Prioritizing areas for habitat conservation in the face of climate and land-use change

by

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Preface

Official statement of work

The first chapter of this thesis was the product of collaboration between myself, my supervisor Dr. Kerr, Laura Coristine and Rosana Soares. The majority of the research, written content, and figures were direct products of my own work; the co-authors provided valuable thematic guidance and topical expertise during the formulation of the manuscript, and provided revisions to the completed manuscript that improved the clarity and flow of the work.

The second chapter of this thesis was the product of primarily my own work, with guidance and manuscript revisions from Dr. Kerr, and generous help from others as acknowledged below.

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Abstract

The selection of sites for biodiversity conservation is best done if it anticipates future challenges and efficiently accomplishes targets, given limited funding for such efforts. The first chapter of this thesis discusses how conservation practitioners might manage and enhance long-term survival for species whose ranges must shift as climate changes, across regions that present significant mobility barriers. I describe recommendations highlighting connectivity, refugia from climate change, adaptation, and restoration within agricultural landscapes in North America, but these recommendations are transferable elsewhere. The second chapter examines patterns of change in agricultural intensity and land price within Canada’s species-rich farmland between 1986 and 2011, and creates sequential cost-efficient plans to conserve resident species-at-risk within that time period, to determine how environmental and cost changes erode the efficiency of conservation plans. While sites initially selected as cost-efficient remained so through time, total plan costs increased, decreasing each plan’s ability to represent all species for a given budget. This emphasizes the urgent need for conservation within Canada’s farmland.

Résumé

Le choix de sites candidats pour la conservation doit répondre à des objectifs de manière efficiente et anticiper les défis possibles vu l’exiguïté des fonds dans ces entreprises. Dans le premier chapitre, je présente les moyens par lesquels les responsables de la conservation pourraient gérer et améliorer les perspectives de survie à long terme des espèces qui doivent migrer, géographiquement, lorsque les changements climatiques dans des régions présentent des obstacles importants à la mobilité de ces espèces. J’y décris les rôles de la connectivité, des refuges, de l’adaptation et de la restauration dans des environnements agricoles en Amérique du Nord, mais ces recommandations s’appliquent aussi ailleurs. Le deuxième chapitre étudie l’évolution des changements d’intensité de l’activité agricole et du prix des terrains agricoles au Canada entre 1986 et 2011 et établit des stratégies séquentielles rentables pour conserver des espèces résidentes en péril durant cette période. J’y détermine l’impact des changements environnementaux et des prix sur l’efficacité des stratégies. Bien que les sites choisis soient demeurés indispensables tout au long de la période, les coûts de mise en œuvre ont augmenté et il y a eu diminution de la faisabilité de chacune des stratégies de conserver des espèces au budget donné. Cela souligne le besoin urgent de conserver la grande variété d’espèces qui s’abritent sur les terres agricoles au Canada.

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General Introduction

Protected areas—defined by the IUCN as "clearly defined geographical space[s], recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley 2008)—are essential elements for preserving the integrity of ecosystems. However, the design, creation and maintenance of protected areas often require significant investments of time and effort, and it is important that a) land that is protected has high conservation value, and b) land that is set aside for conservation will continue to serve conservation purposes through time. Systematic conservation planning, the process of prioritizing locations for protection of biodiversity or ecological function, seeks to achieve these goals (Margules & Pressey 2000; Kukkala & Moilanen 2013) by considering the complementarity of sites chosen for protection (the ability of added sites to contribute previously under-represented features to an existing set of sites; Vane-Wright et al. 1991) and their irreplaceability (the probability that a site must be conserved in order to accomplish a conservation goal; Ferrier et al. 2000).

Much of the foundational literature on systematic conservation planning has focussed on prioritizing land that can protect the highest density of conservation targets (species, habitat types, etc.) where they have historically been found (Kiester et al. 1996; Cabeza & Moilanen 2001; Brooks et al. 2006; Chan et al. 2006; Freemark et al. 2006; Kremen et al. 2008). But as the field has developed, other considerations have emerged. Widely observed shifts in the distributions of species under climate change have led to discussion of how best to maintain protection of such species using protected areas (Hannah et al. 2007; Heller & Zavaleta 2009; Olson & Lindsay 2009; Lemieux et al. 2011; Rissman et al. 2015). Limited resources for conservation initiatives have driven investigations into how conservation costs and benefits can be intergrated into protected area plans (Montgomery et al. 1999; Pirard 2012), and how such plans can be optimized for cost-efficiency (Ando et al. 1998; Naidoo et al. 2006; Polasky et al. 2008; Arponen et al. 2010; Petersen et al. 2015). Finally, prolonged implementation phases following site selection have inspired study into the “cost of waiting” to acquire land (Meir et al. 2004; Strange et al. 2006b; McDonald-Madden et al. 2008). While most articles continue to discuss these and other issues within the context of setting aside remaining, undisturbed land for formal, government-legislated protected areas (e.g. national parks), others have studied these concepts for restoration initiatives (Kumaraswamy & Kunte 2013; Donlan et al. 2014) and private land easements (Newburn et al. 2005; Gerber & Rissman 2012; Rissman et al. 2015). For efficient conservation planning, optimization algorithms have also been developed (e.g. Marxan, Zonation; see Cabeza & Moilanen 2001; Moilanen et al. 2005; Ball et al. 2009), which can, in brief, be described as solving one of two logical problems: finding complementary sites that accomplish the most for a given budget (known also as the maximum coverage problem), or finding sites that accomplish a given conservation target for the lowest “cost” (the minimum set problem; Moilanen & Arponen 2011).

The emerging issues specified above all relate to the long-term sustainability of effective, efficient protected areas and protected area networks. Climate change threatens the long-term effectiveness of protected areas, if those areas are designed without taking into account the expected shift in distributions of many species as climate changes (Hannah et al. 2007; Olson & Lindsay 2009; Kharouba & Kerr 2010; Araujo et al. 2011; Lemieux et al. 2011; Alagador et al. 2014). Likewise, conservation plans that do not efficiently accomplish clearly defined targets per unit cost will be unlikely to succeed in a world of competing land uses, and limited financial and labour resources (Naidoo et al. 2006; Moilanen & Arponen 2011). But more importantly, even for cost-efficient conservation plans, the cost:benefit ratio within a set of locations will change through time if these respective values change, for example if costs associated with acquiring the land rise (Armsworth et al. 2006; Carwardine et al. 2010). This would degrade the efficiency of cost-effective plans through time, and could render them obsolete if such changes are rapid relative to the rate of implementation.

This thesis (in article format) aims to address questions relevant to the field of systematic conservation planning, as they relate to the sustainability issues identified above, within the human dominated areas of North America. As elaborated below, these regions, including the Canadian and north and eastern U.S. Great Plains, the eastern U.S. and the Mixed-Wood Plains in southern Canada, are a high priority for the creation of new conservation areas. These areas have a high density of human impacts that co-occur with a high density of species. While this alone is a concern for the maintenance of biodiversity, the arc of high human footprint that stretches across the continent, both within and north of regions of high species richness, poses a further challenge when considering predicted northward range shifts of many taxa. While the need is great, the challenges to conservation in this region are also formidable; much of the land is used for agriculture, has been disturbed, and is privately held.

The first chapter of this thesis considers the need for restoration in areas of intense human land use across southern Canada and the central and eastern United States, in light of predicted climate change-induced range shifts in many taxa. It then synthesizes existing and potential approaches to protect species and facilitate range shifts under climate change, presenting a conceptual framework that builds from the requirement that habitat supports population growth and individual dispersal. This chapter highlights the importance of focused, cross-border conservation efforts to increase permeability of the landscape for northward range expansion of species in regions of North America where human footprint is substantial. Having established the importance of restoration within the matrix of non-reserve areas in southern Canada as part of the first chapter, the second chapter presents multiple hypothetical cost-efficient conservation plans for the most extensive portion of this non-reserve matrix, Canada’s farmland. This second chapter examines how these plans, designed to protect and recover species-at-risk while minimizing cost based on two cost proxies and one land-use intensity proxy, would have differed at six different years over the 25-year period from 1986 to 2011. The goal here was to inform conservation planners as to how changes in the return-on-investment in nationwide conservation within this region may affect future initiatives.

Chapter 1: Facilitating climate-change-induced range shifts across continental land-use barriers

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Abstract

Climate changes impose requirements for many species to shift their ranges to remain within environmentally tolerable areas, but near-continuous regions of intense human land use stretching across continental extents diminish dispersal prospects for many species. We reviewed the impact of habitat loss and fragmentation on species' abilities to track changing climates and existing plans to facilitate species dispersal in response to climate change through regions of intensive land uses, drawing on examples from North America and elsewhere. We identified an emerging analytical approach that accounts for variation in species' dispersal capacities relative to both the pace of climate change and habitat availability. Habitat loss and fragmentation hinder climatic niche tracking under climate change, particularly for species with narrow habitat tolerances, by impeding both propagule dispersal and population growth. The analytical approach identifies prospective modern-era climatic refugia, where the rate of displacement of climatic niches under climate change has been slower than surrounding areas, and that are defined relative to individual species' needs. The approach underscores the importance of identifying and managing dispersal pathways or corridors through semi-continental land use barriers that can benefit many species simultaneously. The above strategies to facilitate range shifts must account for uncertainties around population adaptation to local environmental conditions. Accounting for uncertainties in climate change and dispersal capabilities among species and expanding biological monitoring programs within an adaptive management

framework are vital strategies that will improve species' capacities to track rapidly shifting climatic conditions across landscapes dominated by intensive human land use.

Introduction

While rapidly changing climates elevate extinction risk (Maclean & Wilson 2011), habitat loss and degradation continue to pose severe threats to many species (Vié et al. 2009; Collen et al. 2012). Across North America, intensive and extensive land uses have eliminated or degraded critical habitats in many of the most biologically diverse areas. The result is that rates of species endangerment in such areas are high (Brown & Laband 2006). Anthropogenic climate change poses a separate array of risks that may interact with habitat loss to accelerate extinction rates still further. While mechanisms governing how, why, and when species respond to changing climatic conditions continue to be discovered (Araujo et al. 2013), strategies to reduce population and species extinctions arising from habitat losses or degradation must clearly account for directional shifts in the underlying environmental factors that often determine the limits of species distributions.

Climate change imposes requirements for geographical range shifts for many species, but land use conversions across broad regions in North America impose a potential dispersal barrier spanning much of the continent (Fig. 1.1). Anticipated warming of 2-5 °C in the next century over this region (IPCC 2013) adds to the complexity of conservation planning, the effectiveness of which will depend in part on the extent to which the impacts of habitat loss and climate change, respectively and interactively, can be mitigated. In this paper we reviewed the impact of habitat loss and fragmentation on species’ abilities to track changing climates. The review focused on the highly developed regions of eastern and central North America as a particularly relevant example where these interactions occur. Human footprint, a metric of human influence

(Sanderson et al. 2002), was assessed within latitudinal bands across North America to illustrate this variation in human-imposed barriers to dispersal. We then reviewed the systematic conservation planning, ecology, and evolution literature for existing conservation planning and management approaches that facilitate species dispersal in response to climate change through regions of intensive land uses, as exemplified by cases in North America and elsewhere. Strategies to manage for changing land use intensities and climate change have evolved rapidly (e.g. Faleiro et al. 2013; Alagador et al. 2014) and have begun to account for an increasingly mechanistic understanding of the factors that govern species' ecoevolutionary and phenotypic responses to complex global change threats (Hoffmann & Sgro 2011).

Climate Change, Range Shifts, and Habitat

The successful expansion of a species' range at the cold range margin depends on the presence of habitat that may be colonized by individual dispersal. Shifts in species' distributions can be modeled as propagule diffusion within a window of suitable climate that moves across a landscape as climates change (Travis 2003; Leroux et al. 2013). Species' distributions must keep pace with this moving climate window to avoid accumulation of climate debts (declines in species/population fitness prospects due to decreased climatic suitability within their occupied space) and potentially extinction (Devictor et al. 2012) by colonizing new areas at expanding range margins even as individuals of populations are lost from retracting warm margins. Species' ability to keep pace depends on its rate of spatial spread, itself a function of individual movement rates and the population growth rate. In mathematical terms, this rate of spread can be modeled by

$$c^* = 2\sqrt{Dr}\ , \tag{1}$$

where $c*$ is the critical rate of spread for tracking the suitable climate, D is the diffusion rate of individuals or rate of individual movement, and r is population growth rate (Leroux et al. 2013). As part of this reaction-diffusion framework for modeling species movement, it is possible to generate predictions for the minimum critical size of a patch of habitat that will permit species persistence, given that both the patch and the species must shift with respect to changing climatic conditions:

$$L_C(q) = \pi\sqrt{D/r}\left(\sqrt{1-\frac{q}{2\sqrt{Dr}}}\right)^{-1} , \qquad (2)$$

where L_C is the minimum critical size of the species' climatic envelope (or area that is climatically tolerable), which moves at pace q. It is then straightforward to show that species persistence depends on whether its rate of movement, c^*, is at least equal to the rate of movement, q, of its tolerable climate. This framework predicts which species will be at risk from climate change, given knowledge of their dispersal rates and observations of shifts in their areas of climatically tolerable habitat, providing a means to include more mechanistic insights into how dispersal affects range shifts due to climate change (developed in Leroux et al. [2013]).

Species' range responses to changing climatic conditions depend on their capacity to disperse (Boulangeat et al. 2012), which relates to habitat availability and connectivity (Leroux et al. 2013). For example, range expansion predictions for the speckled wood butterfly *Pararge aegeria* that included growth rates and a dispersal function accurately predicted the observed difference in range expansion rate between a habitat-rich landscape and a fragmented, habitat-poor landscape (Hill et al. 2001). Cropland (Janin et al. 2009; Ockinger et al. 2012), clearcuts in forested landscapes (Popescu et al. 2012), and urban or built areas (Tremblay & St Clair 2011; Sackett et al. 2012) are pervasive in much of North America (Fig. 1.1) and inhibit the movement of individuals or reduce colonization success in remaining habitat patches for butterflies, toads, songbirds, and prairie dogs. Even for species requiring structurally similar habitats to those that agricultural land uses replaced, such as for grassland species remaining in areas of high-productivity cropland, fragmentation from various land uses isolates populations (Soons & Heil 2002; Torok et al. 2011) and is linked to persistent bird population declines (Sauer et al. 2003). Habitat loss is particularly likely to diminish dispersal capacities of habitat specialists, making it less likely that such species will track shifting climatic conditions successfully (Warren et al. 2001; Travis 2003; Stefanescu et al. 2011). Because intensive land uses effectively filter these species out of changing biological communities and generalists persist more readily or expand their distributions, this land use and climate change interaction accelerates biotic homogenization over broad regions (White & Kerr 2007).

