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Contributed Paper

Assessing the shelf life of cost-efficient conservation plans for species at risk across gradients of agricultural land use

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Abstract: *High costs of land in agricultural regions warrant spatial prioritization approaches to conservation that explicitly consider land prices to produce protected-area networks that accomplish targets efficiently. However, land-use changes in such regions and delays between plan design and implementation may render optimized plans obsolete before implementation occurs. To measure the shelf life of cost-efficient conservation plans, we simulated a land-acquisition and restoration initiative aimed at conserving species at risk in Canada's farmlands. We accounted for observed changes in land-acquisition costs and in agricultural intensity based on censuses of agriculture taken from 1986 to 2011. For each year of data, we mapped costs and areas of conservation priority designated using Marxan. We compared plans to test for changes through time in the arrangement of high-priority sites and in the total cost of each plan. For acquisition costs, we measured the savings from accounting for prices during site selection. Land-acquisition costs and land-use intensity generally rose over time independent of inflation (24–78%), although rates of change were heterogeneous through space and decreased in some areas. Accounting for spatial variation in land price lowered the cost of conservation plans by 1.73–13.9%, decreased the range of costs by 19–82%, and created unique solutions from which to choose. Despite the rise in plan costs over time, the high conservation priority of particular areas remained consistent. Delaying conservation in these critical areas may compromise what optimized conservation plans can achieve. In the case of Canadian farmland, rapid conservation action is cost-effective, even with moderate levels of uncertainty in how to implement restoration goals.*

Keywords: conservation planning, habitat, implementation, land-use change, private lands, resilience, restoration, return on investment

Valoración de la Vida de Anaquel de los Planes de Conservación Rentables para Especies en Riesgo a lo largo de Gradientes de Uso de Suelo Agrícola

Resumen: *Los altos costos de las tierras en las regiones agrícolas garantizan estrategias de priorización espacial que consideran explícitamente los precios de suelo para producir redes de áreas protegidas que cumplan eficientemente con los objetivos. Sin embargo, los cambios en el uso de suelo en dichas regiones y los retrasos entre el diseño del plan y la implementación pueden volver obsoletos a los planes optimizados antes de que ocurra la implementación. Para medir la vida de anaquel de los planes de conservación rentables, simulamos una iniciativa de adquisición y restauración de suelo con miras a la conservación de especies en riesgo en las tierras de cultivo canadienses. Tomamos en cuenta los cambios observados en los costos de adquisición de suelo y en la intensidad agrícola con base en los censos de agricultura hechos desde 1986 hasta 2011. Para cada año de datos, mapeamos con el uso de Marxan los costos y las áreas de prioridad de conservación designadas. Comparamos los planes para analizar los cambios a través del tiempo en el arreglo de los sitios de alta prioridad y en el costo total de cada plan. Para los costos de adquisición medimos los ahorros a partir de la consideración de los precios durante la selección de sitio. Los costos de adquisición de*

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suelo y la intensidad de uso de suelo en general aumentaron con el tiempo sin importar la inflación (24-78%), aunque las tasas de cambio fueron heterogéneas a lo largo del espacio y disminuyeron en algunas áreas. La consideración de la variación espacial en el precio del suelo redujo el costo de los planes de conservación en un 1.73-13.9%, disminuyó la gama de costos en un 19–82%, y creó soluciones únicas para elegir. A pesar del alza en los costos de los planes con el tiempo, la alta prioridad de conservación de las áreas particulares permanecieron consistentes. El retraso de la conservación en estas áreas críticas puede comprometer lo que los planes de conservación optimizados pueden lograr. En el caso de las tierras de cultivo canadienses, la acción rápida de conservación es rentable, incluso con niveles moderados de incertidumbre sobre cómo implementar los objetivos de restauración.

