (1 ha) and more detailed

mapping in general, the proportion of native vegetation in the landscape is now calculated to be about 16% of the region, though this may include sites with degraded understories.

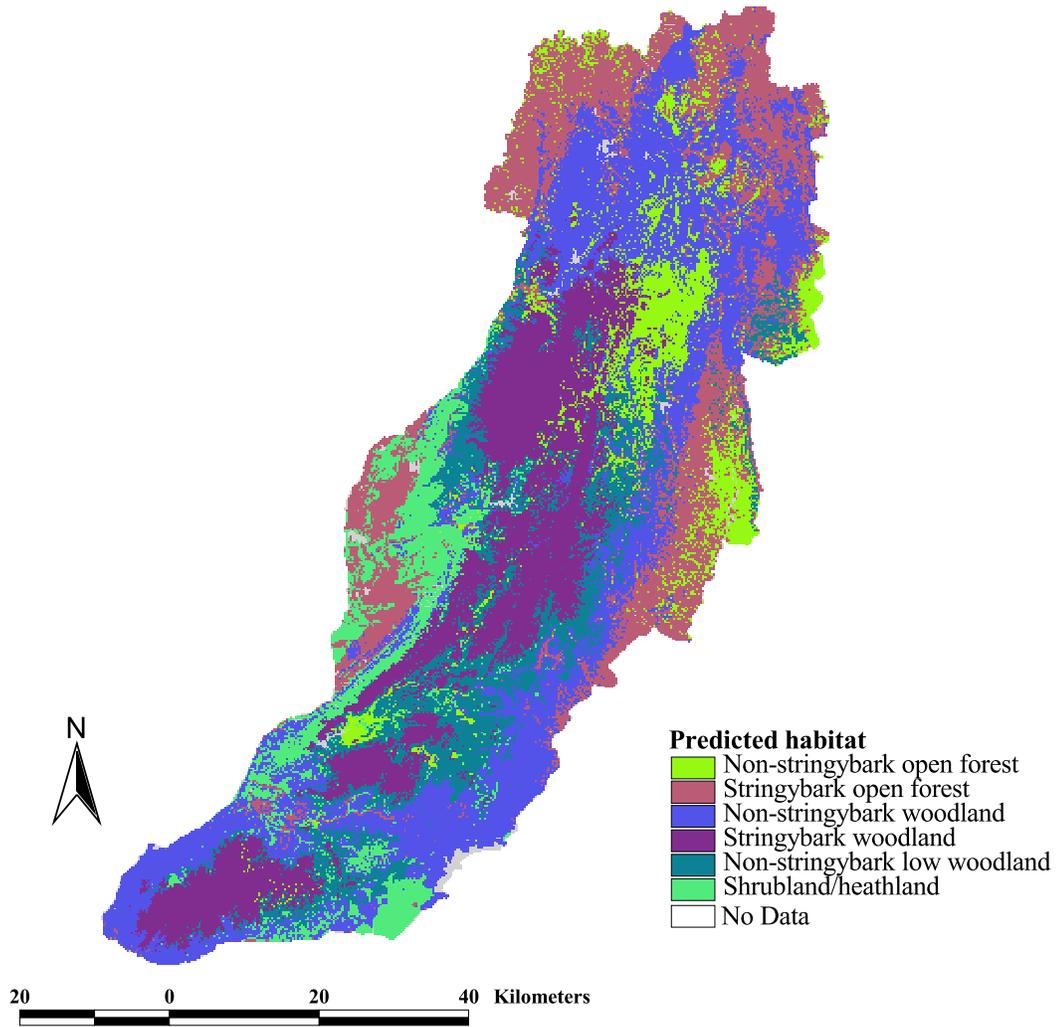
We explore both scenarios with equal site costs and variable site costs, and for the latter, the cost of revegetation is assumed to be a linear function of property values. The South Australian Australian Department of Environment and Heritage extrapolated the property value coverage from values assigned by the South Australia Valuer General. There are a total of 193,239 parcels, with a mean area of 2.92 ha ( $\sigma = 14.92$  ha) (Bagg, *pers. comm.*). We used a vector coverage of land use, compiled by the South Australian Department of Transport, Urban Planning and the Arts in 1991, to exclude sites in our optimization program that are urban areas, reservoirs and quarries. We converted both these vector coverages to rasters (grids) with a 6.25 ha grain size, in accord with the vegetation data. About 10% of the approximately 83,000 sites in the region did not have property value data, so we simply interpolated based on the average of the values within a one-cell neighborhood. The sites with missing property value data are well distributed in the region and are not disproportionately biased to any land use type.

We investigate scenarios where the restored sites can become any one of the habitat types and where the restoration is constrained to the most probable habitat type as derived from a multinomial regression of habitat type as a function of 21 environmental variables (nnet library, S-Plus 2000, MathSoft Inc., 1999) (Venables and Ripley 1999) (Table 3). Of a total of about 1200 existing native vegetation sites, the regression model classified the habitat type correctly in 47% of the site (Figure 4).

<b>Environmental variables</b>
Soil moisture index
Relative short-wave radiation ratio
Soil drainage
Minimum topographic temperature
Maximum topographic temperature
Soil salinity
Soil rockiness
Soil pH
Soil fertility
Mean temperature driest quarter
Mean temperature wettest quarter
Rainfall wettest period
Rainfall seasonality
Rainfall driest period
Minimum temperature coldest period
Minimum temperature warmest period
Mean annual temperature
Mean annual rainfall
Diurnal temperature range
Annual temperature range
Annual moisture index

**Table 3.** Environmental variables used in the multinomial regression of habitat types. For more details, see (Bryan 2000).

# Predicted Vegetation



**Figure 4.** The predicted habitat types as derived from a multinomial regression of environmental variables.

### *Objective function and constraints*

We set our objective to maximize the summed probability of occurrence over all bird species and all revegetated sites in the region, given some budget  $q$ . Let  $\mathbf{y}$  be the original landscape with no revegetation, where each element,  $y_i \in [0, 1]$ . If the site is vegetated, then  $y_i = 1$ , otherwise  $y_i = 0$ . Likewise,  $\mathbf{x}$  is the landscape vector with revegetation added, where each element,  $x_i \in [0, 1]$ . Furthermore,  $\mathbf{h}$  is the habitat type vector, where each element,  $h_i \in [1 \dots 6]$ , is one of the six coarse habitat types for the vegetated sites. Let  $n$  be the number of species under consideration, and  $m$  the number of sites (grid cells) in the landscape. Our control variable is which sites to select for revegetation. The objective function is:

$$\text{Maximize } V(\mathbf{h}) = \left[ \sum_{j=1}^n \sum_{i=1}^m (x_i - y_i) p_{ij}(\mathbf{h}) \right] \quad (1)$$

$$\text{Subject To : } C(\mathbf{x}) = \sum_{i=1}^m c_i (x_i - y_i) \leq q, \quad \sum_{k=1}^6 w_k \geq 0.1m$$

where  $p_{ij}(\mathbf{h})$  is the probability that species  $j$  would occur if site  $i$  was revegetated, which is a function of the habitat in a neighborhood around site  $i$ ,  $c_i$  is the cost of acquisition and/or revegetation for site  $i$ . The second constraint is that the number of sites of each habitat type,  $w_k$ , must be greater or equal to 10% of the total number of sites. The probabilities of occurrence are the fitted probabilities from the logistic regression models (with the range in probabilities standardized from 0.0 to 1.0) and so are calculated from the landscape metrics of the 2 km. neighborhood around and including site  $i$ . We have

chose to weight all species equally. Westphal and Possingham (*submitted*) have explored modifications of the above objective function, such as adding a boundary length penalty and converting probabilities of occurrence to population density with various functional forms. The former is already implicitly incorporated in the logistic regression functions, as most species respond positively to large, compact patches. The decision how to weight boundary length, to reduce management costs for example, in comparison to the probabilities of occurrence is the domain of policy. The conversion of probabilities of occurrence to population density adds one more layer of uncertainty, so, here we confine ourselves to maximizing the summation of probabilities of occurrence. An alternative to the objective function is to make the summation across all vegetated sites, not just the revegetated sites. However, computationally it is more intensive, and exploration showed that it did not significantly change the solutions. We have explored the objective function at three budget sizes (1000, 5000, 10000 ha) and under the scenario where a restored site can become any habitat type (“any habitat”) and where the habitat type is constrained to be the most probable type as calculated from the multinomial regression (“predicted habitat”).

Secondly, we repeated the 1000 ha budget scenarios using property value data. Now the cost of site  $i$ ,  $c_i$ , is the property value (\$/ha), normalized by dividing by the median site value. The “effective” area of a site is the site area (6.25 ha) multiplied by the site property value, divided by the median property value. Property values are an imperfect measure of true revegetation costs, with the true costs of habitat restoration lying somewhere between the equal site cost scenario and the inclusion of property values. Moreover, errors necessarily arise when spatial vector data is converted to raster

coverage and there is discordance between the scale of the properties (average size = 2.92 ha.) and the scale of the planning unit used in the optimization (6.25 ha).

We also modified the above multi-species objective function and explored single-species habitat restoration for three focal species: the Brush Bronzewing (*Phaps elegans*), the Brown Treecreeper (*Climacteris picumnus*) and the Scarlet Robin (*Petroica multicolor*). Possingham and Field (2001) list the Brush Bronzewing and the Brown Treecreeper as being vulnerable to extinction within the next 200 years. Moreover, the Brush Bronzewing can be considered an umbrella species for heathland. The Scarlet Robin is a species of concern, and nationally, the number of sightings has fallen by 21% over the last 20 years (Cogger et al. 2003). We then calculated the corresponding objective function across all species to see how well the single-species solutions approximated that of the whole community.

### *Optimization algorithm*

The number of available locations for restoration,  $L$ , in the MLR is about 70,000. If the budget size is 10000 ha ( $M = 1600$  sites for the equal cost scenario), for example, then

the number of possible locations is:  $\binom{L}{M} = \binom{70000}{1600} \approx 2.74 \times 10^{3310}$ . For the scenario

where the restored site can become any habitat type, the number of combinations is:

$\approx 2.74 \times 10^{3310} \times 6^{1600}$ . The problem is *NP-hard* (Cormen et al. 1990), and so we employ

the iterative heuristic algorithm simulated annealing (Metropolis et al. 1953, Kirkpatrick et al. 1983) to find near-optimal solutions. The concept of simulated annealing is

derived from metallurgy, where a substance is heated and then cooled to obtain a desired crystalline structure.