Designing Reserve Networks for Range Shifts

Alleviating habitat loss will both reduce its biotic impacts directly and improve prospects that species dispersal rates will suffice to track shifting climatic conditions (Heller & Zavaleta 2009; Lemieux et al. 2011). While the continued efficacy of formal protected areas in the face of changing climates and shifting ranges is uncertain (Kharouba & Kerr 2010; D'Amen et al. 2011; Kujala et al. 2011; Johnston et al. 2013), creating and maintaining protected areas continues to be essential for conservation strategies that address climate change because they mitigate other human impacts (Hannah et al. 2007; Lemieux et al. 2011). However, the strategy of prioritizing potential reserves based on species' current distributions is clearly limited by increasingly dynamic species distributions (Williams & Jackson 2007; Hobday 2011); additional, innovative strategies are urgently needed.

Protection along Climate Change Trajectories

Species' capacities to track shifting climates depends strongly on availability of sufficient habitat where species can establish populations beyond their historical range limits and subsequently disperse (Hiley et al. 2013). Protecting or restoring habitat that strategically facilitates range shifts (effectively increasing the c^* term and diminishing the risk of $q > c^*$ in Eq. 2), such as in areas that are poleward or upslope of existing range boundaries or biodiversity hotspots, will reduce extinction risks related to climate change. This creates a unique challenge for conservation planners because a reserve may be only transiently tolerable for constituent species. While many species with broad climatic tolerances will continue to benefit from existing reserve networks, other species may need to use those reserves to shift through landscapes where habitat losses might otherwise hinder or prevent dispersal. If so, arranging individual reserves or managed lands along the expected trajectories of shifting species' niches will improve their likelihood of colonizing new areas (Fig. 1.2) (Lawler 2009; Alagador et al. 2014).

Managing habitats along the trajectory of distribution changes requires prediction of this trajectory in a landscape. For North America east of the Rockies, the trajectories of climate change are largely northward; some converge toward higher elevations like the Appalachian ranges and along northern coastlines (Burrows et al. 2014). However, observations of how climatic niches have shifted across landscapes can provide greater insight than direction and pace; multiple trajectories can be mapped to identify the timing and extent to which these trajectories converge, remain overlapping, and diverge. For example, the rate of displacement of climatic niches under climate change has been calculated (Loarie et al. 2009). From these rates, 50-year trajectories (1960-2009) of climatic niches have been mapped across North America that identify climate “corridors,” where many of these trajectories pass through a single common region (Burrows et al.

2014). If species are expected to track individual climatic niches in a shared direction (if not pace), these common routes of migration imposed by climate change need identification and management. Although geographical range shifts observed to date have not yet been strongly limited by hard geographical boundaries, such as coastlines, region-specific management will be necessary to account for such responses in some areas (e.g. California; [Ackerly et al. 2010]).

Predicting species distributions based on models of future climate (Pyke et al. 2005; Rose & Burton 2009; Kujala et al. 2013b; Loyola et al. 2013) relies on many assumptions (e.g. that the current distributions of species are in equilibrium with climate) or on underlying models with their own assumptions and uncertainties (e.g. about future CO_2 emissions [Buisson et al. 2010]). The accuracy of these predictions are infrequently tested (Crimmins et al. 2013). It is important to validate such models by testing their ability to predict changes over periods of observed climate change (Kharouba et al. 2009; Kerr & Dobrowski 2013; Williams et al. 2013). Finally, shifting climatic niches are not necessarily geographically continuous (Early & Sax 2011), which creates gaps along dispersal pathways that may lead to more complex management requirements.

Connectivity through Corridors, Stepping-Stones, and Translocation

The distribution of dispersal characteristics among species assemblages can inform the nature of potential management interventions. Range shifts in response to climate change are contingent on successful individual dispersal among habitat patches, the probability of which can vary regardless of landscape permeability. Strategies to connect conservation areas must account for potentially enormous variation in target species' intrinsic dispersal abilities (Burke et al. 2011). Some species will successfully disperse through even extremely fragmented landscapes, whereas other species will not disperse rapidly enough to track shifting climatic conditions even if habitats are nearly continuous and subject only to natural disturbances. Among species for which long distance dispersal is unlikely, for example, corridors may be needed (Beier et al. 2008), whereas habitats arrayed as stepping stones may suffice for species that disperse over moderate distances relative to existing geographical barriers (e.g. wind- or bird-dispersed seeds) (Fig. 1.3) (Pearson & Dawson 2005). As a result, strategies to improve connectivity in human-dominated landscapes may range from no intervention at all to managed relocation (Pearson & Dawson 2005; Shoo et al. 2013).

New techniques are required to assemble and evaluate dispersal capacities within large species assemblages and to evaluate methods to facilitate their dispersal across human-impacted landscapes. Burke et al. (2011) assembled consensuses of expert views on species' mobility for 297 butterfly species in United States and Canada, which showed that dispersal capacities varied enormously among species. Some of these species are unlikely, without some form of management intervention (Fig. 1.4), to keep pace with shifting climatic conditions. Interventions to facilitate such geographical range shifts vary relative to species intrinsic dispersal capacities, ranging from no intervention to managed relocation, as well as local land uses and costs. Corridor or stepping stone establishment, through formal protection measures or informal land use management, will often be less intrusive and potentially less costly than managed relocation, depending particularly on whether these landscape features are being retained or must be restored (Hoegh-Guldberg et al. 2008; Shoo et al. 2013). The costs and logistical difficulty of managed relocation increase rapidly as numbers of species requiring relocation increase (Loss et al. 2011), although prohibitively high land costs or inflexible land uses may sometimes cause managed relocations to be relatively economical.

Connectivity is particularly relevant to trans-national conservation issues. In North America, for instance, human-dominated regions of eastern and central North America extend across the border between Canada and the United States and maintenance of landscape connectivity in trans-boundary areas requires international cooperation. There is some precedent for international cooperation in the Great Lakes watershed, through longstanding activities of the International Joint Commission (Hall 2008). Broad-scale initiatives of this kind are similarly exemplified by the Yellowstone to Yukon (Raimer & Ford 2005) and Algonquin to Adirondacks (Stephenson 2001) corridors, but they remain uncommon. Such efforts may need to be expanded particularly in central North America, where the pace of climate change is higher (Loarie et al. 2009) and species consequently experience greater challenges in tracking shifting climatic conditions. Building cooperative management structures between agencies and governments with limited histories of trans-boundary co-operation may be challenging but will likely be indispensable.

Climatic Refugia

Strategies to reduce the geographical displacement rates of species' climatic niches may provide vital benefits that complement widely recognized approaches of facilitating dispersal through human-dominated landscapes. During past climate changes, paleoecological and phylogeographic data indicate that small populations of many species sheltered successfully in climatic refugia and subsequently expanded as climatic conditions allowed (Svenning et al. 2008; Hampe et al. 2013). Identifying similar areas that could buffer impacts of current anthropogenic climate change is an urgent requirement (Ashcroft 2010; Dobrowski 2011; Keppel et al. 2012; Reside et al. 2013). The capacity of a site to act as a refugium depends on the rate of warming within it relative to surrounding areas, the duration and magnitude of climate change, and climatic tolerances of resident biota (Moritz & Agudo 2013).

Biological mechanisms governing species' responses to climate change can inform efforts to identify modern climatic refugia. If these areas are defined as having lower rates of climate change, refugia effectively reduce the rates at which species' climatic envelopes (q, or tolerance niches *sensu* Sax et al. 2013) move relative to species' dispersal rates (c^*). Refugia complement strategies intended to increase species dispersal rates because those rates are measured relative to how quickly areas with suitable climates shift. All other things being equal, the most effective refugia will be relatively large so as to reduce risks of localized, stochastic extinctions and mitigate climate impacts sufficiently well that $q < c^*$ for the duration of the climate change period. In principle, this means refugia can satisfy their technical definition while being spatially dynamic; that is, they act like a habitat corridor that is buffered against climate change impacts. This issue has been little explored (Graham et al. 2010; Rose & Burton 2011). While the roles of refugia in preserving relictual populations during periods of sustained cooling is well known (Hampe et al. 2013; Jurickova et al. 2014), their durability during periods of rapid warming is considerably less certain. Expanded understanding of the distribution and dynamics of refugia relative to recent climate changes and potentially constituent species is urgently needed.

Local adaptation and dispersal

A population is more likely to survive the effects of climate change if it retains sufficient standing variation to enable adaptive shifts in tolerance of changing environmental conditions. These effects are ubiquitous, given that even very long-lived species, like trees, show widespread evidence of local adaptation to climatic conditions (Davis et al. 2005; Franks et al. 2014).

Furthermore, local adaptation to climatic conditions depends on the balance between local selective responses and gene flow (Lenormand 2002), which may shift rapidly in areas where human land uses impose dispersal barriers but climate-change-related selective pressures vary spatially and temporally. Selection can nevertheless shift species' critical thermal limits to the extent that local genetic variation exists. For example, *Drosophila* populations rapidly evolve increased tolerance to stressful abiotic conditions in experimental microcosms (Reusch & Wood 2007). Species' seasonal timing (phenologies) have shifted rapidly over recent decades (Kharouba et al. 2014), responses that reflect phenotypic plasticity and the presence of sufficient genetic variation to permit selection (Berteaux et al. 2004; Bradshaw & Holzapfel 2008; Skelly & Freidenburg 2010). Similarly, variability in heat shock protein expression can be high, suggesting potential responses to strong selection for increasing upper critical temperature (Reusch & Wood 2007). Conversely, recent reviews of thermal thresholds globally suggest there is strong conservatism across taxa in upper thermal limits (Araujo et al. 2013), and shifts in tolerance at species upper thermal limits occur much slower than at their lower thermal limits (Munoz et al. 2014). Maintenance of genetic diversity in support of traits that are critical for adaptive responses to warming (e.g. thermal tolerance), as well as identifying populations with limited adaptive potential (Hoffmann & Sgro 2011), would improve the prospects of successful conservation outcomes.

Yet, climate change may select for differences in dispersal ability, not just thermal tolerances. Warming along species' geographical range limits in fragmented landscapes selected for increased dispersal capacity among insect populations (Hill et al. 2011). In those areas, individuals with greater dispersal capacity would be the first to colonize areas that have newly become climatically suitable, allowing them to escape intraspecific competition (Hargreaves &

Eckert 2014). In contrast, model-based expectations suggest that dispersal can reduce probability of successful adaptation to climate change by exposing species to novel competitors (Norberg et al. 2012). Such apparent mismatches between model-based and field ecological observations can be substantial. However, there is growing evidence that assisted gene flow or management activities that increase dispersal rates are likely to accelerate adaptation to changing climatic conditions, but negative impacts, like outbreeding depression, also present risks that must be recognized and addressed (Sgro et al. 2011; Weeks et al. 2011).

While models that assume strong potential impacts of competition can predict negative impacts of dispersal on population survival, alternative theoretical frameworks have been described (e.g. Leroux et al. 2013) in which dispersal is critical to improve prospects for species survival. This framework was linked to field-based observations to generate predictions of risks related to climate change relative to species' dispersal capacities and climatic tolerances across large areas of North America. Risks associated with outbreeding depression, for instance, may prove larger in populations that are naturally highly fragmented, such as those inhabiting mountainous areas (Hamann & Aitken 2013). Across enormous areas of central North America, however, human land uses have subdivided formerly continuous landscapes that have very little topographical relief (see Fig. 1.1). Increasing dispersal rates among population isolates in such areas would restore gene flow to levels that could have been historically observed, which seems unlikely to yield perverse conservation outcomes in terms of adaptation, especially given the benefits of outcrossing for genetic rescue in isolated and inbred populations of naturally outbreeding species (Frankham 2015).

Planning for Uncertainty

Anthropogenic climate change will impose non-analog conditions in some areas (Williams et al. 2007). These conditions will necessitate management of the effects of extreme events and species responses to previously unobserved environmental conditions (Lemieux et al. 2011). Large areas that include potential climatic refugia are more likely to provide both the shelter and resources species require under such circumstances. Agri-environmental programs used in Europe and the United States (Baylis et al. 2008) can maintain or improve habitat quality for target species within core protected areas and facilitate their dispersal through managed mixed use areas surrounding them (Donald & Evans 2006; Lawson et al. 2012). Accepted systematic conservation planning principles, such as redundant species representation within networks of protected or managed areas, will reduce the likelihood that climate changes will eliminate species from the system (Lemieux et al. 2011; Gillson et al. 2013). Smaller areas can help integrate networks that include widely dispersed large protected areas in regions adjacent to landscapes under highly intensive human use (Hannah 2011), such as across broad expanses of central North America.

To predict species responses to climate change in a way that allows effective targeted approaches (Heller & Zavaleta 2009; Dunlop et al. 2012), observations and mechanisms determining species' responses to recent changes are vital (Kujala et al. 2013a). Long-term monitoring programs (McMahon et al. 2011), like the Breeding Bird Survey (Newman 2011; Sauer et al. 2013), provide measurements of species' responses against historical values. This temporal component provides context and considerably greater biological insight than purely spatial measurements (e.g. Kerr et al. 2007) and is critical if adaptive management (where best practices are determined “through sequential reassessment of system states and dynamic relationships” either actively through experimentation or passively through monitoring and experience [Rist et al. 2013]) is to employ the strongest evidence (Mawdsley 2011). Such management programs should also continue to monitor and manage populations of invasive species while recognizing the increasing difficulty of defining alien and native species in a changing world (Webber & Scott 2012).

Conclusion

New research efforts that integrate mechanistic understanding of species' dispersal relative to the pace of climate change are vital to address conservation challenges posed by the interaction of high intensity human land use with rapid climate change. This framework also provides the basis to identify modern climatic refugia, which can be viewed as areas with low rates of environmental change (or climate velocities) relative to species' dispersal abilities, a dynamic definition of *refugia* relative to anthropogenic climate changes. While management strategies that account for biological variation in dispersal capacities that vary across species assemblages, such as assisted migration for species with the least dispersal capacity or where land costs prohibit use of other approaches, are likely to improve most species' conservation prospects, the same strategies also pose risks to populations that are locally adapted to environmental conditions. Uncertainties around impacts of extreme events and the advent of non-analog conditions, along with the need to account for and retain adaptive potential among target populations and species, represent important areas where research would yield practical benefits.