Palabras Clave: cambio de uso de suelo, hábitat, implementación, planeación de la conservación, rentabilidad de inversión, resiliencia, restauración, tierras privadas

Introduction

Conservation initiatives must seek to balance their economic costs with their intended benefits to biodiversity. Pressures to optimize this trade-off are particularly acute where conservation organizations acquire land by purchase or compensation to owners to manage lands as reserves and that land has been intensively used or has high economic value. Systematic conservation planning (Margules & Pressey 2000) has emphasized the importance of selecting sites to maximize efficiency—that is, to achieve the greatest conservation benefits per unit cost (Laycock et al. 2009; Kukkala & Moilanen 2013). The costs of acquiring lands vary spatially due to multiple economic and social factors, and explicit measurements of those costs (e.g., income from land uses, capital value, and opportunity cost) provide more defensible and transparent conservation plans (Ando et al. 1998; Naidoo et al. 2006; Boyd et al. 2015). Simpler proxies for cost, such as the number of reserves 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). The dollar costs of acquiring lands for conservation can be measured, but areas also differ in their land-use intensity, which affects the effort required to restore and manage an area's ability to sustain sensitive species (Kerr & Cihlar 2004).

The computational challenges of prioritizing areas for conservation or restoration have diminished (Ball et al. 2009; Moilanen et al. 2009; Williams & Johnson 2013), but implementing conservation plans can take decades of fundraising, surveying, and stakeholder negotiations (Meir et al. 2004; McDonald-Madden et al. 2008; Visconti & Joppa 2015). In the intervening period, land uses and economic conditions may change (Barraquand & Martinet 2011; Bowler 2014), as may the likelihood of achieving conservation targets given initial financial commitments and onsite ecological conditions. Changes in land value (via changing economic conditions) or restoration cost (via land-use change) through time can affect the efficiency of initially optimal conservation plans by changing which sites are most important to include in a plan or by changing the total cost of the plan and consequently whether initial conservation targets can still be achieved. If land prices or the potential for habitat recovery changes disproportionately among sites between planning and implementation, then site selections for the efficient solution may also change. Even if the relative importance of sites remains stable through time, rising land-acquisition or restoration costs may cause conservation plans to miss critical areas because funds are insufficient to secure them.

The rates at which the costs of conservation plans change may limit their shelf life, meaning beyond a particular amount of change plans become obsolete relative to cost-efficiency or incomplete relative to conservation goals. Such a change affects how conservation planners select sites and time their acquisition. If changes in the arrangement of priority areas are likely, plans may need to include flexibility in site selection from the outset or require sustained monitoring of land markets for implementation opportunities. Understanding these patterns improves chances that practical, not just expected, cost-efficiency remains high.

Researchers testing how conservation-planning efficiency is affected by stepwise land-use changes in simulated landscapes (Meir et al. 2004; Visconti & Joppa 2015) have focused on wilderness availability and have not considered restoration of converted sites. The cost-efficiency of conservation plans with gradual land acquisition has been explored (Wilson et al. 2006; Underwood et al. 2008), but authors of these studies do not address whether changes in costs alter conservation plans. Although an examination of the sensitivity of systematic conservation plans to arbitrary cost changes by Carwardine et al. (2010) found that priority of important sites remains stable, the changes simulated were not based on expected patterns within the study landscape. Although dynamic optimization allows researchers to model predicted changes in their planning regions (Underwood et al. 2008; Williams & Johnson 2013) and Polasky et al. (2008) modeled future land use to examine changes in return on conservation investment, no one has used observed, temporal patterns of change. Understanding how conservation plans would have changed relative to observed land prices and land-use intensities over the recent past improves understanding of the relationship between cost change and conservation priority and informs predictions of future effectiveness of conservation planning.