To implement this algorithm for our landscape restoration problem, we first select a random restored landscape, and then the algorithm iteratively explores neighboring solutions by randomly adding or deleting sites to the system. Initially, any change is accepted, and as the *temperature* is lowered, the algorithm becomes choosier, rejecting changes that decrease the value of the objective function too much. By the end of the iterations, when the system is “cold”, the algorithm only accepts positive changes. The simulated annealing algorithm for the MLR habitat reconstruction problem is structured as follows:

- I. Set the temperature,  $T$ , which is the acceptance parameter.
- II. Generate a random restoration landscape, excluding those sites that are urban areas, reservoirs or quarries. For every revegetated site, the program searches a neighborhood of 2 km. around it, calculates the landscape metrics, and then determines the probability of occurrence for every species. For the scenario where each restoration site can become any habitat, the habitat type that maximizes the probability of occurrence is selected, within the constraint of having 10% representation for each habitat type. Summed across all sites, this gives the objective function,  $V(\mathbf{x}_1)$ .
- III. Randomly choose a site to delete from and then add to the landscape. Continue adding random sites, if the habitat constraint is not exceeded, until the cost  $C(\mathbf{x}_2) \geq q$ . Delete sites, until  $C(\mathbf{x}_2) \leq q$ . Evaluate the change in the

objective function,  $\Delta V = V(\mathbf{x}_2) - V(\mathbf{x}_1)$ : if  $e^{\frac{\Delta V}{T}} >$  uniform random number  $[0, 1]$ , then accept change,  $\mathbf{x}_1 \leftarrow \mathbf{x}_2$

- IV. If the temperature,  $T$ , has not been lowered for  $y$  iterations, reduce the temperature. Otherwise, the temperature remains unchanged.
- V. Go to step III for the set number of iterations or until the  $V(\mathbf{x}_1)$  is not replaced after  $z$  times.

The temperature reduction is determined by an adaptive cooling schedule (Westphal and Possingham, *submitted*, Huang et al. 1986). The number of times spent at each temperature,  $y$ , is set to 50. Finally, the algorithm terminates if a change is not accepted after 30 iterations ( $z$ ). After one run of the simulated annealing algorithm, the algorithm is repeated, except that only sites adjacent to already restored sites are chosen for possible addition to the restored landscape. The *Boltzmann* probability term of step III is still used to evaluate whether of site is added.

We augmented the simulated annealing algorithm with a *deterministic clustering algorithm (iterative improvement)* after the second pass of the simulated annealing algorithm. The clustering algorithm randomly selects a revegetated site and, if available, revegetates one of its neighbors and deletes a random site elsewhere if it improves the objective function. It continues the process with the other seven neighbors and then repeats the process with the other original revegetated sites, randomly chosen. The algorithm continues to repeat the clustering operation as long as new objective function is at least 5% better than the original objective function before the clustering. It ignores “tabu” sites evaluated in previous iterations of the clustering algorithm. The rationale

behind this clustering algorithm and the second run of the simulated annealing algorithm is that for many species, large contiguous patches are preferred.

Since the simulated annealing algorithm is non-deterministic, each run will generate a different solution. For each scenario and budget size, we ran the algorithm 50 times. All aspects of the optimization program, including the calculation of the landscape metrics, the simulated annealing algorithm and the deterministic clustering algorithm, are written in the C programming language. On an Intel Pentium IV processor, the average time to complete each run of the algorithm ranged from 90 - 400 minutes depending on the budget size.

We compared the near-optimal solutions generated from the optimization algorithms with other heuristics, such as accreting all the area to the largest patch, creating one large patch, creating focal patches of 100 ha, as well the solutions as generated from a defragmentation “scent” algorithm (Loehle 1999), which connects patches and makes them less sinuous. The latter is based on diffusion, where “scent” emanates from vegetated areas. The unrestored sites that have the highest concentrations after a given period of time are restored, within the 10% habitat representation constraint. The size of 100 ha focal patches is arbitrary, but is larger than or equal to the recommended size of patches as derived from some focal species restoration programs for birds in Australia (Watson et al. 2001, Brooker 2002).

## RESULTS

### *Summed irreplaceability*

One way to distill information on solutions obtained using stochastic algorithms is to show the *summed irreplaceability*, that is, over all runs, how many times a site is selected. Though the probability that any site  $i$  is selected in each run is given by a binomial distribution, according to the *Central Limit Theorem*, the number of selections for each site  $i$  over all  $n$  runs approaches a normal distribution. The *summed irreplaceability* of site  $i$  is:

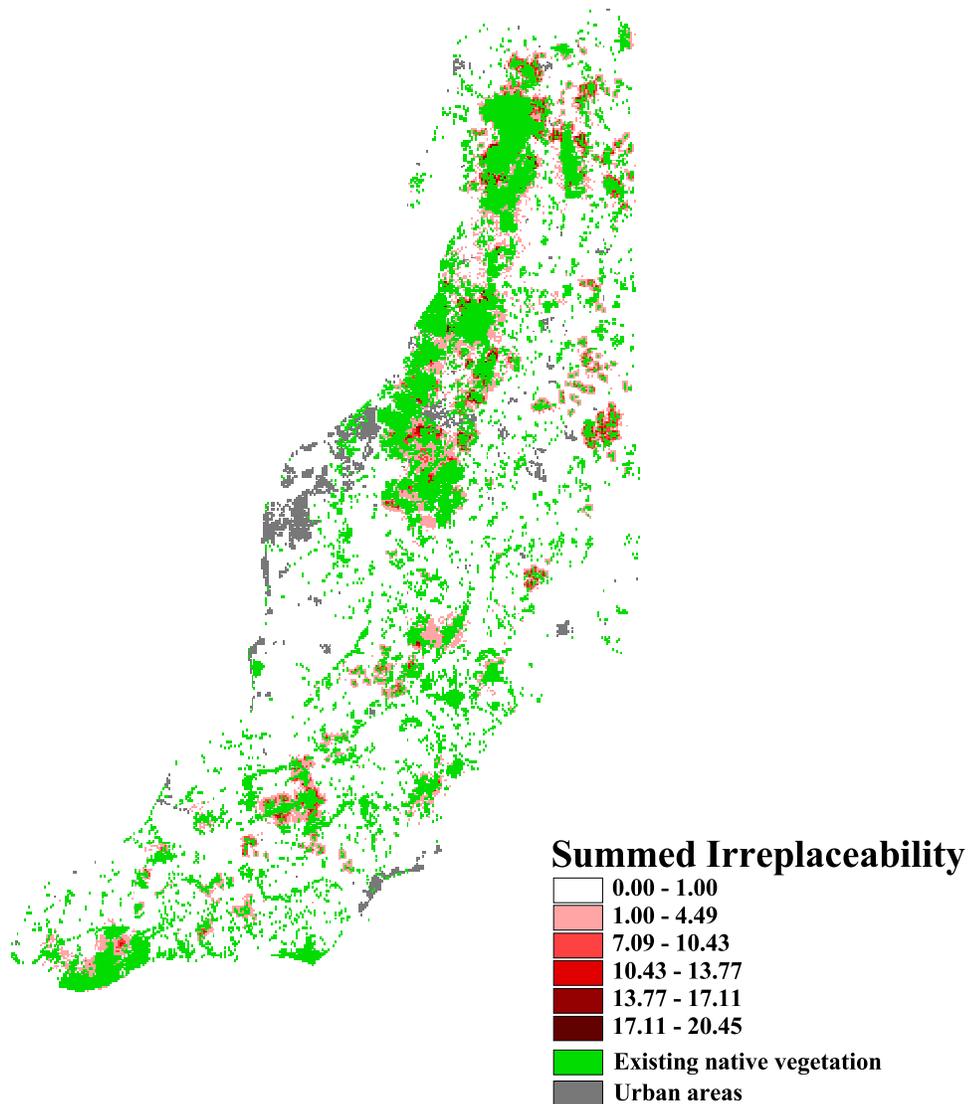
$$I_i^{qn} = \frac{\sum_{i=1}^n S_i}{P_i^{qn}} \quad (2)$$

The summation term in the numerator is the number of times that site  $i$  is selected over  $n$  runs of the algorithm, where  $s_i \in [0,1]$ . The  $p_i^{qn}$  is the 95% confidence interval value for the probability that site  $i$  would be selected at random, given a budget size,  $q$ , and the  $n$  replicates, assuming a normal distribution, with the mean and variance determined by 50 Monte Carlo trials where all available sites are chosen with equal probability. Hence, an  $I_i$  of greater than 1.0 indicates a site is selected on average more frequently than random, with a significance level,  $\alpha = 0.05$ . The sites with high summed irreplaceability are priority sites for revegetation.

Figures, 5-8, show the summed irreplaceability maps for the region. For the equal cost, any habitat scenario, many the highly selected sites are clustered near the largest contiguous blocks of vegetation in the northeast part of the region. Unlike Westphal and Possingham (*submitted*), more of the sites with high summed irreplaceability values are scattered in other parts of the region. This is due to the fact that the specific habitat type of the existing native vegetation is important, not just the presence of large patches. For the predicted habitat scenario, the distribution of highly irreplaceable sites is more confined to the very northern part of the region where there is not only is high density of exiting vegetation but where also most of predicted habitat is non-stringybark woodland, generally the most speciose of the habitat types. When property values are included, for both scenarios there is a general shift toward less expensive sites farther from the metropolitan Adelaide and the highly vegetated, main spine of the MLR.