Some regions with large areas of intact wilderness remain in regions such as northern North America, and strategies discussed here are intended to enable species to reach those areas successfully despite the presence of semi-continental dispersal barriers of intense human land use. Efforts to improve habitat for species in degraded areas are unlikely to yield perverse conservation outcomes, but wilderness areas outside these are also at risk. Extensive and rapid growth of industrial land uses, such as for bitumen oil extraction in the boreal landscapes just beyond North America's central plains, creates potentially impenetrable obstacles to geographical range expansion for some species as well as a growing footprint of comprehensive habitat destruction. This growth over the past decade is a reminder that the existence of expansive wilderness areas is no guarantee of their persistence. Such areas are also experiencing large climate change impacts and these generally grow larger toward the Arctic (IPCC 2013). Thus, species must become progressively better dispersers the further north their ranges extend, leading also to increasing relative impacts of land use changes on species capacities to track shifting climatic conditions in those areas. Wilderness conservation in these few frontier regions that remain must be a high priority. At the least, strategies that facilitate species movement beyond existing human-imposed dispersal barriers are likely to improve species' conservation chances during this epoch of accelerating climate change.

Figures

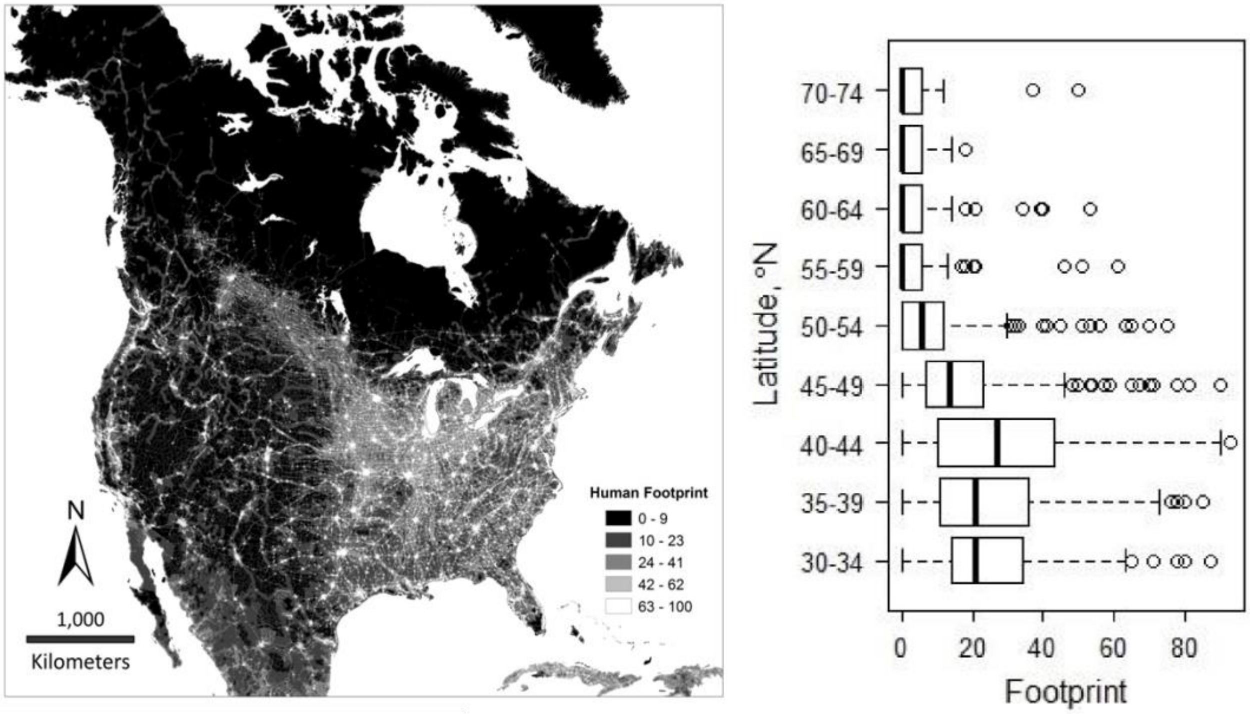

Figure 1.1. Human footprint in North America, expressed as a percentage of the human influence present in each terrestrial biome, measured with a combination of data on population density, human land use and infrastructure, and human access via waterways, rail, and roads (derived from Sanderson et al. 2002). Graph shows median footprint (vertical lines) and interquartile range of footprint values (boxes) relative to latitude (dashed lines, whiskers representing most extreme data point within 1.5 times the interquartile range; circles, outliers). Although footprint appears to be concentrated on the eastern half of the continent, there is a clear peak through the middle of the continent, stretching through central Canada to the Rocky Mountains in the west.

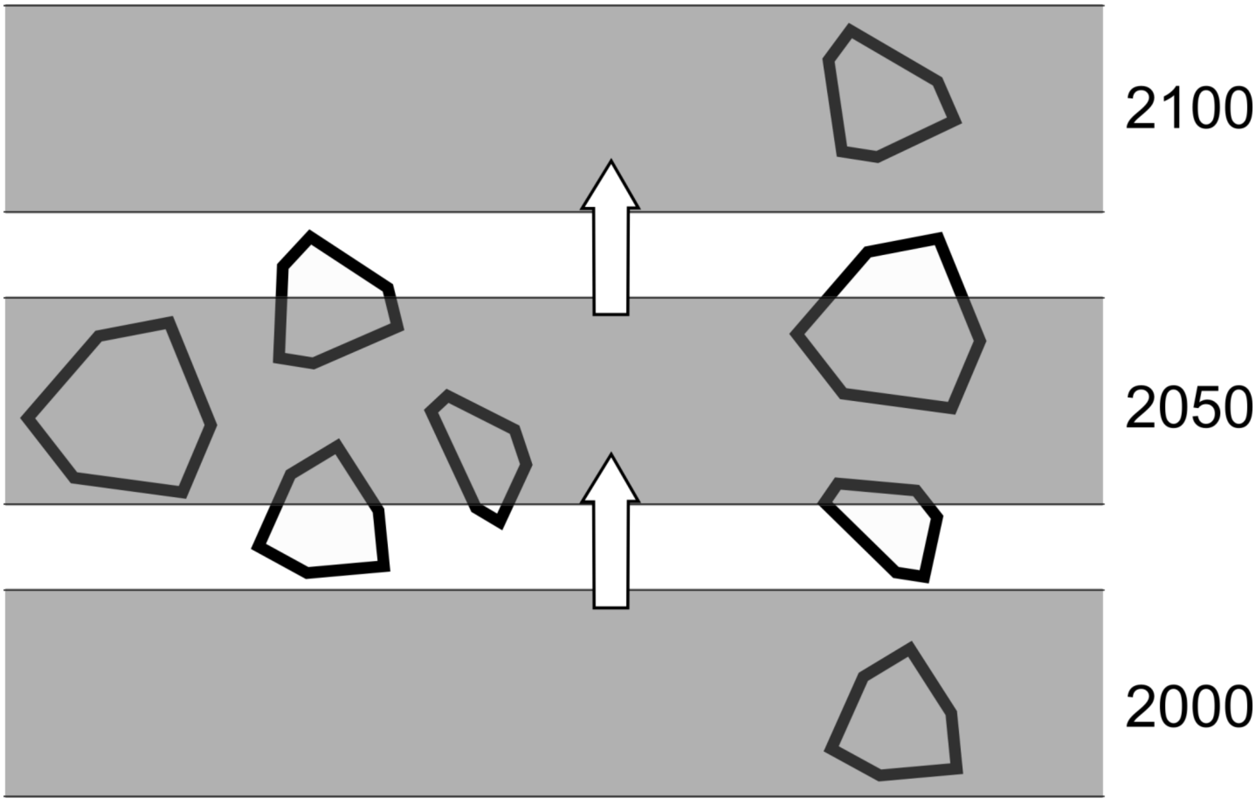

Figure 1.2. A conventionally clustered reserve network (left) and a reserve network stretched along the axis of climatic niche movement (gray, climate windows at 3 periods intended to exemplify significant climate change; arrows indicate direction of climate window movement).

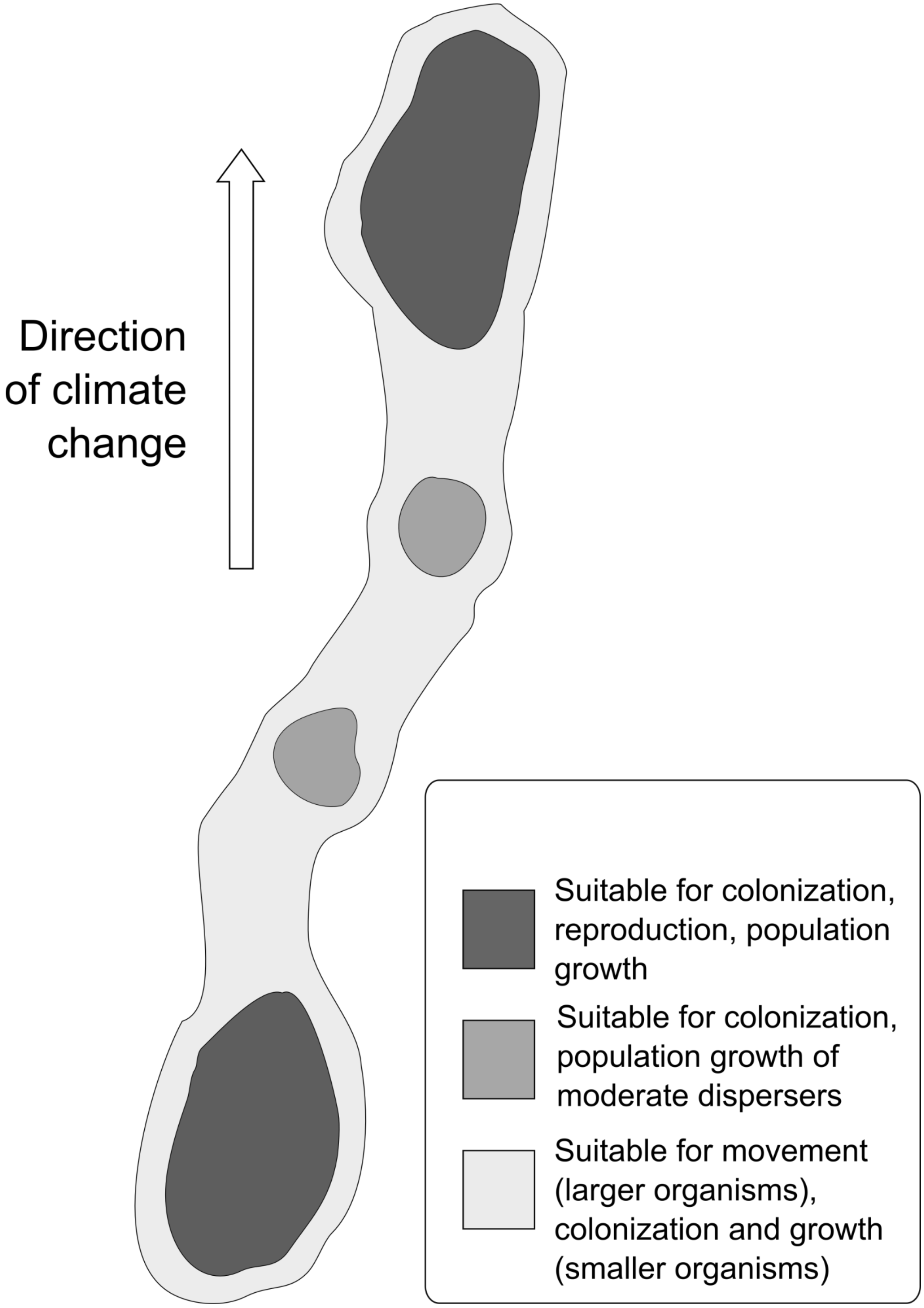

Figure 1.3. Two ways to connect habitat patches (black) for species tracking climate niches moving from bottom to top of the figure: continuous corridors (light grey) and stepping stones (dark grey).

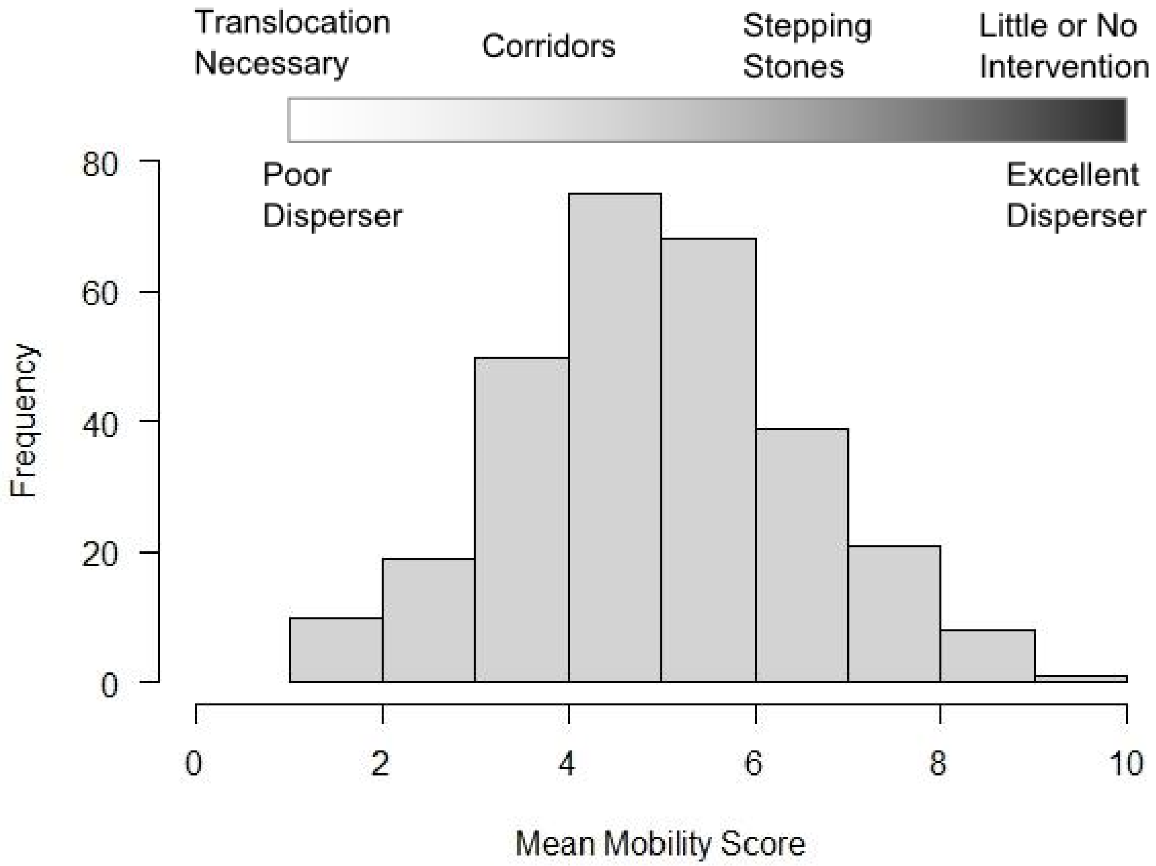

Figure 1.4. Butterfly mobility scores (derived from Burke et al. 2011) highlighting best approaches for habitat connectivity based on dispersal ability.