We tested how restoration and implementation costs for a systematic conservation plan, targeted at cost-efficient recovery of species at risk, have changed over a quarter-century of agricultural intensification and economic changes within the agricultural regions of Canada. These regions extend from the Atlantic to Pacific Ocean, occupy approximately 766,000 km^2, and include much of North America's Great Plains and Mixedwood Plains. These mostly southerly areas have high human population densities and species richness, little protected area (approximately 94,880 km^2 [IUCN & UNEP-WCMC 2015]) and, consequently, the greatest number of species at risk (Kerr & Deguise 2004). Land-use intensities are high relative to adjacent, nonagricultural areas. Climate-change-induced range shifts for many taxa through this landscape suggest that landscape permeability must be improved through further restoration of habitats in southern Canada (Robillard et al. 2015). Federal funding programs such as the Habitat Stewardship Program (https://www.ec.gc.ca/hsp-pih/) encourage habitat-based approaches to protect multiple species at risk within a single conservation area. Integrating costs into habitat conservation plans may allow agencies responsible for recovery to minimize the costs of a given conservation outcome.

We used empirical land prices to first test the cost savings of accounting for price variation when making efficient conservation plans in Canada's farmland. We then examined how recent historical changes in land values affected the stability (the similarity in arrangement over time) of conservation plans and measured the overall cost of efficient plans through time to examine how changes affect species representation in conservation plans with fixed budgets. The latter analysis included a metric of agricultural intensity to explore how increasing demands in habitat restoration could change restoration plans that target species at risk.

Methods

Study Region

The planning region encompassed Canada's agricultural areas, delineated using satellite land-use and -cover information. We divided agricultural areas into 1463 grid cells representing potential conservation sites. Most sites were 470 km^2, but some peripheral sites were smaller (300–322 km^2) (Supporting Information). Sites were the basic spatial units of our analyses for which species presences and per-area costs were assigned. Although sites could be made smaller, information on species' distributions is less reliable at higher resolutions, making such efforts unlikely to represent species' presences reliably within sites.

Simulating Cost-Efficient Conservation Solutions with Marxan

In our analyses, we simulated and compared several efficient conservation plans (referred to here as conservation solutions). These solutions were each produced from multiple runs of the reserve selection tool Marxan (Ball et al. 2009). Marxan identifies sets of sites that together accomplish conservation goals for the lowest cost with a simulated annealing algorithm based on the objective function

$$\sum_{i=1}^{1463} \mathrm{cost}\,(i) + \sum_{j=1}^{91} \mathrm{SPF}\left(j\right) \times \text{penalty}, \qquad (1)$$

where cost is the cost associated with site i, SPF is the species penalty factor assigned to species j, and penalty is calculated by Marxan with a greedy algorithm as the cost of acquiring the least expensive remaining sites containing missing occurrences of that species (example given in Supporting Information). The boundary length modifier, a parameter often used in the objective function to control clustering of reserves, was kept at 0 because at a Canada-wide scale there would be little biological meaning to a clustered reserve set.

To generate each solution, we assigned a minimum occurrence target for each species at risk within the planning region, assigned prices for each site, and included information on which species are found in which sites. We then ran Marxan 1000 times to generate 1000 conservation solutions. We considered the complete solution (i.e., all species targets met) with the lowest cost of these 1000 runs the optimal solution. Marxan also creates a summary table across all solutions to display the frequency with which each site was selected as part of a solution. A set of runs therefore yielded 2 important 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) with a specific cost to implement and the table of selection frequencies by site that illustrated the relative importance of each 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 Prices and Land-Use Intensity as Costs

Cost variables were obtained from the Canadian Census of Agriculture (Statistics Canada 1986–2013) as reported by farm operations. The data are aggregated by census consolidated subdivisions (CCSs), which are census geographic units made up of multiple municipalities.

In separate analyses, we used 2 variables as proxies for the cost of land acquisition: mean per-hectare value of the land's capital (total capital) and mean annual per-hectare gross receipts from farming operations (gross income). Total capital represented dollar costs to purchase a farm's land, buildings, and equipment outright for conservation, whereas gross income was a proxy for the dollar costs of compensating landowners for lost productivity on land set aside for conservation. Net income values were not available at CCS resolution, and derived net income estimates (gross farm receipts minus expenses) were correlated with gross income (coefficient = 0.86–0.97), making gross income a conservative proxy.