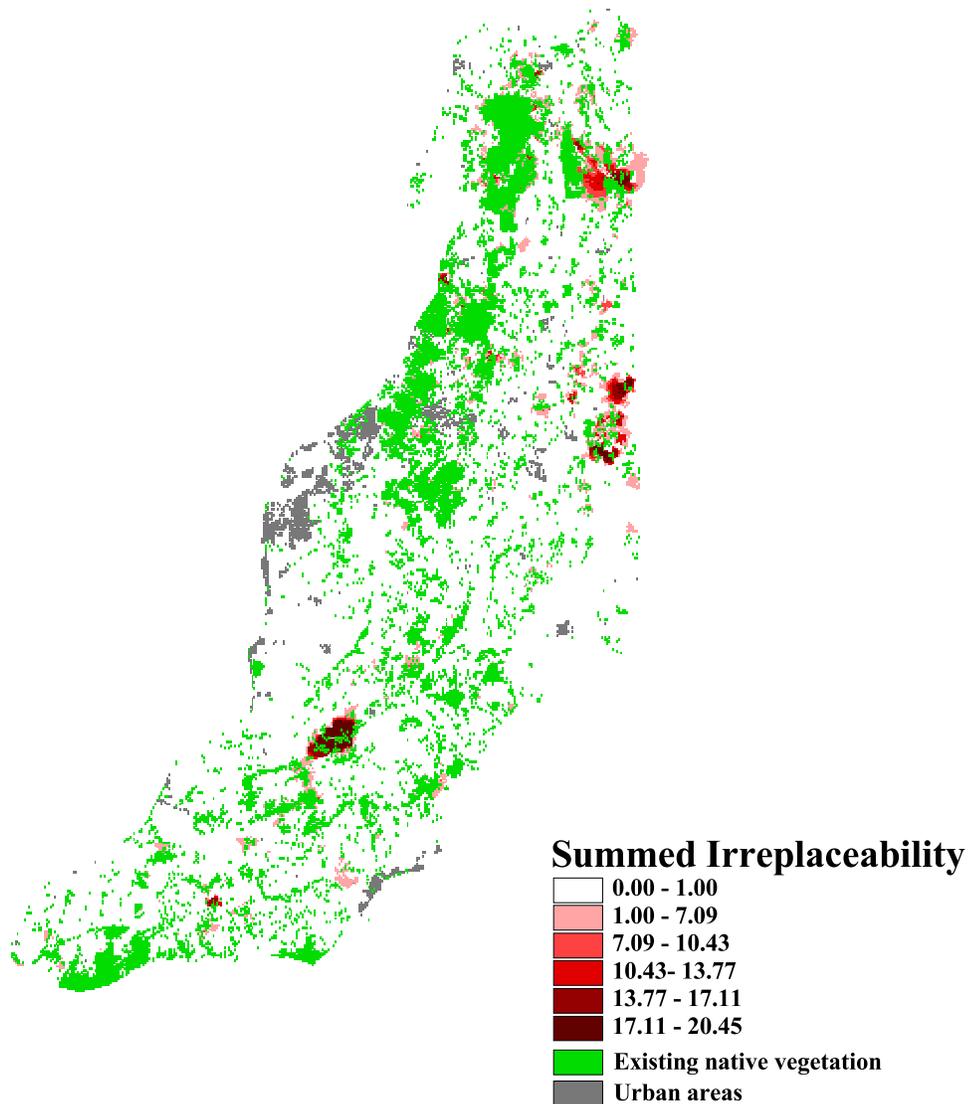
Table 4 shows a matrix of the Gower's similarity index for pairwise comparisons of the summed irreplaceability maps of the various scenarios (Legendre and Legendre 1983). In each pairwise comparison, we included only sites that had a summed irreplaceability value of greater than 1.0 for one of the maps. A Gower's similarity index of 1.0 indicates perfect concordance. Within each scenario but across budget size, the similarity indices are quite high ( $> 0.90$ ), indicating high concordance. In pairwise comparisons, the any habitat, variable site cost scenario is the most highly dissimilar, followed by the predicted habitat scenarios at the 5000 ha and 1000 ha budget sizes.

## MLR Optimal Habitat Reconstruction -10000 ha (Equal site costs, any habitat)



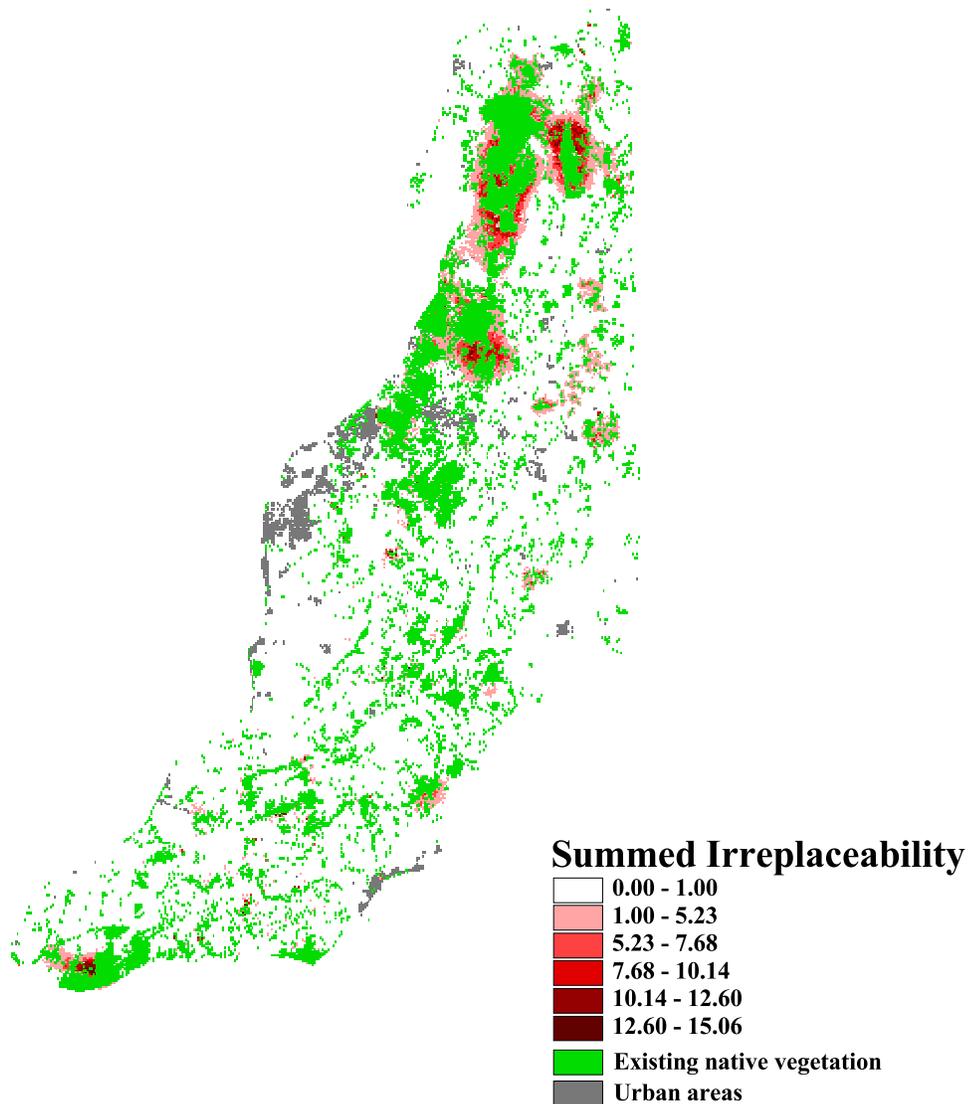
**Figure 5.** Summed irreplaceability for the 10000 ha scenario where each restored site can become any habitat type and the site costs are equal (50 runs).

## MLR Optimal Habitat Reconstruction -10000 ha (Property value, any habitat)



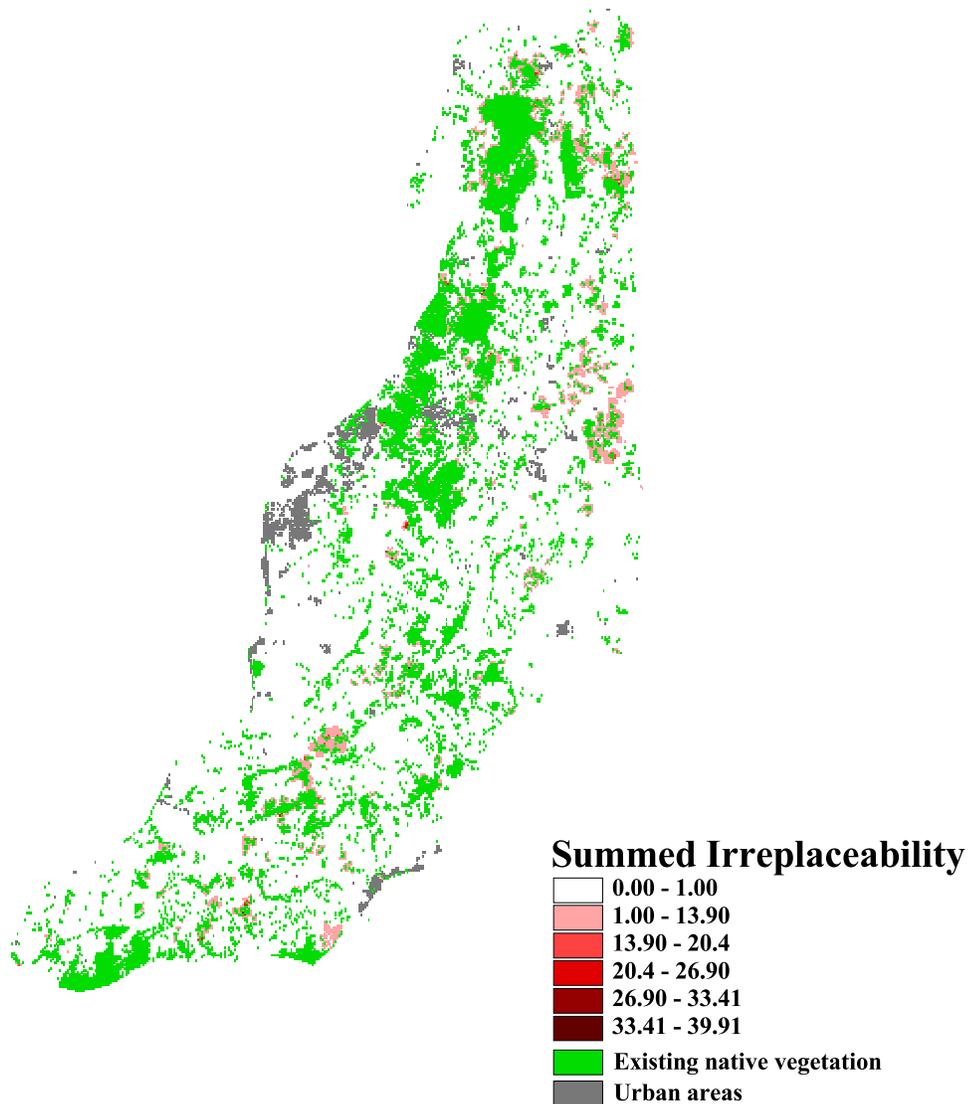
**Figure 6.** Summed irreplaceability for the 10000 ha scenario where each restored site can become any habitat type with property values included (50 runs).