Chapter 2: Assessing the shelf-life of cost-efficient conservation plans in Canada's farmland

Please note: This paper has been formatted for submission to the peer-reviewed journal Conservation Biology.

Appendices referenced are available at the end of the thesis document.

Abstract

The high cost of conservation within agricultural regions warrants systematic planning approaches that explicitly consider land prices when selecting potential sites, to produce reserve sets that accomplish targets efficiently. However, changes in land use within these regions and delays between plan design and implementation may render optimized plans obsolete before implementation occurs. An initiative to acquire and restore habitat for species-at-risk in Canada's farmland was used to measure the shelf-life of cost-efficient conservation plans, given observed changes in two measurements of land acquisition costs and trends in agricultural land use intensity from Censuses of Agriculture (available at 5 year intervals from 1986 to 2011). For each year of data, these "costs" were mapped and conservation plans simulated using the conservation planning decision tool Marxan. Plans were then compared to test for changes through time in a) the arrangement of selected sites for conservation, and b) the total cost of potential conservation plans. For each acquisition cost type, the cost savings of explicitly accounting for prices during site selection were also measured. Results from the separate analyses converged in general trends. Costs of acquiring areas for conservation, and the intensity of land use within them, generally rose substantially, albeit differently between regions. Explicitly accounting for land price variation in space each year added to cost-efficiency, decreased the variability of costs, and increased the number of unique solutions to choose between. While the costs of implementing conservation plans rose rapidly through time, the need

to focus conservation efforts on particular areas remained highly consistent. Delaying conservation action reduces what systematic conservation plans can achieve in a manner that alternative site selection cannot circumvent. Rapid conservation action is cost effective in this case, even with moderate levels of uncertainty in how to implement restoration goals.

Introduction

Conservation initiatives must seek to balance economic costs with benefits. Pressures to optimize this trade-off are particularly acute where land is extensively or intensively used, has high economic value, and is acquired by conservation organizations through purchase or compensation. Systematic conservation planning (Margules & Pressey 2000) has emphasized the importance of selecting sites for protection or management to maximize efficiency - that is, the ability to achieve the greatest conservation benefits per unit cost (Laycock et al. 2009; Kukkala & Moilanen 2013). The costs of acquiring lands vary and explicit measurements of those costs (e.g. the income generated through local land uses, an area's capital value, or some form of opportunity cost) provide more defensible and transparent conservation plans (Ando et al. 1998; Naidoo et al. 2006; Boyd et al. 2015). Simpler estimates of the costs of protecting an area, such as counts of the number of areas required or their sizes, are less likely to provide reliable indications of the economic efficiency of conservation plans (Underwood et al. 2009; Murdoch et al. 2010; Auerbach et al. 2014). While the costs of acquiring lands for conservation purposes can be measured, areas differ also in their land use intensities, which can render some areas far less able to sustain sensitive species without significant restoration efforts (Kerr & Cihlar 2004).

The computational challenges associated with prioritizing areas for conservation or restoration have diminished (Ball et al. 2009; Moilanen et al. 2009), but implementing conservation plans can take many years (Meir et al. 2004; McDonald-Madden et al. 2008;

Visconti & Joppa 2015). In the intervening period, land use changes and intensification may continue (Barraquand & Martinet 2011; Bowler 2014), economic conditions can change, and the likelihood of achieving conservation targets given the initial financial commitments and onsite ecological conditions may change substantially. Cost changes through time can affect the efficiency of initially optimal conservation plans in two ways: by changing which sites are the most important to include in an optimal conservation solution, or by changing the total cost of all sites included in the solution and consequently whether all conservation targets can still be achieved. If land prices or the likelihood that an area retains or can recover important ecological characteristics change relatively among sites in the period between planning and implementation, then site selections for the most efficient (optimal) solution may also change. Even if the relative importance of sites remains constant through time, rising land acquisition or restoration costs may cause conservation plans to leave out critical areas because available funds are insufficient to secure all areas needed for proposed networks.

The rates at which the economic costs of conservation plans—or requirements for restoration—change may limit their life expectancy, or "shelf life", before changing circumstances render them obsolete in terms of cost-efficiency, or incomplete. Such patterns of change will affect how conservation planners select sites and time their acquisition; if changes in priority areas are likely, plans may need to include flexibility in site selection from the outset and/or require sustained monitoring of land markets for an opportune moment to create and implement them. Understanding these patterns will ensure that the actual cost-efficiency remains high, not just the expected efficiency based on prices at the time of planning. Studies testing how conservation planning efficiency is affected by stepwise land use changes in simulated landscapes (Meir et al. 2004; Visconti & Joppa 2015) focus on availability of natural areas, and do not include the possibility of acquiring converted sites for restoration. The cost-efficiency of systematic conservation plans in the context of gradual land acquisition has been explored (Wilson et al. 2006; Underwood et al. 2008), but these studies do not address how changes in costs might alter conservation plans. While one recent study examining the sensitivity of systematic conservation plans to arbitrary changes in cost (Carwardine et al. 2010) found that priority of important sites remained mostly stable, and one study has addressed return on investment in conservation under modelled future land use scenarios (Polasky et al. 2008) no studies to our knowledge have used empirical patterns of change through time. Finally, while dynamic optimization methods have recently allowed researchers to model projected changes in their planning regions (Baker et al. 2004; Underwood et al. 2008; Williams & Johnson 2013), understanding how conservation plans would have changed relative to land prices and land use intensities over the recent past can inform predictions of their future effectiveness.

In this paper, we test how the ecological obstacles and implementation costs for a systematic conservation plan targeted at cost-efficient endangered species recovery have changed over a quarter century of agricultural intensification, within the temperate agricultural regions of Canada. These regions extend from the Atlantic to Pacific Oceans, occupy ~766,000 km^2 (Kerr & Cihlar 2003) and include much of North America's Great Plains and Mixed-wood Plains. These areas have high human population densities and species richness, small, scattered protected areas, and consequently, the greatest number of species-at-risk (Kerr & Deguise 2004; Warman et al. 2004; Freemark et al. 2006). Land-use intensities are extremely high relative to adjacent, non-agricultural areas. Climate change-induced range shifts for many taxa through this matrix suggest that landscape permeability must be improved through the restoration and protection of habitats that can serve as stepping stones for dispersal (Robillard et al. 2015).

While past national conservation strategies have focused on conservation initiatives on private land (http://www.canada.ca/en/campaign/ncp/), there is currently no overarching plan for how national-level conservation goals, such as the protection and restoration of habitat for species at risk across Canada's farmland, might be accomplished systematically.

We used empirical land prices to first test the benefits of accounting for variation in such prices when making efficient conservation plans in Canada's farmland. We then examined how changes in land values through the recent past affect the stability of optimal trade-offs between land costs and conservation benefits and the cost and conservation penalties that result from delaying the implementation of a systematic conservation plan. We measured the change in the overall cost of optimal conservation solutions through time and examined how this affects the effectiveness of conservation plans with a fixed budget. The latter two analyses included a distinct metric of agricultural land use intensity that enabled exploration of how increasing demands for habitat restoration could affect conservation and restoration plans that target species-at-risk.

Methods

Study Region

The planning region of this study was delineated by the agricultural areas in Canada, as determined using agricultural land use/land cover information (Kerr & Cihlar 2003). Agricultural areas were divided into a grid of 1463 cells representing potential sites within which to focus conservation efforts; most cells were 470 km^2 in equal area, but some cells near the periphery of agricultural areas were smaller (300 – 322 km^2; Fig. 2.1). While grid cells could be made smaller, information on species' distributions is progressively less reliable at higher resolutions, making such efforts less likely to represent species' presences reliably within individual landscapes.

Simulating Cost-Efficient Conservation Solutions Using Marxan

Our analyses involved simulation and comparison of multiple efficient conservation plans or "solutions," each the product of multiple runs of a reserve selection algorithm. We used the program Marxan (Ball et al. 2009), which uses a simulated annealing algorithm to find sets of sites that together accomplish a conservation goal for the lowest cost (see Appendix A: Supplemental Methods and Table A.1 for detailed algorithm parameters).

As described below, within Marxan we assigned a minimum occurrence target for all species-at-risk within the planning region, a price for each site, and the measured potential for each site to contribute to meeting the conservation target. We then ran the software 1000 times to generate 1000 possible conservation solutions. The complete solution (i.e. all species targets met; see below) with the lowest cost out of these 1000 Marxan runs is then chosen as the optimal solution, and a summary table across all solutions displays the frequency with which each site was selected as part of a solution. A set of runs therefore yielded two important simulation results: a single best solution with its own particular arrangement of sites, displayed as a list of binary ratings by site (1= "selected", 0= "not selected"), and with a specific cost to implement; and the table of selection frequencies by site, which was used as a proxy for the relative importance of a site as part of an optimal conservation plan.

In all analyses, the results of these simulations under differing spatial cost patterns were compared, to examine how these differences affected the overall arrangement and cost of conservation plans.

Land Price, Land Use Intensity, and Target Species Data

Land Prices and Land Use Intensity

In separate analyses, two different variables were used as a proxy for the cost of conservation land acquisition: the mean per-hectare value of the land's capital (total capital), and the mean per-hectare value of gross receipts from farming operations (gross income). Total capital represented the dollar cost to purchase farmland and equipment outright for the purposes of habitat conservation, whereas gross income represented the dollar cost of compensating landowners for lost productivity on land set aside for habitat conservation.

A third analysis used a proxy for agricultural intensity that represented the estimated relative "cost" to restore land successfully for species-at-risk protection and recovery. This metric, hereafter referred to as land use intensity, was measured as the sum of the mean intensity of fertilizer, herbicide, insecticide and fungicide applications within a site (more detail in Appendix A: Supplemental Methods). Land use intensity contributes to the decline of species in these regions independently of land cover change (Kerr & Cihlar 2004; Gibbs et al. 2009), and creates secondary impacts like invasion by non-native species, that make restoration goals more challenging to achieve (Suding 2011). Land use intensity in this analysis is therefore a relative measurement of effort required to achieve restoration targets. Patterns of change in land use intensity measured using this approach, within arrays of sites reveals trends in the quality and extent of habitat available to species-at-risk in those areas.

Data on economic costs and land use intensity were obtained from the Canadian Census of Agriculture (Statistics Canada 2014) at the level of census consolidated subdivision (CCS). CCS boundary files used to assign spatially-explicit CCS cost values to grid cells were available from the Census of Agriculture from 1986 until 2011 (Statistics Canada 2015), so this became the study’s time range; because census data are available every five years, the years included were 1986, 1991, 1996, 2001, 2006, and 2011, except in the case of gross income, for which values were only available from 1991, 2001, and 2011. Raw reported values in each CCS were converted to per-hectare values by dividing them by the total reported area of farmland within the CCS (in hectares), and rasters of these values by CCS were converted to the area-weighted mean values for each site using zonal statistics in ArcGIS. All dollar values were converted to 2011 Canadian dollar equivalents using the consumer price index (Statistics Canada 2014) to account for inflation.

Species

Each simulation attempted to select sites for protection of habitat for those terrestrial species at risk. Species were included if a) they were listed under Canada’s Species at Risk Act (SARA); b) a historical range map was available for that species from the Canadian Wildlife Service (Canadian Wildlife Service 2012); c) 50% or more of their historical range was determined to consist of human-dominated land uses (urban or agricultural), as determined from validated land use observations derived from satellite data (Kerr & Cihlar 2003); d) the historical range overlapped our grid of sites such that the species could benefit directly from conservation plans centered on agricultural landscapes. This resulted in a total of 91 species to be included: 52 vascular plants, 13 birds, 8 insects, 8 reptiles, 4 mammals, 4 amphibians, and 2 non-vascular plants (see Appendix A, Table A.2 for full list).

Sites that could provide potential habitat (if selected for restoration) for recovery of a given species were identified by overlapping the planning region with historical range maps of each species at risk. It was assumed that sites overlapping the range of a given species-at-risk contained land parcels that could be restored to provide a suitable habitat patch for the species, thereby increasing its available habitat area, and that such parcels would be available within a chosen site to be set aside for habitat. The willingness of a landowner to enter into a conservation agreement is an important practical consideration at the planning stage (Meir et al. 2004; McDonald-Madden et al. 2008; Knight et al. 2011), but no such measurements have been undertaken nationally to permit assessment of this issue in analyses conducted here. We assume that all grid cells, which are large relative to farm sizes, contain sites where landowner cooperation is achievable.

The conservation target as assigned in Marxan was to create a set of reserves that collectively provide a certain minimum number of occurrences of every species (where a site overlapping with a species range map was considered an occurrence) for the lowest cost. This was done for three different minimum levels of representation: one, four, and seven occurrences for each species. Species that were found to occur in fewer sites than the occurrence target prescribed were assigned a target equal to their total number of occurrences. The above target levels were selected to create solutions that covered a wide range of conservation effort, without having that effort exceed the maximum number of sites available for half or more of the target species. Running simulations for three different target levels allowed us to average, at every year for a given cost type, site selection frequencies generated across the three target levels (1, 4 and 7 occurrences). This average selection frequency is similar to the “average optimacity” metric (Wilhere et al. 2008), which measures the relative importance of a site in a conservation plan, independent of the ambitiousness of occurrence targets.

Each unique combination of “cost” type (including land use intensity), year, and species target, represents one “scenario” within which conservation plans were generated.

Measuring Efficiency Gains of Cost-Explicit Planning

Given the challenges of assessing conservation costs over broad areas and through time (Naidoo & Adamowicz 2006; Naidoo & Ricketts 2006; Ban et al. 2009), past conservation planning efforts have aimed to minimize the area or number of sites protected, using these values to replace spatially explicit land prices and permitting site-specific costs to be ignored (e.g. Araújo et al. 2002; Pressey et al. 2004). We explored whether efforts to include land prices were likely to yield a cost savings within our study system, by comparing the acquisition costs of conservation solution sets generated when differences in site prices were considered against the costs of a null model that treated all sites as equivalent in price during selection.