In a third analysis, we used a proxy for agricultural intensity that estimated relative cost to restore land for recovery of species at risk. This metric (hereafter land-use intensity) was calculated as the sum of mean intensity of fertilizer, herbicide, insecticide, and fungicide applications within a site. Proportion of woodland, an important factor in land-use intensity for many ecosystems, could not be measured consistently with census data and was not included. Pesticides and fertilizer contribute to species declines in these regions (Kerr & Cihlar 2004; Gibbs et al. 2009), and fertilizer combined with disturbance creates secondary impacts, such as invasion by non-native species (Alpert et al. 2000), which challenge restoration goals (Suding 2011). Land-use intensity in this analysis was a unitless and relative measure of effort required to achieve restoration targets and complements land-acquisition cost metrics to represent more fully the array of costs involved in habitat conservation. Patterns of land-use intensity change measured this way reveal trends in habitat quality for species at risk. We considered total capital, gross income, and land-use intensity separate cost types. Analyzing other costs inherent in conservation, including transaction, ongoing monitoring, and nonrestorative management costs, was beyond the scope of our analysis.

The CCS boundary files used to assign cost values to sites were available from the Census of Agriculture from 1986 until 2011 (Statistics Canada 1986–2011), so this became the study's time range. Census data are available in 5-year intervals. We included data from 1986, 1991, 1996, 2001, 2006 to 2011 except for gross income, for which values were available for only 1991, 2001, and 2011. Raw values in each CCS were converted to per-hectare values by dividing them by total reported area of farmland per CCS, and rasters of these values were converted to area-weighted mean values for each site in ArcGIS. Dollar values were converted to constant 2011 Canadian dollars using the consumer price index (Statistics Canada 2014) to account for inflation.

Species

Each simulation selected sites for potential habitat protection for terrestrial species at risk of extinction. We chose 91 species at risk from across the study region (52 vascular plants, 13 birds, 8 insects, 8 reptiles, 4 mammals, 4 amphibians, and 2 bryophytes) for inclusion in analyses (inclusion criteria, species list, and species richness map given in Supporting Information).

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 (Canadian Wildlife Service 2012). We assumed sites overlapping the range of a given species contained land parcels that could be restored to provide new habitat for the species, thereby increasing available habitat, and that such parcels would be available within a chosen site to be set aside for restoration.

The conservation target as assigned in Marxan was creation of a set of reserves that collectively provide a certain minimum number of occurrences of every species (where a site overlapping a species' range was considered 1 occurrence) for the lowest cost. This was done for 3 different minimum target representation levels: 1, 4, and 7 occurrences per species. Species that occurred in fewer sites than the occurrence target 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 exceeding the maximum numbers of sites available for at least half the target species. Running simulations for 3 different target levels allowed us to average, at every year for a given cost type, site selection frequencies generated across target levels. This average selection frequency resembled the "average optimacity" measurement (Wilhere et al. 2008) of relative site importance in a conservation plan across effort levels. Each unique combination of cost type, year, and species target represented one scenario within which conservation plans were generated.

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), many conservation planning efforts aimed to minimize the area or number of sites protected, rather than accounting for spatially explicit land prices (e.g., Araújo et al. 2002; Pressey et al. 2004). We explored whether efforts to consider land prices yielded cost savings within our study system by comparing acquisition costs of conservation solution sets generated when differences in site prices were considered against those of a null model that treated all sites as equivalent in price during selection.