## MLR Optimal Habitat Reconstruction -10000 ha (Equal cost, predicted habitat)



**Figure 7.** Summed irreplaceability for the 10000 ha scenario where each restored site can become only its predicted habitat type and the site costs are equal (50 runs).

## MLR Optimal Habitat Reconstruction -10000 ha (Property value, predicted habitat)



**Figure 8.** Summed irreplaceability for the 10000 ha scenario where each restored site can become only its predicted habitat type with property values included (50 runs).

	<b>Any (1000)</b>	<b>Any (5000)</b>	<b>Any (10000)</b>	<b>Any, PV (1000)</b>	<b>Predicted (1000)</b>	<b>Predicted (5000)</b>	<b>Predicted (10000)</b>	<b>Predicted, PV (1000 ha)</b>
<b>Any (1000)</b>	----- -	0.93	0.93	0.85	0.95	0.89	0.91	0.92
<b>Any (5000)</b>	0.93	----- -	0.92	0.80	0.94	0.86	0.84	0.93
<b>Any (10000)</b>	0.93	0.92	-----	0.81	0.95	0.87	0.82	0.94
<b>Any, PV (1000)</b>	0.85	0.80	0.81	-----	0.90	0.77	0.79	0.88
<b>Predicted (1000)</b>	0.95	0.94	0.95	0.90	-----	0.95	0.95	0.93
<b>Predicted (5000 ha)</b>	0.89	0.86	0.87	0.77	0.95	-----	0.94	0.90
<b>Predicted (10000)</b>	0.91	0.84	0.82	0.79	0.95	0.94	-----	0.91
<b>Predicted, PV (1000 ha)</b>	0.92	0.93	0.94	0.88	0.93	0.90	0.91	-----

**Table 4.** Matrix of the Gower's Similarity Index for pairwise comparisons of the summed irreplaceability maps of the various scenarios. The values in the parentheses are the budget sizes in hectares (Any = any habitat, predicted = predicted habitat, PV = property value).

### *Comparison with other heuristics*

The question always remains as to whether optimality is important. That is, if the optimal solution is only marginally better than simple rules, then the optimization approach is extraneous. Table 5 shows a comparison of the objective function values between the multi-species optimization solution and the single-species solutions and other simple heuristics for the equal cost scenarios.

Only considering the scenarios where the alternative landscape heuristics were able to satisfy the habitat representation constraint, then the alternative landscape heuristics had objective function values that ranged from 48 – 73% of the near-optimal values from the simulated annealing algorithm. Simply randomly distributing habitat across the landscape performs poorly, with objective values less than 50% of that of the near-optimal solutions. Though we have not exhausted the possibilities of simple rules for revegetation that one could intuit, it is likely that other simple rules would be inadequate as well. These results indicate the utility of adopting a decision-theory framework with iterative heuristic algorithms for landscape design problems. The single-species solutions poorly approximate the multi-species solutions, with objective function values that are only 63 – 91% the *a priori* multi-species scenarios. The Brown Treecreeper performs better than the other two species as a surrogate for the community that we have considered.

We did not compare the solutions for the variable cost scenarios, because they resulted in highly varying numbers of revegetation sites. A strategy may be poor because fewer restoration sites are selected (and hence more expensive); however, the other

revegetation costs, which may a function of the number of sites, may be lower. Likewise, a fairly good strategy would be to select simply the least expensive sites based on property values, but that would lead to a fragmented landscape with a low objective value per site ratio and the subsequent costs of revegetation would be obviously quite high. Our goal for including property values as a surrogate for costs is to indicate how the resulting optimal restoration landscape may differ greatly with variable site costs.

	<b>Heuristic</b>								
<b>Scenario</b>	SA (multi-species)	SA (Scarlet Robin)	SA (Brown Treecreeper)	SA (Brush Bronzewing)	Scent algorithm	Largest patch	One large patch	Focal patch (100 ha)	Random
Any (1000)	2937 (54)	1981 <sup>a</sup> (31)	2525 <sup>a</sup> (70)	1857 <sup>a</sup> (37)	2112 <sup>b</sup>	1985 <sup>a</sup> (168)	1562 <sup>a</sup> (203)	1403 <sup>a</sup> (147)	1251 <sup>a</sup> (41)
Any (5000)	14685 (157)	————	————	————	9882 <sup>b</sup>	9601 <sup>a</sup> (666)	8582 <sup>a</sup> (916)	7070 <sup>a</sup> (335)	6346 <sup>a</sup> (69)
Any (10000)	29370 (288)	————	————	————	18613 <sup>b</sup>	18948 <sup>a</sup> (1019)	17792 <sup>a</sup> (1485)	14197 <sup>a</sup> (415)	12847 <sup>a</sup> (93)
Predicted (1000)	2837 (104)	2090 <sup>a</sup> (27)	2573 <sup>a</sup> (88)	1929 <sup>a</sup> (36)	2073 <sup>b</sup>	2692 <sup>ac</sup> (421)	2090 <sup>ac</sup> (462)	1448 <sup>a</sup> (112)	1281 <sup>a</sup> (36)
Predicted (5000)	14151 (249)	————	————	————	9741 <sup>b</sup>	13337 <sup>ac</sup> (1483)	7902 <sup>a</sup> (757.87)	7429 <sup>a</sup> (310)	6592 (68)
Predicted (10000)	28292 (309)	————	————	————	1823 <sup>b</sup>	26378 <sup>ac</sup> (2909)	16067 <sup>a</sup> (2232)	15257 <sup>a</sup> (1588)	13528 (137)
<sup>a</sup> Solution mean is significantly different from near-optimal multi-species mean, as determined from a two-sample test with unequal variances ( $p < 0.05$ ) (Zar 1999) <sup>b</sup> Solution is outside the 95% confidence interval of the mean of the near-optimal multi-species solution (Zar 1999) <sup>c</sup> The habitat type 10% representation criterion is not met									

**Table 5.** A comparison of the objective function values of the near-optimal simulated annealing (SA), multi-species solution with single-species solutions and other heuristics. Standard deviations are in parentheses. Each heuristic was run 50 times. The values in the parentheses are the budget sizes in hectares (Any = any habitat, predicted = predicted habitat).

### *Landscape characterization*

Another way to render information on the revegetated landscapes is to characterize their configuration, including the number of existing and new revegetated patches and patch connectivity, which is displayed in Table 6. The mean patch sizes for the optimization scenarios refer only to patches that have some portion that is new revegetated area. Likewise, the connectivity measure only includes revegetated patches. The average size of revegetated patches ranges from 112 – 598 ha, compared to the average patch size of 35 ha in the present, unvegetated landscape. This is less than the average size of the revegetated patch found in Westphal and Possingham (*submitted*), where only a binary landscape was considered. Now the probabilities of occurrence are also a function of the habitat types not just the landscape configuration alone, and more sites are selected away from the main spine of the MLR. The percent of revegetated area that is in the form of new patches ranges from 5 – 22%; generally accreting area to existing patches is the more favorable tack. The percentage is higher in the any habitat, equal site cost scenario because the restored sites are distributed more widely across the MLR. The mean nearest neighbor distance is reduced (MNN) about 70% at small budget sizes, but at larger budget sizes, there is no significant difference from the present unvegetated landscape.

In terms of the percentage of each habitat type, only non-stringybark woodland and stringybark woodland exceed the 10% criterion. Under the any habitat scenario, more revegetated sites are stringybark woodland, while under the predicted habitat scenario, more sites are non-stringybark woodland. This illustrates the complexity of the

species responses to the landscape and how varying the habitat constraints changes the solution results. The near-optimal solutions result in summed probabilities of occurrence in the restored sites that are increased from 50 – 130% over the present unvegetated landscape. Adding the additional factor of variable site costs results in solutions with lower average probabilities of occurrence.

<b>Objective Function*</b>	<b>Budget size (ha)</b>	<b>Revegetation Area (ha)</b>	<b>MPS total (ha)</b>	<b>MPS new (ha)</b>	<b>MPS existing (ha)</b>	<b>% New Patch</b>	<b>MNN (m)</b>	<b>Avg. % Occurrence</b>
Any	1000	-----	598 (84)	8 (2)	882 (123)	13 (4)	62 (18)	63 (1)
	5000	-----	176 (16)	7 (0)	348 (28)	21 (3)	129 (13)	63 (1)
	10000	-----	112 (10)	7 (0)	260 (17)	22 (3)	202 (27)	63 (1)
Any, PV	1000	6454 (680)	417 (44)	11 (6)	598 (70)	5 (3)	73 (56)	45 (5)
Predicted	1000	-----	698 (90)	7 (1)	990 (144)	9 (3)	66 (22)	61 (2)
	5000	-----	234 (18)	7 (1)	395 (36)	9 (1)	102 (19)	61 (1)
	10000	-----	135 (9)	7 (0)	264 (19)	10 (1)	158 (29)	61 (1)
Predicted habitat, Property values	1000	1872 (688)	298 (36)	7 (3)	389 (41)	11 (4)	97 (52)	40 (6)

<b>Objective Function*</b>	<b>Budget size (ha)</b>	<b>% ns1</b>	<b>% str1</b>	<b>% ns2</b>	<b>% str2</b>	<b>% ns3</b>	<b>% ns4</b>
Any	1000	11 (0)	10 (0)	27 (4)	31 (4)	10 (0)	10 (0)
	5000	12 (1)	10 (0)	21 (3)	37 (3)	10 (0)	10 (0)
	10000	16 (2)	10 (0)	18 (2)	36 (3)	10 (2)	10 (0)
Any, PV	1000	10 (0)	10 (0)	12 (2)	48 (2)	10 (0)	10 (0)
Predicted	1000	11 (0)	11 (0)	39 (8)	19 (8)	11 (0)	10 (0)
	5000	10 (0)	10 (0)	41 (5)	19 (5)	10 (0)	10 (0)
	10000	10 (0)	10 (0)	41 (4)	19 (4)	10 (0)	10 (0)
Predicted, PV	1000	12 (2)	15 (3)	33 (4)	18 (3)	12 (2)	10 (1)
Present landscape		13	15	25	17	20	9
	<b>Area (ha)</b>	<b>MPS (ha)</b>	<b>MNN (m)</b>	<b>Avg. % Occur.</b>			
Present landscape	78369	35	194	27			

**Table 6.** Summary of the landscape characteristics for the five scenarios (over 50 runs of the algorithm). Standard deviations are in parentheses (Any = any habitat, predicted = predicted habitat, PV = property value).