The relationship between land costs and numbers of species per site strongly affects whether including land price information will likely increase efficiency of the planning process relative to focussing solely on benefits, like species representation (Naidoo et al. 2006). If land costs and species numbers per site are negatively correlated, it is less likely that including costs will provide new information on how to prioritize restoration efforts, as high species numbers will correspond to a high benefit:cost ratio. Conversely, weak or positive correlations between land costs and richness would make land cost information likely to be informative for cost-efficient planning. We tested for a relationship between land prices and species richness among sites to explore this issue for each combination of year and acquisition cost type (total capital or gross income). We conducted this analysis using data in years where this relationship was most strongly positive and most strongly negative for each cost type. A highly constrained species target (7 occurrences) was assigned to the year with the most negative coefficient per cost type, and a liberal species target (1 occurrence) was assigned to the year with the most positive coefficient. This was done to generate a particularly conservative comparison and a nonconservative comparison per cost type. We conducted a Welch's t-test on simulations using these values to compare the mean cost of the price-ignored solutions to the mean cost of solutions generated when price was taken into account.

The differences in total plan cost produced by this analysis as described above would represent a suite of reserves that are only 1 hectare each in area, equivalent to 0.01km^2, which are <5th percentile for existing protected area size in the study region. For each comparison, we used an example reserve size of 7.7km^2 to show the possible cost savings for a realistically ambitious set of reserves. An area of 7.7km^2 represents the 3rd quartile of protected area sizes within or near the planning region, according to recent data from the World Database of Protected Areas (IUCN & UNEP-WCMC 2015).

Comparing Solution Arrangements, Cost, and Feasibility through Time

We assessed how the arrangement and total cost of optimally efficient solutions might change through time by running Marxan for the multiple years available for each cost type. Here, land use intensity is treated as a "cost" alongside the acquisition cost metrics, but is presented in unitless intensity values rather than dollars. The distribution of target species was assumed constant throughout all scenarios.

Arrangement

We measured the agreement between the average selection frequency values throughout the planning region in the first year with the same values in subsequent years, to calculate whether the spatial distribution of selection frequencies changed through time, for each cost type. The concordance correlation coefficient (Lin 1989), which incorporates both association and agreement between two measures, produced identical results to a simple Pearson's coefficient, indicating that the slopes of the relationship between selection frequency values in the first year and those in subsequent years were close to 1. A Spearman's rank correlation was used to measure the agreement in these values between the initial year and subsequent years, and linear regressions to estimate the rate of change in the agreement with the initial solution from the first time period to the last.

Cost and Feasibility

We calculated the median, minimum and maximum total cost of the solutions generated in each scenario, and plotted these through time within a given cost type and target level, to assess whether the budget required to accomplish the targets changed over the study period. If the cost increased over time, we then re-ran all scenarios for that cost type using the median cost in the first year as a budget cap for subsequent years, and calculated how many species or species occurrences became "unprotected" by the budgetary shortfall incurred over that time interval. The overall cost of a solution could exceed the budget cap, but would incur a penalty to the cost-efficiency score for that run.

In each simulation, we assumed that acquisition of land within all chosen sites took place within a single time step; modelling the stepwise acquisition of land parcels was beyond the scope of this analysis. We did not assume that all land within a chosen grid cell would be set aside for habitat conservation; by using mean per hectare prices within each site, we made the analysis flexible with respect to reserve size.

Results

Acquisition costs and land use intensity varied temporally and spatially, with most sites becoming more expensive or more difficult to recover through time (Fig. 2.2). Mean prices and land use intensity across all sites usually increased with time (Table 2.1). Mean land use intensity decreased in 1991 relative to 1986, but then climbed above 1986 values from 1996 onward. This unique decline did not appear to be related to a decline in a particular agricultural input (i.e. fungicide only, fertilizer only) that year, but rather from a decline in both pesticide and fertilizer intensity, particularly in the southern core of the prairie sites in the planning region (Fig. B.1 in Appendix B: Supplemental Results).

Regions of high richness did not coincide strongly with areas of high or low acquisition cost across the study region (Table 2.2). However, species-rich regions did coincide with more intense agricultural practices, and areas where land use intensity was increasing.

For acquisition costs, the scenario most expected to benefit from the consideration of land prices, and the scenario least expected to benefit from land price consideration, both demonstrated statistically-significant cost savings by explicitly including price (all $p << 0.001$; Table 2.3). While data in some years were not normally distributed, a Wilcoxon rank sum test yielded qualitatively similar results ($p << 0.001$). In some cases, the proportional gains in mean cost-efficiency across runs were small (e.g. 1-2% of the total cost). However, in cases modelled here relying on sets of $7.7km^2$ reserves, even small gains in efficiency led to large cost savings. Furthermore, for all scenarios, run sets that ignored explicit land prices produced solutions that had the same number of sites and therefore the same cost, whereas run sets accounting for the variability of prices contained solutions that could be identified as more or less expensive.

For all scenarios, the agreement between the distribution of selection frequencies among sites in the first year and the distribution of selection frequencies in subsequent years remained high throughout the study period (Table 2.4). While statistically significant declines in agreement through time were detected for land use intensity and total capital, rates of decline for all cost types represented a loss of less than 5% in the similarity of the final distribution of values to the initial distribution. These linear rates of change are also likely to over-estimate rates of change in later years, since many cost-target combinations exhibited a slight non-linear loss that levelled off over time. Similar comparisons of the single best solutions at each year using the kappa statistic of agreement found steeper rates of decline in similarity (Table B.1; 4.2-31.5% losses).

For both land acquisition cost types at all target levels, the total cost of the best reserve set increased in every successive year (see Fig. 2.3a-c for 4-occurrence target results). This trend was generally present in the reserve sets based on land use intensity, but with the same slight dip present in year 1991 as observed for mean site values. Most yearly increases in cost were significantly higher than the variability in total costs within a given set of 1000 solutions, and the minimum (best solution), median and maximum total costs for these solution sets all displayed the same trend of increase. While in some scenarios for total capital and gross income, cost increases in a few sites affected total cost of plans across all sites more strongly, excluding these sites from the analysis revealed a similar trend toward increasing costs through time (Fig. B.2).

The capacity of a fixed budget to accomplish representation goals eroded through time considerably more than purely through inflationary cost increases. For all cost types and target levels, using the median total cost of the optimal 1986 solution as a constraint led to species being lost from the reserve set and remaining species occurring less often (except in the year 1991 for land use intensity; Fig. 2.3d-f). In the case of total capital with the goal to protect at least 7 sites for each species, the initial 1986 budget failed to protect 129 occurrences of 43 different species by 2011 (73% of total occurrences represented, 53% of species fully represented). The trends of change in cost and capacity to accomplish representation goals through time did not differ noticeably between target levels within a given cost type despite predictable differences in absolute values (Fig. B.3, B.4).

Discussion

Conservation costs can change rapidly and cause systematic conservation planning objectives to become unachievable. This study examines how known past changes in the spatial patterns of land value and land use intensity through time affect the outcome of cost-efficient conservation planning. We aimed to uncover central tendencies in these patterns by repeating our analyses for two types of land acquisition cost, a land use intensity proxy, and multiple conservation target levels; among these variables, the trends were broadly similar.

Our approach enabled us to identify an erosion of conservation return on investment over time with respect to cost changes. As demonstrated, costs can be assessed economically, using fixed costs based on the necessity of land acquisition, but can also be measured relative to land use intensity. Whether conservation plans focus on habitat restoration or simply protecting existing habitats, lands can be purchased outright or management rights can be transferred for conservation. We focus here on agricultural landscapes, which are subjected to a particular array of land use practices that contribute distinctly to species endangerment (such as fertilizer and pesticide applications), and where land values at a point in time depend on both current land use practices and the complexities of international commodities markets. However, approaches similar to ours could apply readily to other environments, such as forested landscapes where the value of forest leases could be assessed through time.

The rate at which conservation costs will change in the future will necessarily be subject to substantial uncertainty (Carwardine et al. 2010; Barraquand & Martinet 2011). Analyses of how those costs have shifted through the recent past, as performed here, can provide guidance around the "shelf life" of newly created conservation plans. Of course, such analyses are not possible without comprehensive, regularly collected environmental and socio-economic data. It is important to stress the need to continue monitoring land use and land prices through vehicles such as the Canadian Census of Agriculture, at a time when Canada's ability to collect such data has been in flux (Death of evidence 2012; Walton-Roberts et al. 2014). As long as an up-to-date record of economic and land use patterns is maintained, similar analyses can be conducted into the future.

The stability through time of the spatial distribution of critical areas for cost-efficient conservation suggests that these areas are indispensable for the recovery of species at risk in these regions. This result presents an opportunity to focus conservation and restoration activities stably on a relatively small number of regions. On the other hand, our results also highlight the risk of continued land use intensification in areas that emerge so consistently as high-priority areas for restoration (similar to observations of priority conservation areas under climate change by Olson & Lindsay 2009). While land use intensity in temperate regions contributes to species endangerment and hinders their recovery, and vulnerability to such threats highlights the importance of conservation in nearby sites (Lawler et al. 2003), intensification could also make eventual recovery of species at risk in these areas a practical impossibility by eliminating residual habitats that could serve as nuclei for restoration efforts and by eliminating even many small-bodied species through very high pesticide application rates. This poses a challenge to conserve and restore habitat in these regions while the return-on-investment remains high.

The diminishing rate of return on funds applied to systematic conservation plans for a given target through time is a concern when viewed in the context of existing funds for smaller-scale initiatives. For example, assuming an area of ~7.7km^2 per site acquired, our study found that in 1986, conservation plans that restored habitat for at least one occurrence of 91 species-at-risk could be accomplished for as little as $181,721,001 in 2011 constant dollars when replacing capital. This is the most expensive cost type considered here, and yet this plan cost is still comfortably below the amount provided to the Nature Conservancy of Canada by the federal government in 2007 as part of the Natural Areas Conservation Program ($225,000,000, or $241,950,672.64 in 2011 constant dollars; http://www.budget.gc.ca/2007/plan/bptoc-eng.html). Our results show however, that by 2006, the year before this one-time contribution, accomplishing the same conservation goal while replacing capital would cost at minimum $347,428,235, and in 2011 would cost at least $461,829,445, nearly twice the value of the one-time gift and about two-thirds of the entirety of funds raised for the program to-date (http://www.natureconservancy.ca/en/what-we-do/conservation-program/).

While using Canada-wide species at risk representation goals resulted in a coarse analysis, national-scale systematic conservation plans have been shown to cost less overall than multiple, separate regional conservation plans (Strange et al. 2006a). Nevertheless, the particular solutions created in this study were for the purpose of revealing changes through time under changing economic and land use scenarios; they are not meant to be considered definitive maps of where conservation efforts must be focussed. Other factors could make site selection more complex. For example, our study could not account for range shifts that may occur among target species following climate change (Kujala et al. 2011; Coristine & Kerr 2015; Robillard et al. 2015). However, because the remaining habitats for many species-at-risk in southern Canada are undetectably small when measured using satellite data (Kerr & Deguise 2004), restoring habitat to promote species-at-risk recovery will increase these species' ability to endure potential challenges associated with changing climatic conditions (Olson & Lindsay 2009; Robillard et al. 2015).

In an increasingly dynamic world where conservation resources are finite, ensuring that conservation planning is cost-efficient and robust to both economic uncertainty and land use intensification will maximize return on investment. Our study is intended to guide conservation initiatives seeking to account for how land acquisition schedules will affect their ability to achieve targets. When applied to our study system, it indicates an urgent need to begin setting aside habitat within areas where the opportunities for representation of species-at-risk are high relative to costs; the sooner such lands are acquired, the greater the return on investment in species recovery. Applied elsewhere, approaches to understanding the “shelf-life” of systematic conservation planning solutions can bring conservation organizations closer to realizing habitat protection targets on shorter timescales. The costs of conservation rise rapidly, as can the risks of irreversible biodiversity losses. The clear message is that delays diminish the effectiveness of the most careful conservation plans and erode the value of limited funds available to achieve them.

Figures and Tables

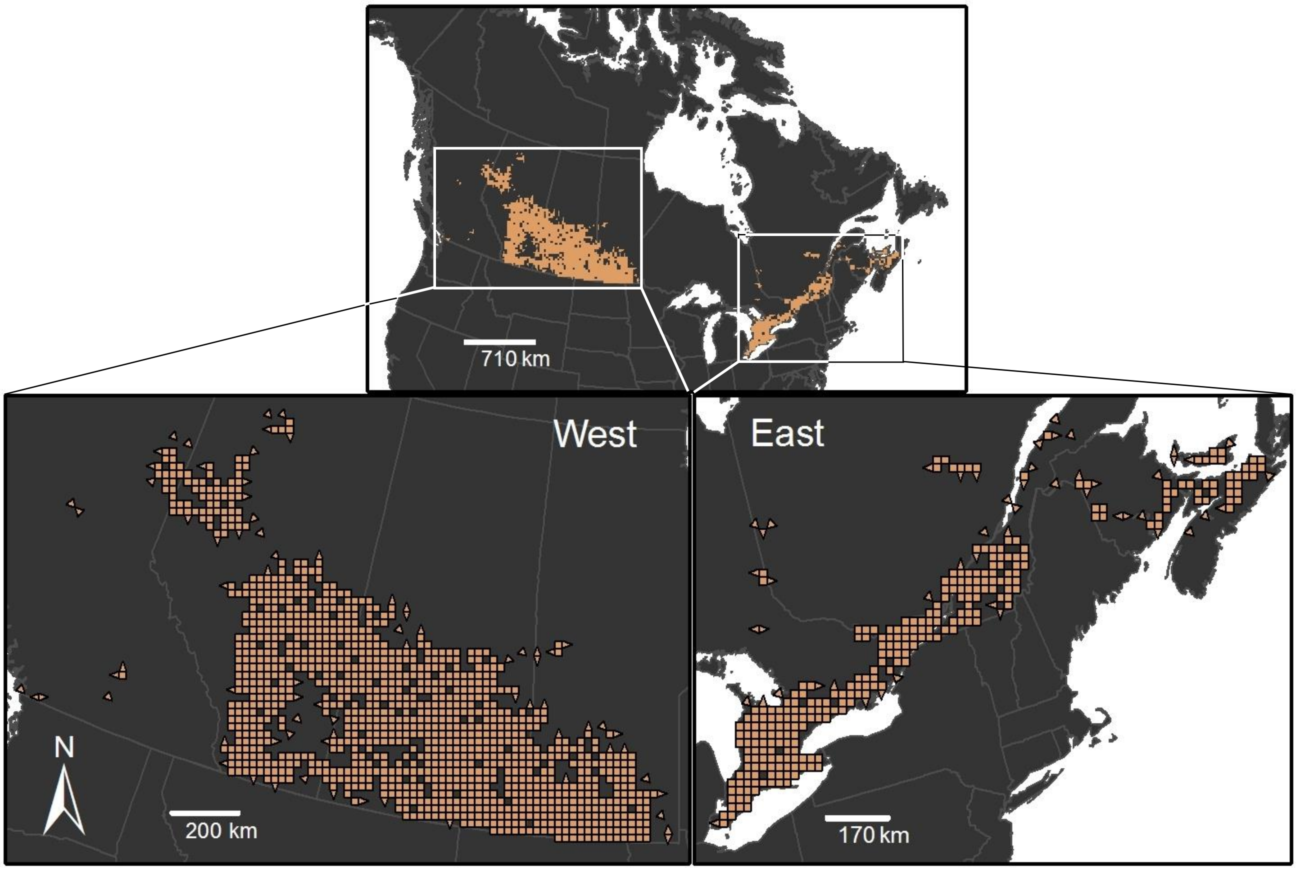

Figure 2.1. Map of the planning region showing the grid of possible sites to select for conservation/restoration.