## DISCUSSION

### *The use of a decision theory framework*

We have shown how the problem of habitat reconstruction can be formalized in a decision-theory framework, where the objective and constraints are explicitly expressed. A decision-theory framework is a rigorous, repeatable and transparent methodology and forces one to be precise in terms of goals and the compartmentalization of the problem, and in this sense, has much heuristic value as well. Yet a decision-theory tool is a decision-support aid not a decision-maker. The maps on priority sites and the landscape configuration characteristics of the restored landscapes that we have presented are not sacrosanct. There obviously are other social and political factors that impress upon the problem. They are not even platonic ideals, as with any modeling exercise, often as many important factors are absent as those that are included. Our work is an impressionistic understanding of strategic revegetation in the MLR and the methodology is flexible. It can be elaborated or altered in several ways, such as: the modification of the planning unit scale, finer or different habitat type divisions, variable species weighting, the delineation of “verboden” sites, the inclusion of a criterion based on assuring a certain level of representation of restoration sites in all subregions of the MLR, the use of a pre-European vegetation map instead of the predicted habitat types, more detailed site costs and updated species distribution models, which could include patch-level variables. However, the absence of perfect information on a system does not

preclude the use of decision-support tools, as decisions in conservation biology usually have to be with a certain exigency.

There has often been a disconnect in conservation between economics and ecology, and the decision theory framework, it must be emphasized, allows one to easily incorporate costs. It is difficult to *a priori* assign site costs, and we have presented two extrema here. The equal site cost scenarios implicitly assume that revegetation costs are much greater than property acquisition, which do not vary across the region. Of course, revegetation cost may be a function of the spatial context of the site, such as the distance from Adelaide or the proximity to areas of native vegetation, as well as the environmental variables of the site. Property value is an imperfect measure of sites costs, as there is no inclusion of revegetation costs. In fact there may no relationship between a site's property value and the ability to restore that site. Owners of high value properties (e.g. hobby farms, tourist-related properties) may be willing to revegetate, as there may be some value added effects. However, others, such as vineyards may be unwilling to cede productive lands.

There are a plethora of heuristics that may be effective in optimal habitat restoration problems, including genetic algorithms, tabu search, stochastic evolution, simulated evolution, great deluge, hybrid approaches and simple greedy algorithms (Sait and Youssef 1999, Bettinger 2002). We have chosen simulated annealing because of its simplicity. In reserve design, for example, there has been some criticism of iterative heuristics in favor of the use of integer linear programming (Rodrigues 2000, 2002); however, as is the case with any interesting landscape design problem, such as

revegetation in this paper, non-linearities in the response variable effectively preclude the use of these integer linear programming.

### *Species distribution models*

The probability functions of species occurrence in the landscape implicitly assume that where a species is present there is suitable habitat and that its distribution is static. The species may be in a declining non-equilibrium state, confined to remnant areas that have a low suitability. Metapopulation theory tells us that a survey of occupancy may not necessarily indicate habitat suitability (Hanski 1998, Hanski 1999). Moreover, there are false positive and more likely, false negative survey errors. Not all presences are equivalent, but without information on source-sink dynamics (Pulliam 1988, 1996) or population density, we have no way of addressing this problem. It would certainly be much more desirable to have some measure of population viability as our objective function. However, for most species there is a dearth of the requisite data for spatially-explicit population dynamic models, particularly dispersal information (Beissinger and Westphal 1998). In most regions, distribution data will be used *faute de mieux*. Some studies have shown that short-term persistence at least can be predicted from distribution data (Gates 2000, Araujo 2002). Our approach assumes that revegetation can duplicate the original microhabitat, such as the species assemblage and structural characteristics. Furthermore, this framework is the “if you build it they will come” approach and excludes the dynamics of species spread into newly revegetated areas. The diffusivity to newly revegetated areas may vary across the region.

*Biodiversity surrogates and representativeness*

Our goal has been to derive optimal habitat reconstruction strategies for birds in the Mount Lofty Ranges, though other species could easily be added if the data exist. Though we have used results from logistic regression analyses of distribution data, simple rules based on expert opinion can be used where there is a paucity distribution data. We have chosen species that are well representative of the avian community, and most of those species with isolated or partially isolated populations were included. However, as the results of the single-species scenarios indicate, it would be myopic to think that the results are applicable to the whole community. Unfortunately, due to the paucity of data, we were unable to include some rare species, such as the Black-chinned Honeyeater (*Melithreptus gularis*), Beautiful Firetail (*Emblema bellum*) and Flame Robin (*Petroica phoenicea*). Extrapolation of our results to other taxa would also most likely be errant. Surrogate schemes have proved rather inadequate in conserving other taxa. In a thorough review Andelman and Fagan (2000) examined the efficiency of umbrella species, flagship species and other taxon-based surrogate schemes in various regions of the United States and concluded that none of them performed better than random in terms of capturing other species or protecting habitat.

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# Appendix I

An example of the SDP metapopulation model used to look at optimal pasture mowing strategies in Chapter 2. The basic model is the same for the Southern Emu-wren work in Chapter 1. Written in the C programming language.

```
/*Start with 4 identical patches; exact patch geometry unimportant (spatially-implicit).
The extinction is a function of the time since last mowing; recolonization is global Levins-type.
State space: metapopulation pattern, vector of patch quality; total cost*/

/* The .h files are header files that the program reads. They are libraries that have specific predefined
functions */
#include <stdio.h>
#include <math.h>
#include <stdlib.h>
#include <assert.h>
#include <time.h>
#include "nrutil.h"

/* Below are defined constants and functions that will be used*/

#define N 4 /* 4 patches on hypothetical rectangular landscape */
#define T 20 /* Model will run for 20 yrs. with a 1 year time step */
#define popstates 16 /* 2^N number of states for the whole metapopulation -
each patch can either be occupied or not */
#define min(x, y) (((x) < (y)) ? (x) : (y))
#define max(x,y) (((x) > (y)) ? (x) : (y))
#define mow 625 /* # habitat quality states (4) ^ # number of patches (4) */
#define BUDGET 100 /* Total number of allowable mows over 100 yrs - ceiling is mow every patch each
year. This is varied. */
#define param 8
#define totalstrats 16 /* Each patch can be mowed or not, so 2^N total strategies at each time step */
#define emin 0.0
#define emax 1.0
#define max_m 1.0
#define min_m 0.0
#define sumoccupy 5 /* 4 patches - max summed occupancy is 4 */
#define sumhab 20 /* Maximum habitat value for each patch is 5, which is the lowest habitat quality. */
#define SWAP(a,b) itemp=(a);(a)=(b);(b)=itemp;
#define M 7
#define NSTACK 50
#define maxmow 4.0 /* 4 patches - maximum number that can be mowed at each time step is 4 */

void indexx(unsigned long n, float arr[], unsigned long indx[]);
void sort5(unsigned long n, float ra[], float rb[], float rc[], float rd[], float re[]);
double **ext_colon(int S[popstates][N+1],
int landscape[mow][N+1], int mgt[totalstrats][N+1], int mowstate, int stratcombo, double mowkill);
```

```

int main(void) /* Main function in the C language*/
{
    /* Below is the initialization of all the variables/parameters */

    int landscape[mow][5];
    int strat[totalstrats][5];
    int S[popstates][5];
    int mowstate, stratcombo;
    int a, b, c, d, h, i, j, k, l, z, t, all, y, w, q;
    int hab[N], feasible;
    double ***V1; /* Value in Bellman's equation. A 3-D array: budget, population state, landscape state */
    double ***V0; /* Value in Bellman's equation. A 3-D array: budget, population state, landscape state */
    double ***M0, ***M1; /* Other 3-D arrays: budget, population state, landscape state*/
    double **Tr; /* Matrix of state transition probabilities */
    double expmow[sumoccupy][sumhab][2], extprob[sumoccupy][sumhab][2],
    stratmow[sumoccupy][sumhab][2], weight, mowkill;
    double **sum, value, **numbmows, **realex;
    int nexthab, minstrat;
    int ***beststrat;
    FILE *ofp, *ofp2, *ofp3, *ofp4, *ofp5, *ofp6, *ofp7, *ofp8, *ofp9, *ofp10, *ofp11, *ofp12, *ofp13, *bud1,
    *bud2, *bud3, *bud4; /* Files that program prints to */
    float temparray1[mow], temparray2[mow], temparray3[mow], temparray4[mow], temparray5[mow];

    ofp = fopen("sdp_butterfly.txt", "w");
    ofp2 = fopen("sdp_butterfly_expectmow_mowkill1.txt", "w");
    ofp3 = fopen("sdp_butterfly_extprob_mowkill1.txt", "w");
    ofp4 = fopen("sdp_butterfly_strat_mowkill1.txt", "w");
    ofp5 = fopen("sdp_butterfly_expectmow_mowkill2.txt", "w");
    ofp6 = fopen("sdp_butterfly_extprob_mowkill2.txt", "w");
    ofp7 = fopen("sdp_butterfly_strat_mowkill2.txt", "w");
    ofp8 = fopen("sdp_butterfly_expectmow_mowkill3.txt", "w");
    ofp9 = fopen("sdp_butterfly_extprob_mowkill3.txt", "w");
    ofp10 = fopen("sdp_butterfly_strat_mowkill3.txt", "w");
    ofp11 = fopen("sdp_butterfly_expectmow_mowkill4.txt", "w");
    ofp12 = fopen("sdp_butterfly_extprob_mowkill4.txt", "w");
    ofp13 = fopen("sdp_butterfly_strat_mowkill4.txt", "w");
    bud1 = fopen("sdp_butterfly_budget_viability1.txt", "w");
    bud2 = fopen("sdp_butterfly_budget_viability2.txt", "w");
    bud3 = fopen("sdp_butterfly_budget_viability3.txt", "w");
    bud4 = fopen("sdp_butterfly_budget_viability4.txt", "w");

    M0 = malloc(popstates * sizeof(double *)); /* Malloc is the dynamic allocation of memory for the
    matrices. */

    for(i = 0; i <= popstates - 1; ++i){
        M0[i] = malloc(mow * sizeof(double));
    }
    for(i = 0; i <= popstates - 1; ++i){
        for(j = 0; j <= mow - 1; ++j){
            M0[i][j] = malloc(BUDGET* sizeof(double));
        }
    }
}