Table 2.1. Mean price across all sites within the planning region, for the mean per hectare value of capital on (total capital), the mean gross income generated from (gross income), and the relative land use intensity in each site, through time.

Cost Type	**Mean Cost Across Sites**					
	1986	**1991**	**1996**	**2001**	**2006**	**2011**
Total capital ($)	3259	3370	3522	4085	4654	5814
Gross income ($)	--	634.6	--	811.4	--	917.1
Land use intensity	0.7630	0.6953	0.7926	0.8273	0.8409	0.9485

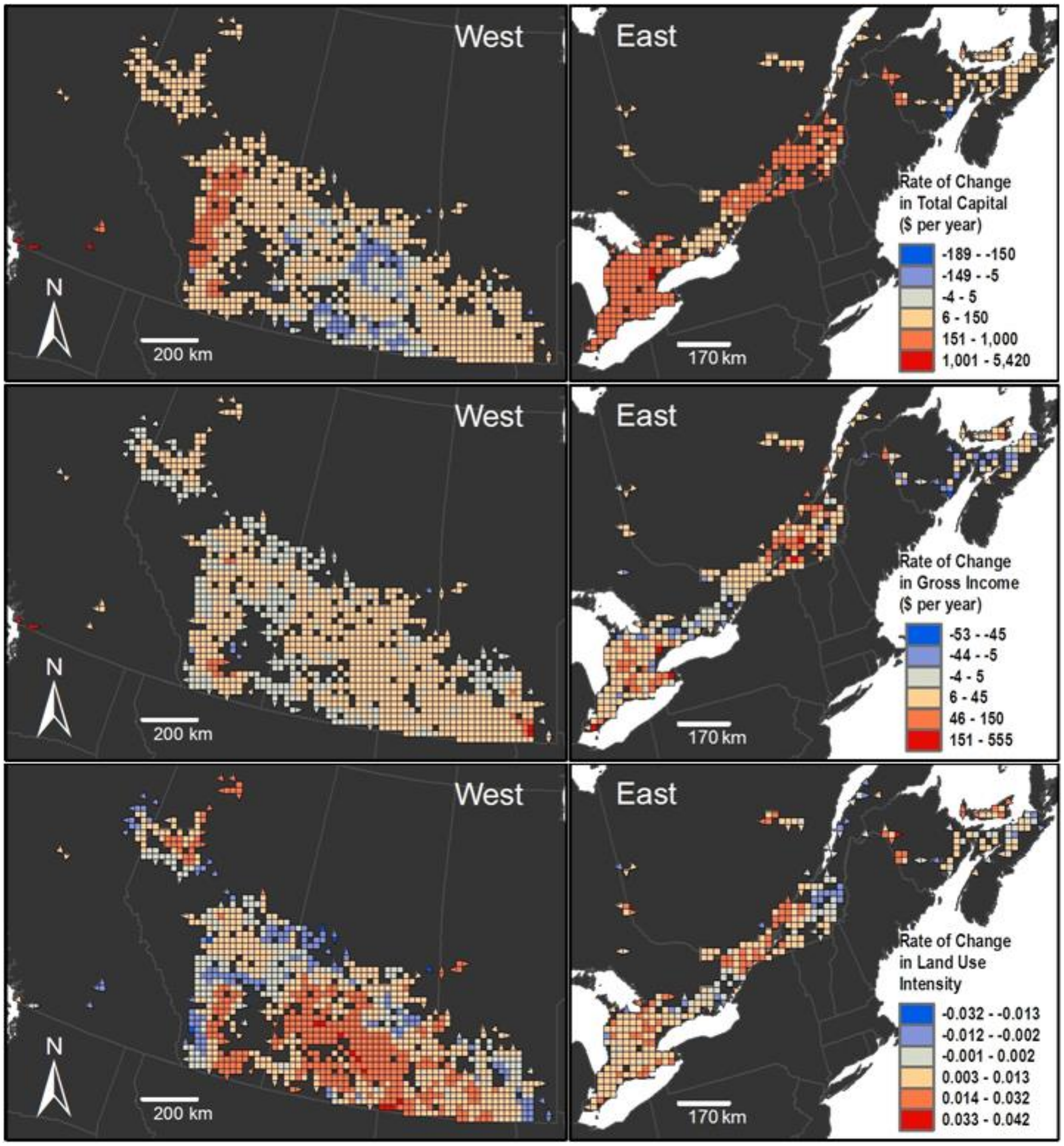

Figure 2.2. Rate of change in a) total capital per hectare, b) gross income per hectare in 2011 constant dollars, and c) relative land use intensity per hectare. Total capital and land use intensity rates are for the period from 1986 to 2011, measured as the slope of the regression line through values at 5-year intervals (1986, 1991, etc.); gross income rates are for the period from 1991 to 2011, measured as the slope of the regression line through values at 10-year intervals (1991, 2001, 2011).

Table 2.2. Pearson's coefficient of the correlation between price and target species richness at all sites within the planning region (Canada's farmland; n=1463). Cost-years chosen for the analysis of the benefits of including variability in price are indicated by an asterix (*). Statistically significant coefficients are presented in bold type.

Cost Type	**Year**	**Coefficient**
Total capital	1986	0.029*
	1991	-0.036*
	1996	-0.027
	2001	-0.021
	2006	-0.031
	2011	-0.021
	Slope over all years	-0.038
Land use intensity	1986	**0.297**
	1991	**0.201***
	1996	**0.282**
	2001	**0.334**
	2006	**0.365**
	2011	**0.374***
	Slope over all years	**0.385**
Gross income	1991	-0.031*
	2001	-0.008
	2011	-0.006*
	Slope over all years	0.033

Table 2.3. Differences between the mean total implementation cost of solutions generated while accounting for variation in site prices, and the mean total realized cost of solutions generated while ignoring price variation. For all t-test comparisons, $p<<0.001$.

Scenario		**Mean Cost ($)**		**Difference ($)**	**%**	**Difference for 7.7km^2 sites ($)**
		Costs considered	Costs ignored			
Total capital	1986, 1 occurrence	2.40×10^5	2.56×10^5	1.55×10^4	6.46	1.195×10^7
	1991, 7 occurrences	1.03×10^6	1.04×10^6	1.77×10^4	1.73	1.366×10^7
Gross income	2011, 1 occurrence	9.13×10^4	1.04×10^5	1.27×10^4	13.9	9.772×10^6
	1991, 7 occurrences	2.08×10^5	2.12×10^5	4.51×10^3	2.17	3.472×10^6

Table 2.4. Amount of agreement in mean selection frequency of all sites between the initial year and subsequent years measured using Spearman's rank correlation coefficient, and the linear rate of change in agreement across the study period.

Cost Type	**Agreement in Mean Selection Frequency of All Sites with Initial Values**						**Slope**	**P-value**
	1986	**1991**	**1996**	**2001**	**2006**	**2011**		
Total capital	1	0.91	0.88	0.86	0.85	0.84	**$-1.45\text{x}10^{-03}$**	0.009
Gross income	--	1	--	0.92	--	0.91	$-1.67\text{x}10^{-03}$	0.137
Land use intensity	1	0.89	0.90	0.92	0.88	0.90	**$-1.39\text{x}10^{-03}$**	0.030

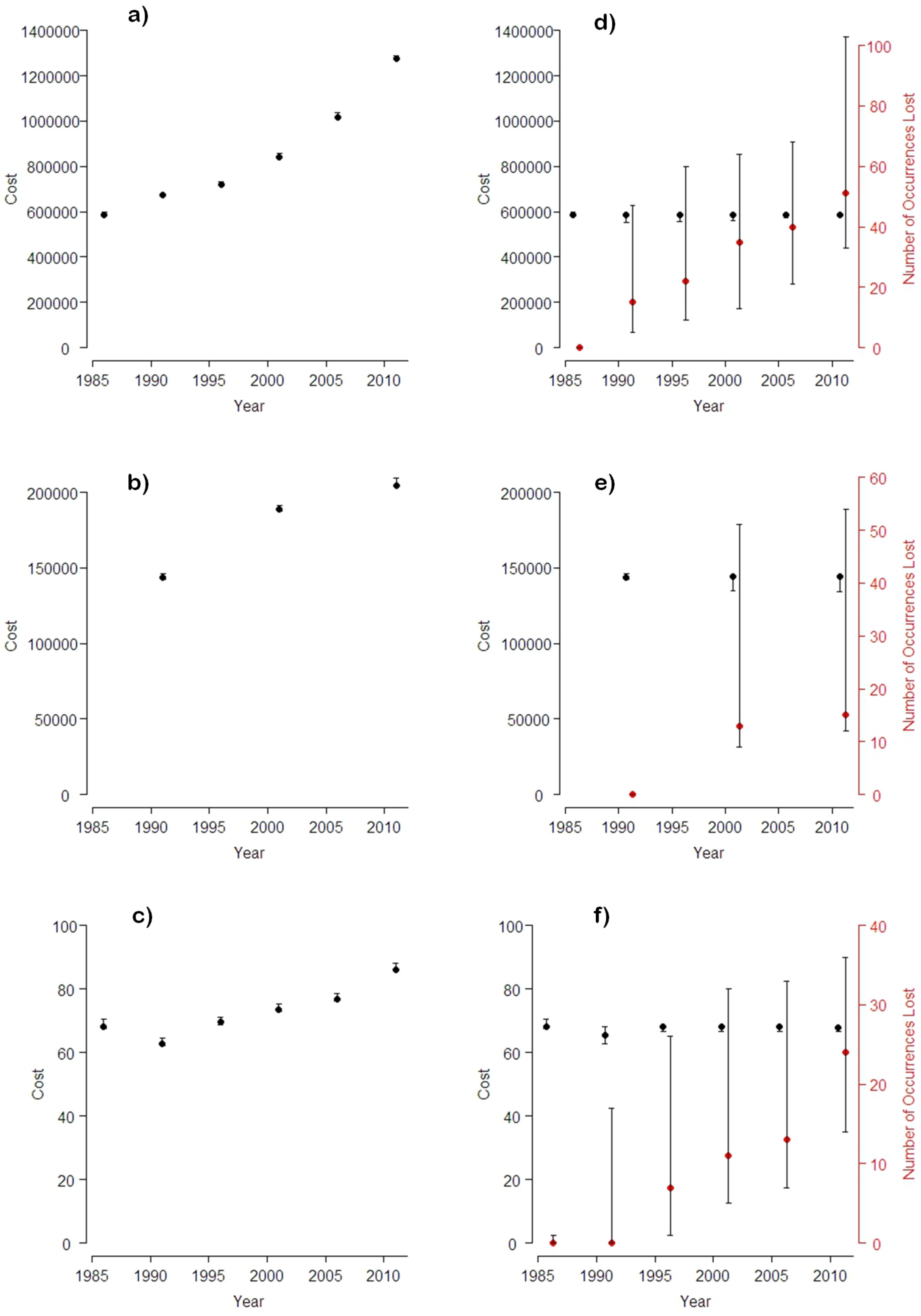
a)
Cost
1400000
1200000
1000000
800000
600000
400000
200000
0
1985
1990
1995
2000
2005
2010
Year
d)
Number of Occurrences Lost
100
80
60
40
20
b)
200000
150000
100000
50000
e)
60
50
40
30
10
c)
f)

Figure 2.3. Changes in overall cost and feasibility of cost-efficient conservation solutions through time, for the 4-occurrence species representation target. Left: Median cost of 1000 conservation solutions generated by Marxan using a) total capital, b) gross income, and c) land use intensity, when all occurrence targets have been met. Right: Cost of solution (black circles) and number of occurrences lost from a solution (red circles) generated by Marxan using d) total capital, e) gross income, and f) land use intensity, when solution cost is constrained based on the minimum cost in the initial year. Bars denote the full range of values (minimum to maximum observed).

General Conclusion

To maintain biodiversity protection under changing climate and as species' ranges shift, there must be increased protection of habitat within the human-dominated regions of North America. The first chapter of this thesis presented many ways this can be done strategically, including, for example, protection along climate change trajectories, and within areas of predicted climate stability. For many of these approaches, the restoration of the matrix within which conservation areas are embedded, currently devoted to agricultural uses, will be a key priority. Indeed, for many species, restoration alone could significantly improve population persistence prospects as climate changes. But initiatives to increase habitat protection and restoration within the agricultural matrix must be cost-efficient, and must be robust to the challenges of delayed implementation in a landscape of dynamic land uses. When it comes to conservation of species-at-risk, our findings from the second chapter suggest that in Canada, the locations of critical areas for efficient species-at-risk conservation have remained stable in the recent past despite changes in the relative costs to acquire and restore land within them. What has not remained stable is the extent to which such efficient conservation plans are feasible; the cost and required restoration effort within the most efficient solutions has increased over the observed 25-year time period. The observed increase in land use intensity within these high-priority areas also suggests that threats are increasing in close proximity to many species-at-risk.

Systematic conservation planning requires a multifaceted understanding of the problems to be solved within a given planning region. By synthesizing current climate-change adapted conservation strategies within a framework that emphasizes habitat as an underlying mechanism for species persistence and dispersal in a patch landscape, our research demonstrates practical ways forward in protecting habitat for range-shifting species. It also provides clear advice that can improve conservation planning decisions, by demonstrating that delays in action can cause costs to spiral quickly upward, making targets more difficult to achieve and compromising the efficient use of conservation funds. Other factors, like the probability of human-wildlife conflicts at protected area margins (Goswami et al. 2014), landowner willingness to sell or enter into conservation agreements on private land (Knight et al. 2011), and competing values in regional land use plans (Freudenberger et al. 2013), will also need to be incorporated into particular real-world conservation initiatives. However, because of the pervasiveness of climate change as a threat to the integrity of protected areas (Hannah et al. 2007; Hobday 2011; Alagador et al. 2014), and because conservation funds have been severely limited throughout Canada and internationally (McCarthy et al. 2012; Donlan et al. 2014), these findings concern some of the most universally relevant considerations for conservation planning in human-dominated areas.