```

```

}
M1 = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    M1[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        M1[i][j] = malloc(BUDGET* sizeof(double));
    }
}

V0 = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    V0[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        V0[i][j] = malloc(BUDGET* sizeof(double));
    }
}

V1 = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    V1[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        V1[i][j] = malloc(BUDGET* sizeof(double));
    }
}

Ext1 = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    Ext1[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        Ext1[i][j] = malloc(BUDGET* sizeof(double));
    }
}

Ext0 = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    Ext0[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        Ext0[i][j] = malloc(BUDGET* sizeof(double));
    }
}

sum = malloc(popstates * sizeof(double));
    for(i = 0; i <= popstates - 1; ++i){
        sum[i] = malloc(totalstrats * sizeof(double));}

numbmows = malloc(popstates * sizeof(double));
    for(i = 0; i <= popstates - 1; ++i){
        numbmows[i] = malloc(totalstrats * sizeof(double));}

```

```

realext = malloc(popstates * sizeof(double));
    for(i = 0; i <= popstates - 1; ++i){
        realext[i] = malloc(totalstrats * sizeof(double));}

beststrat = malloc(popstates * sizeof(double *));
for(i = 0; i <= popstates - 1; ++i){
    beststrat[i] = malloc(mow * sizeof(double));}
for(i = 0; i <= popstates - 1; ++i){
    for(j = 0; j <= mow - 1; ++j){
        beststrat[i][j] = malloc(BUDGET* sizeof(double));
    }
}

for(q = 0; q <= 3; ++q){ /* Four different scenarios regarding the probability that the subpopulation is
extirpated due to mowing */

if(q == 0)
    mowkill = 1.0;
if(q == 1)
    mowkill = 0.5;
if(q == 2)
    mowkill = 0.25;
if(q == 3)
    mowkill = 0.01;

/* LANDSCAPE STATES: HOW LONG SINCE LAST MOWING; MAXIMUM IS 5, MINIMUM IS 1 */

h = 0; /* Initialize all different management. states */
for(i = 1; i <= 5; ++i){ /* Patch 1: 5 possible states */
    for(j = 1; j <= 5; ++j){ /* Patch 2 */
        for(k = 1; k <= 5; ++k){ /* Patch 3 */
            for(l = 1; l <= 5; ++l){ /* Patch 4 */
                landscape[h][0] = i;
                landscape[h][1] = j;
                landscape[h][2] = k;
                landscape[h][3] = l;
                landscape[h][4] = i+j+k+l; /* Sum of the habitat states of the four
patches */

                temparray1[h+1] = i;
                temparray2[h+1] = j;
                temparray3[h+1] = k;
                temparray4[h+1] = l;
                temparray5[h+1] = i+j+k+l;
                ++h;
            }
        }
    }
}

sort5(mow, temparray5, temparray1, temparray2, temparray3, temparray4); /* Sort arrays, lowest
landscape[h][4] to highest */

for(i = 0; i <= mow - 1; ++i){
    landscape[i][0] = (int) (temparray1[i+1]);

```

```

        landscape[i][1] = (int) (temparray2[i+1]);
        landscape[i][2] = (int) (temparray3[i+1]);
        landscape[i][3] = (int) (temparray4[i+1]);
        landscape[i][4] = (int) (temparray5[i+1]);
    }

    /* MGT VECTOR: WHICH PATCHES ARE TO BE MOWED: EACH PATCH CAN BE MOWED OR
    NOT */

    h = 0;
    for(i = 0; i <= 1; ++i){ /* Patch 1: 1 is mow, 0 is leave alone */
        for(j = 0; j <= 1; ++j){ /* Patch 2 */
            for(k = 0; k <= 1; ++k){ /* Patch 3*/
                for(l = 0; l <= 1; ++l){ /* Patch 4 */
                    strat[h][0] = i;
                    strat[h][1] = j;
                    strat[h][2] = k;
                    strat[h][3] = l;
                    strat[h][4] = i+j+k+l;
                    ++h;
                }
            }
        }
    }

    /* POPULATION STATES: PATCH OCCUPANCY: EACH PATCH CAN BE OCCUPIED (1) OR NOT
    (0) */

    z = 0; /* A matrix of states; 1 occupied, 0 unoccupied; this
    gives all possible patterns for the metapopulation. */
    for (a = 0; a <= 1; ++a){ /* Patch 1 */
        for(b = 0; b <= 1; ++b){ /* Patch 2 */
            for(c = 0; c <= 1; ++c){ /* Patch 3 */
                for(d = 0; d <= 1; ++d){ /* Patch 4 */

                    S[z][0] = a;
                    S[z][1] = b;
                    S[z][2] = c;
                    S[z][3] = d;
                    S[z][4] = a+b+c+d;

                    temparray1[z+1] = a;
                    temparray2[z+1] = b;
                    temparray3[z+1] = c;
                    temparray4[z+1] = d;
                    temparray5[z+1] = a+b+c+d;

                    ++z;
                }
            }
        }
    }

    sort5(popstates, temparray5, temparray1, temparray2, temparray3, temparray4); /* Sort array as before. */

    for(i = 0; i <= popstates - 1; ++i){
        S[i][0] = (int) (temparray1[i+1]);
        S[i][1] = (int) (temparray2[i+1]);

```

```

        S[i][2] = (int) (temparray3[i+1]);
        S[i][3] = (int) (temparray4[i+1]);
        S[i][4] = (int) (temparray5[i+1]);
    }

    for(z = 0; z <= mow - 1; ++z){
        if((S[z][0] == 1) && (S[z][1] == 1) && (S[z][2] == 1) && (S[z][3] == 1)){
            all = z; /* All patches occupied */
        }

        for(i = 0; i <= sumoccupy - 1; ++i){ /* Initializing matrices to 0 which will be used later */
            for(j = 0; j <= sumhab - 1; ++j){
                expmow[i][j][0] = 0;
                expmow[i][j][1] = 0;

                extprob[i][j][0] = 0;
                extprob[i][j][1] = 0;

                stratmow[i][j][0] = 0;
                stratmow[i][j][1] = 0;
            }
        }

        /* INITIALIZATION OF THE VALUE OF THE METAPOPOPULATION FOR EVERY BUDGET,
        LANDSCAP STATE AND POPULATION STATE: if at the end of the time horizon, at least one patch is
        occupied, then the metapopulation has a value of 1, else it is 0 */

        for(z = 0; z <= mow - 1; ++z){
            for(i = 0; i <= popstates - 1; ++i){
                for(j = 0; j <= BUDGET - 1; ++j){
                    if((S[i][0] == 1) || (S[i][1] == 1) || (S[i][2] == 1) || (S[i][3] == 1)){
                        V1[i][z][j] = 1.0;
                        Ext1[i][z][j] = 1.0; }

                    else {
                        V1[i][z][j] = 0.0;
                        Ext1[i][z][j] = 0.0; }

                }
            }
        }

        /* SDP BACKSTEPPING – CORE OF THE PROGRAM */

        for(t = T - 1; t >= 0; --t){ /* Iterate backwards from time T-1 to 0, where T is the time horizon */
            for(y = 0; y <= BUDGET - 1; ++y){ /* BUDGET – y = available budget */
                for(z = 0; z <= mow - 1; ++z){ /* Evaluate for each mowing (habitat) state */
                    for(k = 0; k <= totalstrats - 1; ++k){ /* Loop over each strategy */

```

```

feasible = y + strat[k][0] + strat[k][1] + strat[k][2] + strat[k][3];

if(feasible > BUDGET - 1){
    for(j = 0; j <= popstates - 1; ++j){
        sum[j][k] = 0;}
    }

if(feasible > BUDGET - 1)
    continue; /* The number of mows for strategy can not exceed the available budget. If so, continue
to next strategy*/

if(strat[k][0] == 1) /* patch 1 */
    hab[0] = 1;
else
    hab[0] = min(5, landscape[z][0] + 1); /* If the patch is mowed, habitat quality in the next time step
is 1, else it is existing habitat quality plus 1, with maximum of 5 */

if(strat[k][1] == 1) /* patch 2 */
    hab[1] = 1;
else
    hab[1] = min(5, landscape[z][1] + 1); /* If the patch is mowed, habitat quality in the next time step
is 1, else it is existing habitat quality plus 1, with maximum of 5 */

if(strat[k][2] == 1) /* patch 3 */
    hab[2] = 1;
else
    hab[2] = min(5, landscape[z][2] + 1); /* If the patch is mowed, habitat quality in the next time step
is 1, else it is existing habitat quality plus 1, with maximum of 5 */

if(strat[k][3] == 1) /* patch 4 */
    hab[3] = 1;
else
    hab[3] = min(5, landscape[z][3] + 1); /* If the patch is mowed, habitat quality in the next time step
is 1, else it is existing habitat quality plus 1, with maximum of 5 */

mowstate = z;
stratcombo = k;

/* CALL TO EXTINCTION-RECOLNIZATION FUCNTION BELOW */

Tr = ext_colon(S, landscape, strat, mowstate, stratcombo, mowkill); /* Returns a matrix of probabilities
for every population state i to population state j, given that that metapopulation is in z habitat (mowing)
state now, the strategy is k, and the mowing extirpation probability is q */

for(a = 0; a <= mow - 1; ++a){ /* When you do a management strategy, you change
the mowing state. Here you are finding the next habitat state. */

    if((landscape[a][0] == hab[0]) && (landscape[a][1] == hab[1]) &&
        (landscape[a][2] == hab[2]) && (landscape[a][3] == hab[3]) )