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Appendix A: Supplemental Methods

Creating the land use intensity metric

Four variables from the Canadian Census of Agriculture were used to calculate the land use intensity metric: the total reported area of land within a Consolidated Census Subdivision (CCS) applied with a) fertilizer, b) herbicide, c) fungicide, and d) insecticide. Each of these values was divided by the total reported area of farms within the CCS, to yield a measure of the proportion of farm area applied with these inputs.

Insecticides and fungicides were reported together in the 1986 and 1991 census as area applied with pesticide. In order to split this value into a reasonable estimate of insecticide and fungicide applications, we assumed no spatial overlap between areas applied with insecticide and areas applied with fungicide, and that the reported values represented the sum of the two mutually exclusive areas. We then found the proportion of the summed area of insecticide and fungicide allotted to each input type in 1996 within each CCS, and used these proportions to divide up the total area applied with pesticide in 1986 and 1991 into the two components. These split values were then divided by the total farm area to yield the proportion of area applied with insecticide and fungicide, separately.

For each CCS, the values for each input type were summed together to create the land use intensity value. These values by CCS were then rasterized using ArcGIS, and the zonal statistics tool was used with our grid of ~470km^2 sites to calculate the mean land use intensity value within each of these sites based on the values in the CCSs that the site overlapped with. These values at the site level were used as cost inputs to Marxan.

Running Marxan

The objective function

Marxan (Ball et al. 2009) employs an objective function to assign values to the conservation solutions it creates. For this study, in most cases this function can be simplified to:

$$\sum_{Sites=1}^{i} Cost + \sum_{Species=1}^{j} SPF \times Penalty$$

where Cost is the price or level of land use intensity associated with each individual site, i, SPF is the species penalty factor assigned to each species, j (calibrated SPF values described below), and Penalty is the additional cost required to represent any underrepresented species (estimated as the cost of the least expensive remaining planning units representing the missing occurrences of that species). In these simple scenarios, the score for a solution that meets all species occurrence targets will be equal to the overall cost of the solution (i.e. the sum of the cost in all sites chosen). In the scenarios of this study where a budget cap is used, a cost threshold penalty was added to this equation when a solution exceeds the assigned cost threshold. For more information, see the Marxan User's Manual (Game & Grantham 2008) and the Marxan Good Practices Handbook (Ardron et al. 2010).

Calibration of technical parameters

In order to ensure that Marxan was calibrated to find many effective solutions that were as efficient as possible, two main parameters were calibrated for each scenario: the number of iterations of simulated annealing performed for each run (number of iterations), and the value of the species penalty factor (SPF). The boundary length modifier (BLM), a parameter in the objective function used to control the amount of clustering among proposed sites, was kept at 0, since at the scale of this analysis, there would be little biological meaning to a clustered reserve set.

The number of iterations of simulated annealing per run was calibrated to similarly constrain the variability of solutions found by Marxan at each run of the program. The number of iterations was increased if the difference between the most and least costly solution in a set was too great (e.g.

greater than ~15%) or if the least costly solution was not well represented in the solution set (e.g. if the least costly solution appeared only once in the solution set and variability in solution costs was relatively high). This was done for each cost-year combination separately, and was kept constant across years for that grouping (see Table A.1).

The species penalty factor (SPF) was calibrated in order to limit the number of infeasible solutions generated (solutions that failed to meet the occurrence target for at least one species), without overemphasizing the importance of the SPF in Marxan's objective function, relative to the importance of the cost of sites. Calibration runs began with all species assigned an SPF of 1.0, producing a solution set with many infeasible solutions. Species whose occurrence targets were not met were then assigned small increases in SPF (between 0.001 and 0.1 depending on the scenario), with solution sets generated iteratively until all species were assigned adequate penalty factors to be sufficiently represented in most runs. The threshold allowance for the number of infeasible solutions in a set was ~5% or lower.

The number of runs was determined based on what was deemed an optimal compromise between running time and sample size limits. One thousand runs was determined to provide a substantial sample of solutions per scenario (especially considering the low variability of solutions due to the large numbers of iterations per run), without being overly cumbersome to run for 45 different scenarios.

During the feasibility analysis using a budget cap, the default cost penalty threshold parameters were used, as they were found to adequately constrain the cost of solutions, however it did increase the variability in the cost of solutions slightly.

Species List

See Table A.2.

Note: Because some sites within the planning region had no target species, their selection frequency in all scenarios and analyses was predictably 0. However, keeping such sites in the analyses was not found to mask patterns of change within the sites that did contain target species.

Table A.1. Numbers of iterations of simulated annealing per run, for each cost-target combination.

Cost - Target	Number of Iterations
Land use intensity 1	100 k
Land use intensity 4	200 k
Land use intensity 7	100 k
Total capital 1	200 k
Total capital 4	1 mill
Total capital 7	100 k
Gross income 1	200 k
Gross income 4	200 k
Gross income 7	200 k

Table A.2. Species included in the minimum occurrence targets for Chapter 2 (total=91).

Species name	**Marxan species ID**	**Taxon**
Agalinis aspera	53007	Vascular plant
Agalinis gattingeri	53009	Vascular plant
Agalinis skinneriana	53006	Vascular plant
Aletris farinosa	52010	Vascular plant
Ambystoma jeffersonianum	12001	Amphibian
Ammannia robusta	53002	Vascular plant
Anaxyrus fowleri	13002	Amphibian
Anthus spragueii	32006	Bird
Apalone spinifera	62004	Reptile
Aristida basiramea	53019	Vascular plant
Athene cunicularia	33001	Bird
Bidens amplissima	51014	Vascular plant
Buchloë dactyloides	52003	Vascular plant
Bryoandersonia illecebra	53013	Non-vascular plant
Buchnera americana	53025	Vascular plant
Calcarius ornatus	32009	Bird
Carex lupuliformis	53028	Vascular plant
Castanea dentata	53030	Vascular plant
Celtis tenuifolia	52020	Vascular plant
Cephalanthera austiniae	52021	Vascular plant
Charadrius melodus circumcinctus	33005	Bird
Chimaphila maculata	53034	Vascular plant
Cicuta maculata var. *victorinii*	51015	Vascular plant
Cirsium hillii	52022	Vascular plant
Cirsium pitcheri	53101	Vascular plant
Colinus virginianus	33008	Bird
Copablepharon grandis	21001	Insect
Copablepharon longipenne	23009	Insect
Cornus florida	53037	Vascular plant
Cypripedium candidum	53038	Vascular plant
Dalea villosa var. *villosa*	52005	Vascular plant
Desmognathus ochrophaeus	13004	Amphibian

Desmognathus ochrophaeus (Great Lakes / St. Lawrence population)	12002	Amphibian
Dipodomys ordii	43001	Mammal
Eleocharis geniculata (Great Lakes population)	53042	Vascular plant
Empidonax virescens	33010	Bird
Enemion biternatum	52023	Vascular plant
Eremophila alpestris strigata	33011	Bird
Erynnis persius persius	23010	Insect
Eurybia divaricata	52024	Vascular plant
Fabronia pusilla	53004	Non-vascular plant
Frasera caroliniensis	53045	Vascular plant
Fraxinus quadrangulata	51018	Vascular plant
Gentiana alba	53046	Vascular plant
Gentianopsis virgata ssp. *victorinii*	52025	Vascular plant
Gymnocladus dioicus	52026	Vascular plant
Halimolobos virgata	52027	Vascular plant
Hemileuca sp.	23013	Insect
Hesperia ottoe	23014	Insect
Hibiscus moscheutos	51019	Vascular plant
Hydrastis canadensis	52028	Vascular plant
Icteria virens virens	33027	Bird
Iris lacustris	52006	Vascular plant
Isotria medeoloides	53049	Vascular plant
Isotria verticillata	53050	Vascular plant
Justicia americana	52031	Vascular plant
Lanius ludovicianus excubitorides	32017	Bird
Liatris spicata	52032	Vascular plant
Liparis liliifolia	52034	Vascular plant
Lupinus rivularis	53060	Vascular plant
Magnolia acuminata	53061	Vascular plant
Morus rubra	53065	Vascular plant
Numenius americanus	31012	Bird
Pantherophis gloydi (Carolinian population)	63002	Reptile

Pantherophis spiloides (Great Lakes population)	62001	Reptile
Phrynosoma hernandesi	63005	Reptile
Plantago cordata	53073	Vascular plant
Plestiodon fasciatus (Carolinian population)	63011	Reptile
Plestiodon septentrionalis	63004	Reptile
Pooecetes gramineus affinis	33020	Bird
Prodoxus quinquepunctellus	23017	Insect
Regina septemvittata	63009	Reptile
Reithrodontomys megalotis dychei	43002	Mammal
Calcarius mccownii	31005	Bird
Schinia avemensis	23019	Insect
Schinia verna	22005	Insect
Solidago riddellii	51034	Vascular plant
Solidago speciosa	53103	Vascular plant
Symphyotrichum praealtum	52047	Vascular plant
Symphyotrichum prenanthoides	52008	Vascular plant
Symphyotrichum sericeum	52048	Vascular plant
Taxidea taxus jacksoni	43003	Mammal
Thamnophis butleri	63014	Reptile
Tradescantia occidentalis	52049	Vascular plant
Trichophorum planifolium	53092	Vascular plant
Trillium flexipes	53093	Vascular plant
Triphora trianthophora	53094	Vascular plant
Tyto alba	32003	Bird
Vaccinium stamineum	52050	Vascular plant
Viola pedata	53099	Vascular plant
Vulpes velox	42001	Mammal

Appendix B: Supplemental Results

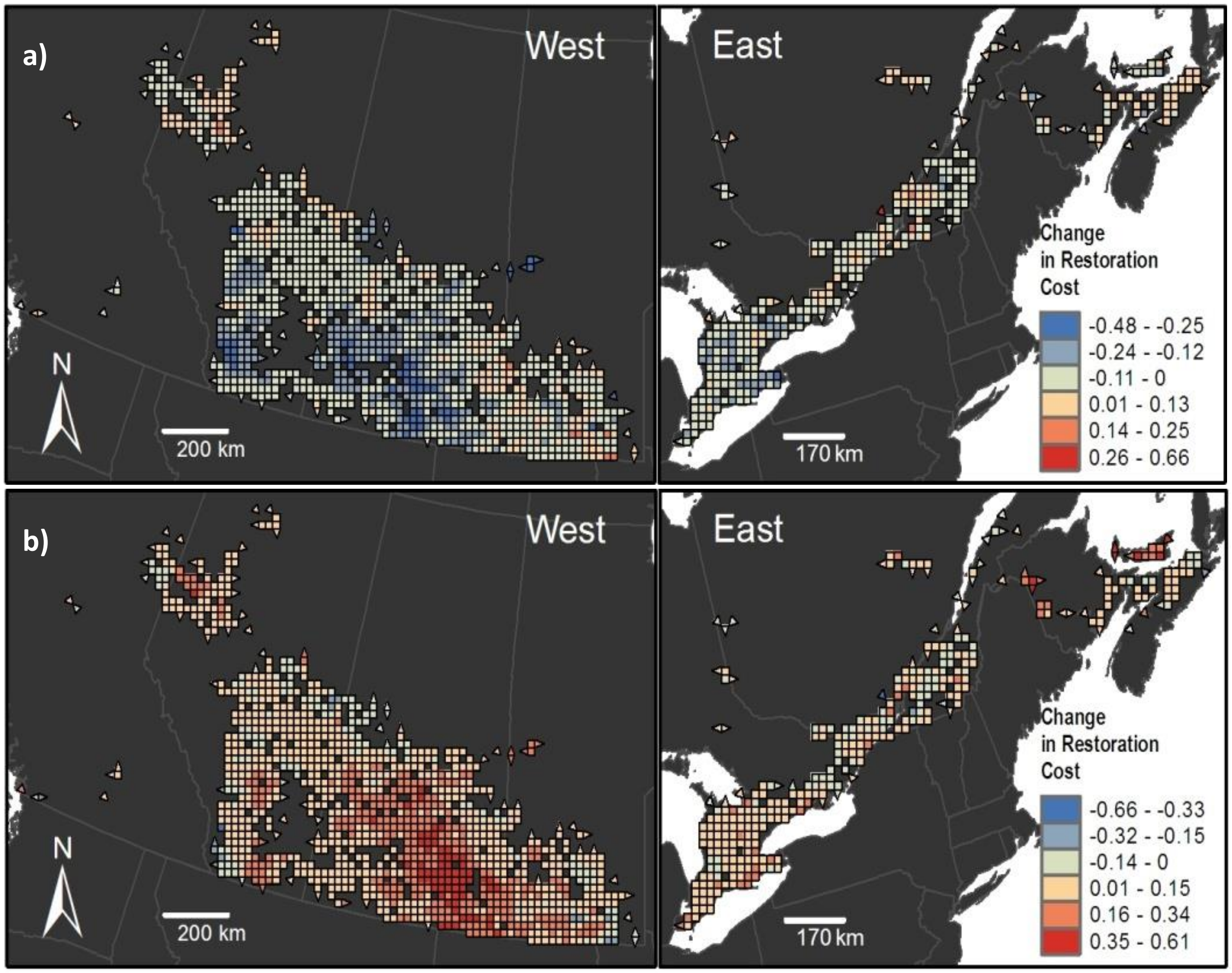


Figure B.1. Change in land use intensity from a) 1986 to 1991, and b) 1991 to 1996.

Table B.1. Change in agreement (using Cohen's kappa coefficient) between best solutions through time. Slopes statistically significant from zero in bold.