```

```

        nexthab = a;}

for(i = 0; i <= popstates - 1; ++i){ /* Evaluate over all possible population states. */

sum[i][k] = 0.0;
numbmows[i][k] = 0.0;
realex[i][k] = 0.0;

    for(j = 0; j <= popstates - 1; ++j){
        sum[i][k] += Tr[j][i]*V1[j][nexthab][feasible]; /* The value of the metapopulation after
strategy k is implemented when it is in i population state is the weighted sum (weighted by the transition
probabilities) of the values of the states that it can transition to. The value is also the probability that the
metapopulation remains extant. */

        realext[i][k] += Tr[j][i]*Ext1[j][nexthab][feasible];

        if(t == T-1)
            numbmows[i][k] = strat[k][4]; /* Adding up the number of mows for this k
strategy */
        else
            numbmows[i][k] += (Tr[j][i]*M1[j][nexthab][feasible]); /* This weighted sum
is the expectation of the total number of mowings over the time periods so far. */
        }

numbmows[i][k] = numbmows[i][k] + strat[k][4]; /* Plus the current mows */

}

for(i = 0; i <= popstates - 1; ++i){ /* Release memory */
    free(Tr[i]);
}
free(Tr);

} /* End of strategy loop */

for(i = 0; i <= popstates - 1; ++i){ /* Find the optimal strategy for each population state */
    beststrat[i][z][y] = 0; /* Initialize to 0 */
    V0[i][z][y] = sum[i][0]; /* Initialize to 0 */
    M0[i][z][y] = numbmows[i][0];
    minstrat = strat[0][4];

    for(k = 0; k <= totalstrats - 1; ++k){

        if( (sum[i][k] - V0[i][z][y] > 0.00001) || ((sum[i][k] == V0[i][z][y]) && (strat[k][4] < minstrat)) ){
            /* If the strategy is greater than current best strategy (with some precision error) or it is equal to
the current best strategy but its number of mows is smaller, then it becomes the new best strategy.

            beststrat[i][z][y] = k;

```

```

        minstrat = strat[k][4];
        V0[i][z][y] = sum[i][k];

        M0[i][z][y] = numbmows[i][k];

        Ext0[i][z][y] = realext[i][k];
    }
} /* End of strategy loop */

} /* End of population states loop */
} /* End of mowing state (habitat) loop */

} /* End of budget loop */

for(i = 0; i <= popstates - 1 ; ++i){ /* For each population state in best habitat state, printing out the
objective function value, the expected number of mows, and best strategy */

    printf("%s%15s%5d\n", "Obj function as %: all habitat = 1", "pop state", i);
    printf("%f\n", ((V0[i][0][0])*100));
    fprintf(ofp, "%s%15s%5d\n", "Obj function as %: all habitat = 1", "pop state", i);
    fprintf(ofp, "%f\n", ((V0[i][0][0])*100) );

    printf("%s\n", "Extinction Probability as %: all habitat = 1");
    printf("%f\n", ((1.00 - V0[i][0][0])*100));
    fprintf(ofp, "%s\n", "Extinction Probability as %: all habitat = 1");
    fprintf(ofp, "%f\n", ((1.00 - V0[i][0][0])*100));

    printf("%s\n%d\n", "strat", beststrat[i][0][0]);
    fprintf(ofp, "%s\n%d\n", "strat", beststrat[i][0][0]);

    printf("%s\n", "Expected Number of Mows: all habitat = 1" );
    printf("%f\n", M0[i][0][0]);
    fprintf(ofp, "%s\n", "Expected Number of Mows: all habitat = 1" );
    fprintf(ofp, "%f\n", M0[i][0][0]);

    for(y = BUDGET- 1; y >= 0; --y){ /* Printing objective function value at three time points for
various budget sizes when all patches are occupied */
        if( (q == 0) && (y <= 50) && (t == 15) && (i == 15) )
            fprintf(bud1, "%d%s%f%s%f\n", (BUDGET - 1) - y, ",", V0[i][0][y]*100, ",",
                M0[i][0][y] );

        if( (q == 1) && (y <= 50) && (t == 10) && (i == 15) )
            fprintf(bud2, "%d%s%f%s%f\n", (BUDGET - 1) - y, ",",
                V0[i][0][y]*100, ",", M0[i][0][y]);

        if( (q == 2) && (y <= 50) && (t == 0) && (i == 15) )
            fprintf(bud3, "%d%s%f%s%f\n", (BUDGET - 1) - y, ",",
                V0[i][0][y]*100, ",", M0[i][0][y]);

        if( (q == 3) && (y <= 50) && (t == 0) && (i == 15) )
            fprintf(bud4, "%d%s%f%s%f\n", (BUDGET - 1) - y, ",",
                V0[i][0][y]*100, ",", M0[i][0][y]);
    }
} /* End of population states loop */

```

```

if( t == 0 ) { /* For each unique-valued summed mowing and summed population state at time t = 0,
summing up the expected number of mows, the best strategy, and the viability. Since some mowing and
population states have the same summed values, this is used to calculate an average for each unique-valued
state below */

```

```

    for(j = 0; j <= mow - 1; ++j){
        for(i = 0; i <= popstates - 1; ++i){
            expmow[ S[i][4] ][ landscape[j][4]-1 ][0] += M0[i][j][0];
            expmow[ S[i][4] ][ landscape[j][4]-1 ][1] += 1.0;
            extprob[ S[i][4] ][ landscape[j][4] -1][0] += (1.0 - Ext0[i][j][0]);
            extprob[ S[i][4] ][ landscape[j][4] -1][1] += 1.0;

            z = beststrat[i][j][0];
            stratmow[ S[i][4] ][ landscape[j][4] -1][0] += strat[ z ][4];
            stratmow[ S[i][4] ][ landscape[j][4] -1][1] += 1.0;

        }
    }

```

```

for(i = 0; i <= sumoccupy - 1; ++i){
    for(j = 3; j <= sumhab - 1; ++j){
        if(expmow[i][j][1] != 0) /*Averaging for each unique-valued summed habitat state and
summed population state */

```

```

            expmow[i][j][0] = (expmow[i][j][0])/(expmow[i][j][1]);
            if(extprob[i][j][1] != 0)
                extprob[i][j][0] = (extprob[i][j][0])/(extprob[i][j][1]);
            if(stratmow[i][j][1] != 0)
                stratmow[i][j][0] = (stratmow[i][j][0])/(stratmow[i][j][1]);

```

```

/* Printing the expected number of mows, best strategy and extinction probability for
each unique-valued summed habitat and population state */

```

```

if(q == 0){
    fprintf(ofp2, "%d%%s%5d%%s%10f\n", j+1, "", i, "", expmow[i][j][0]);
    fprintf(ofp3, "%d%%s%5d%%s%10f\n", j+1, "", i, "", extprob[i][j][0]);
    fprintf(ofp4, "%d%%s%5d%%s%10f\n", j+1, "", i, "", stratmow[i][j][0]);}
if(q == 1){
    fprintf(ofp5, "%d%%s%5d%%s%10f\n", j+1, "", i, "", expmow[i][j][0]);
    fprintf(ofp6, "%d%%s%5d%%s%10f\n", j+1, "", i, "", extprob[i][j][0]);
    fprintf(ofp7, "%d%%s%5d%%s%10f\n", j+1, "", i, "", stratmow[i][j][0]);}
if(q == 2){
    fprintf(ofp8, "%d%%s%5d%%s%10f\n", j+1, "", i, "", expmow[i][j][0]);
    fprintf(ofp9, "%d%%s%5d%%s%10f\n", j+1, "", i, "", extprob[i][j][0]);
    fprintf(ofp10, "%d%%s%5d%%s%10f\n", j+1, "", i, "", stratmow[i][j][0]);}
if(q == 3){
    fprintf(ofp11, "%d%%s%5d%%s%10f\n", j+1, "", i, "", expmow[i][j][0]);
    fprintf(ofp12, "%d%%s%5d%%s%10f\n", j+1, "", i, "", extprob[i][j][0]);
    fprintf(ofp13, "%d%%s%5d%%s%10f\n", j+1, "", i, "", stratmow[i][j][0]);}

```

```

    }
}
}

```

```

/* ESSENCE OF THE SDP BACKSTEP */
Now V0 becomes V1 for the next time step. That is, the value calculated for the best
strategy from the penultimate time step, T - 1, is used to calculate for the value for
each strategy in the T - 2 time step, etc. until T = 0*/

```

```

    for(y = 0; y <= BUDGET - 1 ; ++y){
        for(z = 0; z <= mow - 1 ; ++z){
            for(i = 0; i <= popstates - 1 ; ++i){
                V1[i][z][y] = V0[i][z][y];
                M1[i][z][y] = M0[i][z][y];
                Ext1[i][z][y] = Ext0[i][z][y];
            }
        }
    }

} /* End of time loop */

} /*End of q (mowing extirpation probability) loop*/

```

```

fclose(ofp); /*Closing files */
fclose(ofp2);
fclose(ofp3);
fclose(ofp4);
fclose(ofp5);
fclose(ofp6);
fclose(ofp7);
fclose(ofp8);
fclose(ofp9);
fclose(ofp10);
fclose(ofp11);
fclose(ofp12);
fclose(ofp13);
fclose(bud1);
fclose(bud2);
fclose(bud3);
fclose(bud4);

```

```

return 0;
} /*End of main() function */

```

```

/* EXTINCTION-RECOLONIZATION FUCNTION */

```

```

double **ext_colon(int S[popstates][5],
int landscape[mow][5], int strat[totalstrats][5], int mowstate, int stratcombo, double mowkill)
{

```

```

double m[N][popstates]; /* Colonization probability of each patch [N][states] */
double mu[N]; /* Extinction probability of each patch [N]*/

```

```

double **E; /* Extinction. matrix, where states = 2^N [states][states]*/
double **C; /* Colonization matrix, where states = 2^N [states][states]*/
double **Tr;
double *colon, *ext;