Cost Type	**Occurrence Target**	**Agreement of Best Solution with Best Initial Solution**						**Slope**	One-tail P	adjusted R^2
		1986	**1991**	**1996**	**2001**	**2006**	**2011**			
Total capital	1	1.00	0.91	0.86	0.69	0.74	0.69	**-1.26x10^{-02}**	0.004	0.832
	4	1.00	0.94	0.93	0.94	0.93	0.94	-1.69 **x10**$^{-03}$	0.112	0.174
	7	1.00	0.95	0.93	0.94	0.93	0.97	-1.11 **x10**$^{-03}$	0.222	-0.059
Gross income	1	--	1.00	--	0.88	--	0.79	**-1.06 x10^{-02}**	0.020	0.992
	4	--	1.00	--	0.93	--	0.92	-3.93 **x10**$^{-03}$	0.142	0.627
	7	--	1.00	--	0.97	--	0.95	**-2.66 x10^{-03}**	0.018	0.994
Land use intensity	1	1.00	0.82	0.75	0.72	0.77	0.69	**-9.79 x10^{-03}**	0.021	0.610
	4	1.00	0.99	0.96	0.99	0.91	0.96	-2.46 **x10**$^{-03}$	0.063	0.353
	7	1.00	0.98	0.96	0.96	0.96	0.96	**-1.66 x10^{-03}**	0.009	0.730

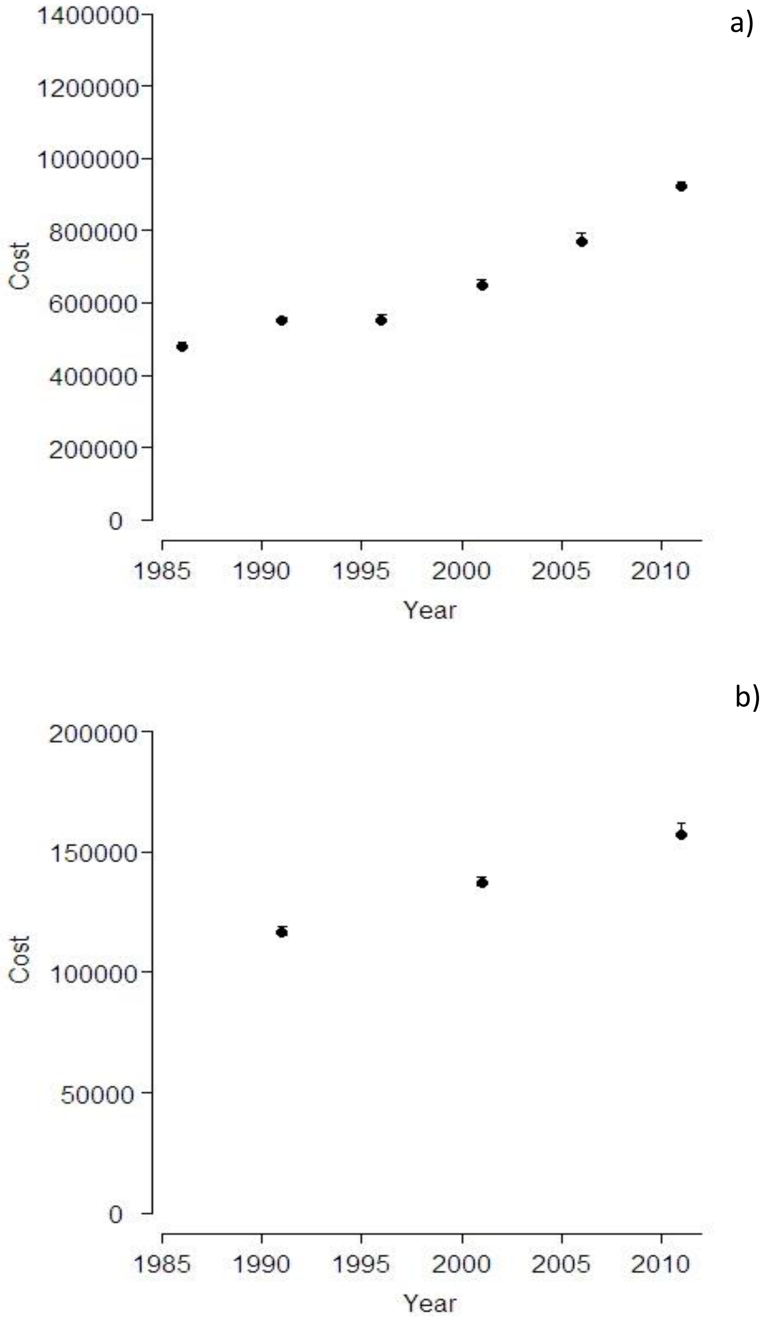
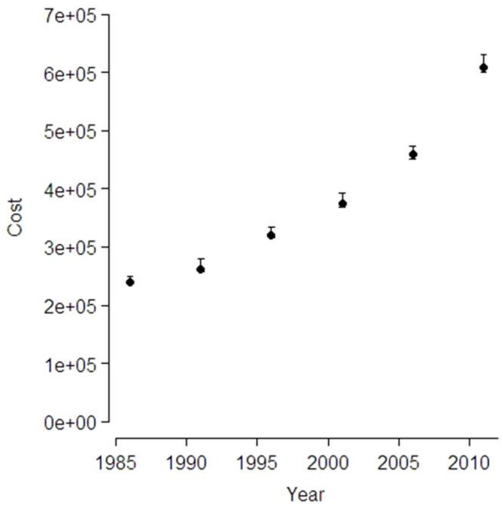


Figure B.2. Change in total cost of best solutions for a) total capital and b) gross income when highly influential sites removed.


7e+05
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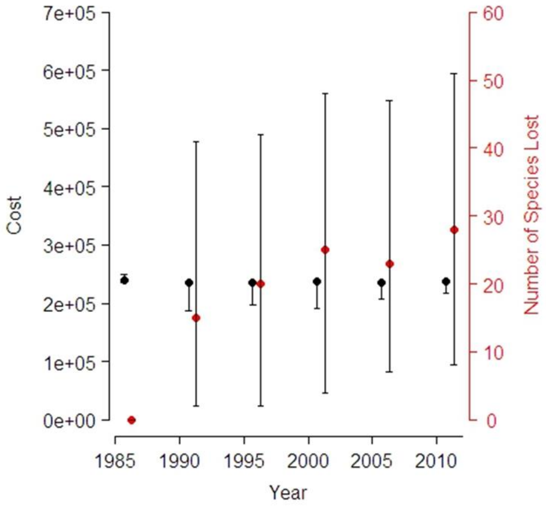
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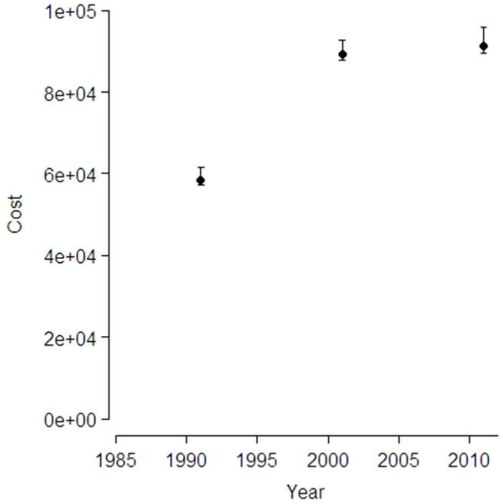
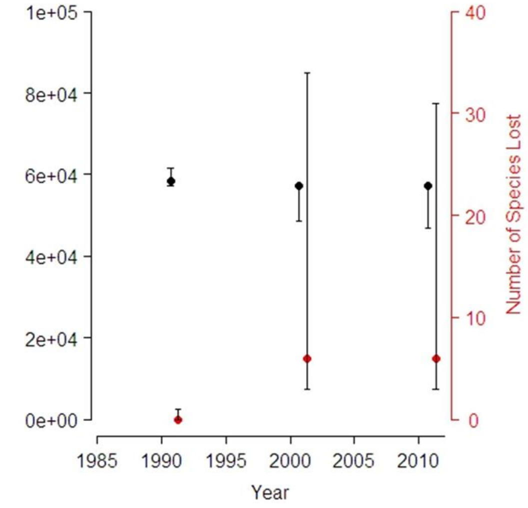
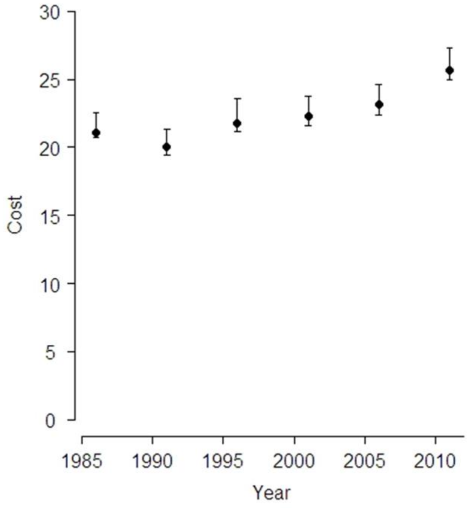
40
30
20
10
0
Number of Species Lost
1985
1990
1995
2000
2005
2010
Year


1e+05
8e+04
6e+04
4e+04
2e+04
0e+00
Cost
1985
1990
1995
2000
2005
2010
Year


1e+05
8e+04
6e+04
4e+04
2e+04
0e+00
Cost
40
30
20
10
0
Number of Species Lost
1985
1990
1995
2000
2005
2010
Year


30
25
20
15
10
5
0
Cost
1985
1990
1995
2000
2005
2010
Year

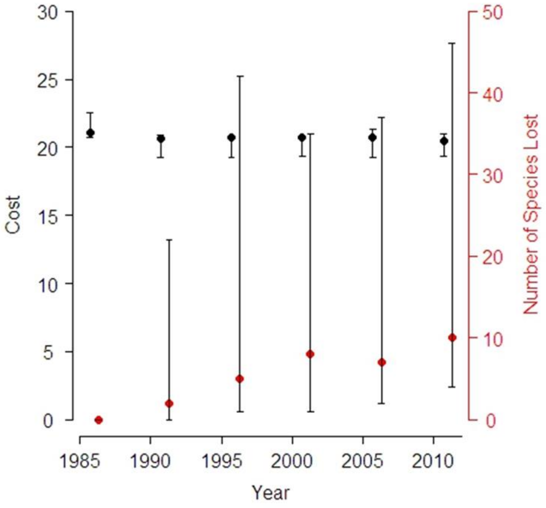

30
25
20
15
10
5
0
Cost
50
40
30
20
10
0
Number of Species Lost
1985
1990
1995
2000
2005
2010
Year

Figure B.3. Changes in overall cost and feasibility of cost-efficient conservation solutions through time, for the 1-occurrence species representation target. Left: Median cost of 1000 conservation solutions generated by Marxan using a) total capital, b) gross income, and c) land use intensity, when all occurrence targets have been met. Right: Cost of solution (black circles) and number of occurrences lost from a solution (red circles) generated by Marxan using d) total capital, e) gross income, and f) land use intensity, when solution cost is constrained based on the minimum cost in the initial year. Bars denote the full range of values.

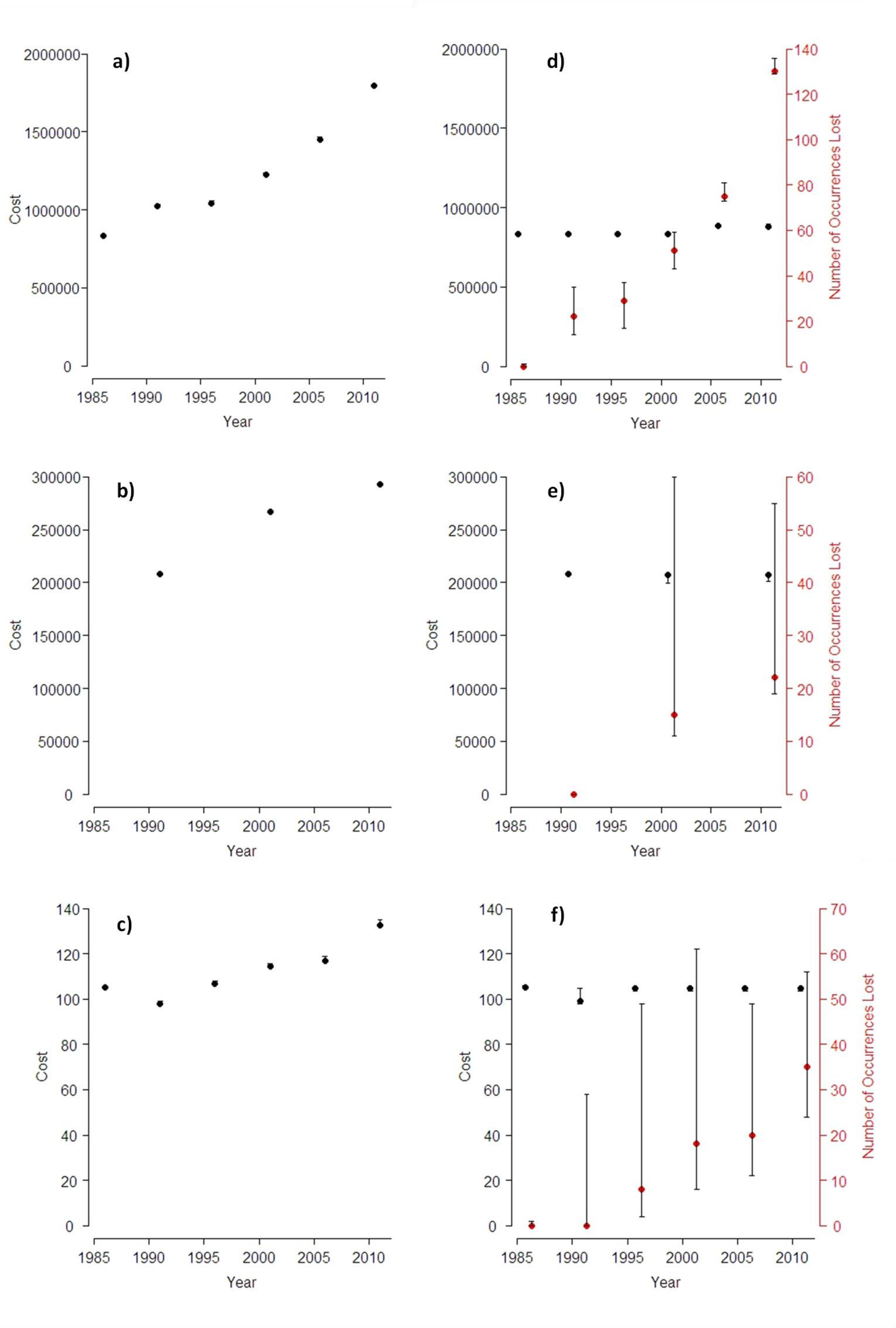

a)
2000000
1500000
1000000
500000
0
Cost
1985
1990
1995
2000
2005
2010
Year
d)
2000000
1500000
1000000
500000
0
140
120
100
80
60
40
20
0
Number of Occurrences Lost
b)
300000
250000
200000
150000
100000
50000
0
e)
60
50
40
30
20
10
c)
140
120
100
80
60
40
20
0
f)
70
60
50
40
30
20
10
0

Figure B.4. Cost Changes in overall cost and feasibility of cost-efficient conservation solutions through time, for the 7-occurrence species representation target. Left: Median cost of 1000 conservation solutions generated by Marxan using a) total capital, b) gross income, and c) land use intensity, when all occurrence targets have been met. Right: Cost of solution (black circles) and number of occurrences lost from a solution (red circles) generated by Marxan using d) total capital, e) gross income, and f) land use intensity, when solution cost is constrained based on the minimum cost in the initial year. Bars denote the full range of values.