```

```

int i, j, z, k;
double recolonprod[popstates][N];
double sumext, sumrec;
double m_interval = max_m - min_m;
double e_interval = (emax - emin);
int correct;

for(z = 0; z <= popstates - 1; ++z){ /*Calculating recolonization probability of each patch, as a function of
the population state (occupancy) and mowing state of the metapopulation */
    for(i = 0; i <= N - 1; ++i){
        m[i][z] = 0;

        for(j = 0; j <= N - 1 ; ++j){

            if(i == j)
                correct = 0; /* A patch can't contribute migrants to itself */
            else
                correct = 1;
            if( strat[stratcombo][j] == 1) /* If a patch is mowed, it can produce dispersers */
                recolonprod[j][z] = 0;
            else
                recolonprod[j][z] = S[z][j]*(max_m - ((landscape[mowstate][j] -
1)*(m_interval/4.0)))*correct; /* The 'production' of dispersers by patch j when the metapopulation is in
mowing state z */

            m[i][z] += (recolonprod[j][z]); /* Recolonization probability of patch i with landscape
state z */

        }

        if((strat[stratcombo][i] == 1) )
            m[i][z] = 0;
        else
            m[i][z] = m[i][z]/(N-1);
    }
}

for(i = 0; i <= N -1; ++i){ /* Now the extinction probability of patch i */

    if(landscape[mowstate][i] != 5) /* Probability can not be infinity */
        mu[i] = (1/(10.0 - ((landscape[mowstate][i] - 1)*2.5)))
        + ((1.0 - (1/(10.0 - ((landscape[mowstate][i] - 1)*2.5))) ))*strat[stratcombo][i]*mowkill);
    else
        mu[i] = 1.0;

    /* The extinction probability is a function of the habitat state of patch i. If the patch is mowed, it can
escape extirpation with a probability of 1 - mowkill */
}

```

```

}

ext = malloc(N * sizeof(double));
E = malloc(popstates * sizeof(double *));
assert(ext != NULL);
assert(E != NULL);
for(i = 0; i < popstates; ++i){
    E[i] = malloc(popstates * sizeof(double));
    assert(E[i] != NULL);}

for(i = 0; i <= popstates - 1; ++i){ /* The transition matrix for the transition from population state i to j
through extinction */
    sumext = 0;

    for(j = 0; j <= popstates - 1; ++j){
        E[j][i] = 1;
        for(k = 0; k <= N - 1; ++k){
            if((S[i][k] == 0) && (S[j][k] == 0)){
                ext[k] = 1.0;} /* Probability that patch i unoccupied in time t, and then j is
unoccupied in time t+1, due to extinction */
            if((S[i][k] == 1) && (S[j][k] == 0)){
                ext[k] = mu[k];} /* Probability that patch i occupied in time t+1, and then j is
unoccupied in time t+1, due to extinction */

            if((S[i][k] == 1) && (S[j][k] == 1)){
                ext[k] = 1 - mu[k];}
/* Probability that patch i occupied in time t, and then j is occupied in time t+1, due to extinction */

            if((S[i][k] == 0) && (S[j][k] == 1)){
                ext[k] = 0;}
/* Probability that patch i unoccupied in time t, and then j is occupied in time t+1, due to extinction */

            E[j][i] = ext[k]; /* Multiplying probabilities together across all patches */
        }
        sumext += E[j][i];
    }
}

free(ext);

colon = malloc(N * sizeof(double));
assert(colon != NULL);
C = malloc(popstates * sizeof(double *));
assert(C != NULL);

for(i = 0; i < popstates; ++i){
    C[i] = malloc(popstates * sizeof(double));
}

for(i = 0; i <= popstates - 1; ++i){ /* The transition matrix for the transition from population state i to j
through recolonization. */

```

```

sumrec = 0;
for(j = 0; j <= popstates - 1; ++j){
    C[j][i] = 1;
    for(k = 0; k <= N - 1; ++k){
        if((S[i][k] == 0) && (S[j][k] == 0)){
            colon[k] = 1 - m[k][i];}
/* Probability that patch i unoccupied in time t, and then j is unoccupied in time t+1, due to recolonization
*/
            if((S[i][k] == 1) && (S[j][k] == 0)){
                colon[k] = 0;}
/* Probability that patch i occupied in time t, and then j is unoccupied in time t+1, due to recolonization */
            if((S[i][k] == 1) && (S[j][k] == 1)){
                colon[k] = 1;}
/* Probability that patch i occupied in time t, and then j is occupied in time t, due to recolonization */
            if((S[i][k] == 0) && (S[j][k] == 1)){
                colon[k] = m[k][i];}
/* Probability that patch i unoccupied in time t, and then j is occupied in time t+1, due to recolonization */
            C[j][i] *= colon[k]; /* Multiplying probabilities together across all patches */
        }
        sumrec += C[j][i];
    }
}

free(colon);

Tr = malloc(popstates * sizeof(double *));
for(i = 0; i < popstates; ++i){
    Tr[i] = malloc(popstates * sizeof(double));}
assert(Tr != NULL);

for(i = 0; i <= popstates - 1; ++i){ /* Full transition matrix. First extinction then recolonization */
    for(j = 0; j <= popstates - 1; ++j){ Tr[j][i] = 0.0;
        for(z = 0; z <= popstates - 1; ++z){ /* Probability o going from population state i to j
with an intermediate population state z */
            Tr[j][i] += (C[j][z])*E[z][i];
        }
    }
}

for(i = 0; i <= popstates - 1; ++i){
    free(E[i]);
    free(C[i]);
}
free(C);
free(E);

return Tr;
}

/*TWO FUCNIONS USED IN SORTING ARRAYS FROM NUMERICAL REPCIES IN C */

```

```

void indexx(unsigned long n, float arr[], unsigned long indx[])

```

```

/* Indexes an array arr[1..n], i.e., outputs the array indx[1..n] such that arr[indx[j]] is
in ascending order for j = 1;2;: :;N. The input quantities n and arr are not changed. */
{

unsigned long i, indxt, ir = n, itemp, j, k ,l = 1;
int jstack=0, *istack;
float a;

istack = ivector(1,NSTACK);
for (j = 1; j <= n; j++) indx[j] = j;
for (;;) {
if (ir-1 < M) {
for (j = l+1 ; j <= ir ; j++) {
indxt = indx[j];
a = arr[indxt];
for (i = j-1 ; i >= l; i--) {
if (arr[indx[i]] <= a) break;
indx[i+1] = indx[i];
}
indx[i+1] = indxt;
}
if (jstack == 0) break;
ir = istack[jstack--];
l = istack[jstack--];
} else {
k = (l + ir) >> 1;
SWAP(indx[k] , indx[l+1] );
if (arr[indx[l]] > arr[indx[ir]]) {
SWAP(indx[l] , indx[ir])
}
if (arr[indx[l+1]] > arr[indx[ir]]) {
SWAP(indx[l+1], indx[ir])
}
if (arr[indx[l]] > arr[indx[l+1]]) {
SWAP(indx[l], indx[l+1])
}
i = l + 1;
j = ir;
indxt = indx[l+1];

a = arr[indxt];
for (;;) {
do i++; while (arr[indx[i]] < a);
do j--; while (arr[indx[j]] > a);
if (j < i) break;
SWAP(indx[i], indx[j])
}
indx[l+1] = indx[j];
indx[j] = indxt;
jstack += 2;
if (jstack > NSTACK) nerror("NSTACK too small in indexx.");
if (ir-i+1 >= j-l) {
istack[jstack] = ir;
istack[jstack-1] = i;
ir = j-l;
}
}
}

```

```

} else {
istack[jstack] = j-1;
istack[jstack-1] = 1;
l = i;
}
}
}
free_ivector(istack,1,NSTACK);
}

```

/\* If you want to sort an array while making the corresponding rearrangement of several or many other arrays, you should first make an index table, then use it to rearrange each array in turn. This requires two arrays of working space: one to hold the index, and another into which an array is temporarily moved, and from which it is redeposited back on to itself in the rearranged order. For 3 arrays, the procedure looks like this: \*/

```

void sort5(unsigned long n, float ra[], float rb[], float rc[], float rd[], float re[])
/*Sorts an array ra[1..n] into ascending numerical order while making the corresponding re-
arrangements of the arrays rb[1..n] and rc[1..n]. An index table is constructed via the
routine indexx. */
{
void indexx(unsigned long n, float arr[], unsigned long indx[]);
unsigned long j, *iwksp;
float *wksp;
iwksp = lvector(1,n);
wksp = vector(1,n);
indexx(n, ra, iwksp); /*Make the index table.*/
for (j = 1;j <= n; j++) wksp[j] = ra[j]; /*Save the array ra.*/
for (j = 1;j <= n; j++) ra[j] = wksp[iwksp[j]]; /*Copy it back in rearranged order.*/

for (j = 1;j <= n; j++) wksp[j] = rb[j]; /*Ditto rb.*/
for (j = 1;j <= n; j++) rb[j] = wksp[iwksp[j]];

for (j = 1;j <= n; j++) wksp[j] = rc[j]; /*Ditto rc.*/
for (j = 1;j <= n; j++) rc[j] = wksp[iwksp[j]];

for (j = 1;j <= n; j++) wksp[j] = rd[j]; /*Ditto rd.*/
for (j = 1;j <= n; j++) rd[j] = wksp[iwksp[j]];

for (j = 1;j <= n; j++) wksp[j] = re[j]; /*Ditto re.*/
for (j = 1;j <= n; j++) re[j] = wksp[iwksp[j]];

free_vector(wksp,1,n);
free_lvector(iwksp,1,n);
}

```

## Appendix II

Pictures of the Southern Emu-wren (*Stipititurus malachurus intermedius*) and habitat



Male

(Courtesy of Marcus Pickett)



**Female**

(Courtesy of Marcus Pickett)



**Male close-up**

(Marcus Pickett)



**Male**

(Marcus Pickett)



**Long skeletal tail**

(Marcus Pickett)



**Typical Fleurieu Peninsula swamp**

(M.I. Westphal)

# Appendix III

## Photos of the Mount Lofty Ranges



(M.I. Westphal)



(M.I. Westphal)



(M.I. Westphal)

## **Michael**

By Hugh P. Possingham

Michael is the salt in SEL

Michael salt socialisation food  
Too little: bland utilitarian spiceless  
Too much: gag inedible

Michael salt friend wound  
Sharp pain, healing, strengthening

Michael salt heart crystal  
Pure, simple, misunderstood

*It was late, late in the evening,  
The lovers they were gone;  
The clocks had ceased their chiming,  
And the deep river ran on.*

- W.H. Auden, *As I Walked Out One Evening*