We limited cost savings comparisons to 2 scenarios per cost type: one least expected to benefit from considering price variations (conservative) and one most expected to benefit from considering price variations (nonconservative). The more negative the correlation between land costs and numbers of target species per site, the less likely that including land-price information will increase efficiency of the planning process (Naidoo et al. 2006). The conservative and nonconservative scenarios chosen were therefore those for which a Pearson's correlation coefficient for land price and target species richness was most negative and most positive, respectively, and where the representation target was most ambitious (7 occurrences) and least ambitious (1 occurrence), respectively (Supporting Information).

We conducted a Welch's t test to assess whether the mean cost of price-ignored solutions was higher than the mean cost of solutions generated when price was considered in prioritization.

Because our cost types are per hectare, the reported differences in total plan cost would be for suites of only 1-ha (0.01 km^2) reserves, which are less than the 5th percentile of existing protected area size in the study region (IUCN & UNEP-WCMC 2015). For each comparison, we therefore also calculated the cost of 7.7-km^2 reserves to show the possible savings for a realistically ambitious reserve set. A 7.7-km^2 area represents the 3rd quartile of protected area sizes within or near the planning region (IUCN & UNEP-WCMC 2015).

Comparing Solution Arrangements, Cost, and Feasibility through Time

We assessed how the arrangement and total cost of cost-efficient solutions changed through time by running Marxan for all years available for each cost type. The distribution of target species was assumed to be invariant through time.

We measured the agreement between average selection-frequency values throughout the planning region in the first year relative to subsequent years to calculate whether spatial distributions of site selection frequencies changed for each cost type. We used a Spearman's rank correlation (Supporting Information) to measure agreement in these values between the initial and subsequent years and linear regressions to estimate rates of change in agreement through time.

We calculated median, minimum, and maximum total costs of the 1000 solutions generated in each scenario, and plotted these through time for each cost type and target level to assess whether budgets required to reach conservation targets changed over the study period. If costs increased over time, we assessed whether solutions with a given budget, adjusted for inflation, became less effective through time by incorporating a budget cap into the analysis and calculating how many species or species occurrences were omitted from solutions constrained by the cap. As an intuitive benchmark, we used the first year's median solution cost as the budget cap for subsequent years. The overall cost of a solution could exceed the budget cap but would incur a penalty to the cost-efficiency score for that run equivalent to

$$\text{amount over threshold} \times \left(14e^{t}-14\right), \qquad (2)$$

where t is the time during the run (range 0–1) (see Supporting Information for details).

In each simulation, we assumed that land acquisition within chosen sites took place within a single time step; modeling the stepwise acquisition of land parcels was beyond the scope of our analyses. We did not assume that all land within a chosen 300–470 km^2 site would be set aside for habitat conservation. By using mean per-hectare prices within each site, the analysis was flexible with respect to final reserve size within a site.

Results

Acquisition costs and land-use intensity varied through time and spatially; many, but not all, sites became progressively more expensive or difficult to recover (Figs. 1a–c). Mean cost across sites increased with time (Table 1) except in 1 cost-year (land-use intensity in 1991) (Supporting Information).

Acquisition costs were not related to numbers of species within sites (Pearson r for total capital was −0.036 to 0.029 and for gross income was −0.031 to −0.0061). However, land-use intensity was higher in areas with more species at risk (Pearson's r 0.20–0.37) and in areas where land-use intensity increased (Pearson's r for the slope 0.38).

For acquisition costs, the scenario most expected to benefit from consideration of spatial-land-price variation and the scenario least expected to benefit from this consideration both demonstrated cost savings in their solution sets when price was considered explicitly (Table 2). A Wilcoxon rank sum test (given non-normal data) yielded similar results ($p \ll 0.001$). In some cases, the proportional mean cost savings were small (e.g., 1–2% of the total cost), and in most cases there was a small overlap between the range of generated solution costs in the ignored and included sets. However, for all scenarios, run sets that ignored explicit land prices produced solutions that had the same number of sites and therefore the same reported area cost, whereas run sets accounting for price variability contained solutions that could be differentiated as more or less expensive. The latter run sets were also less variable in their actual costs;

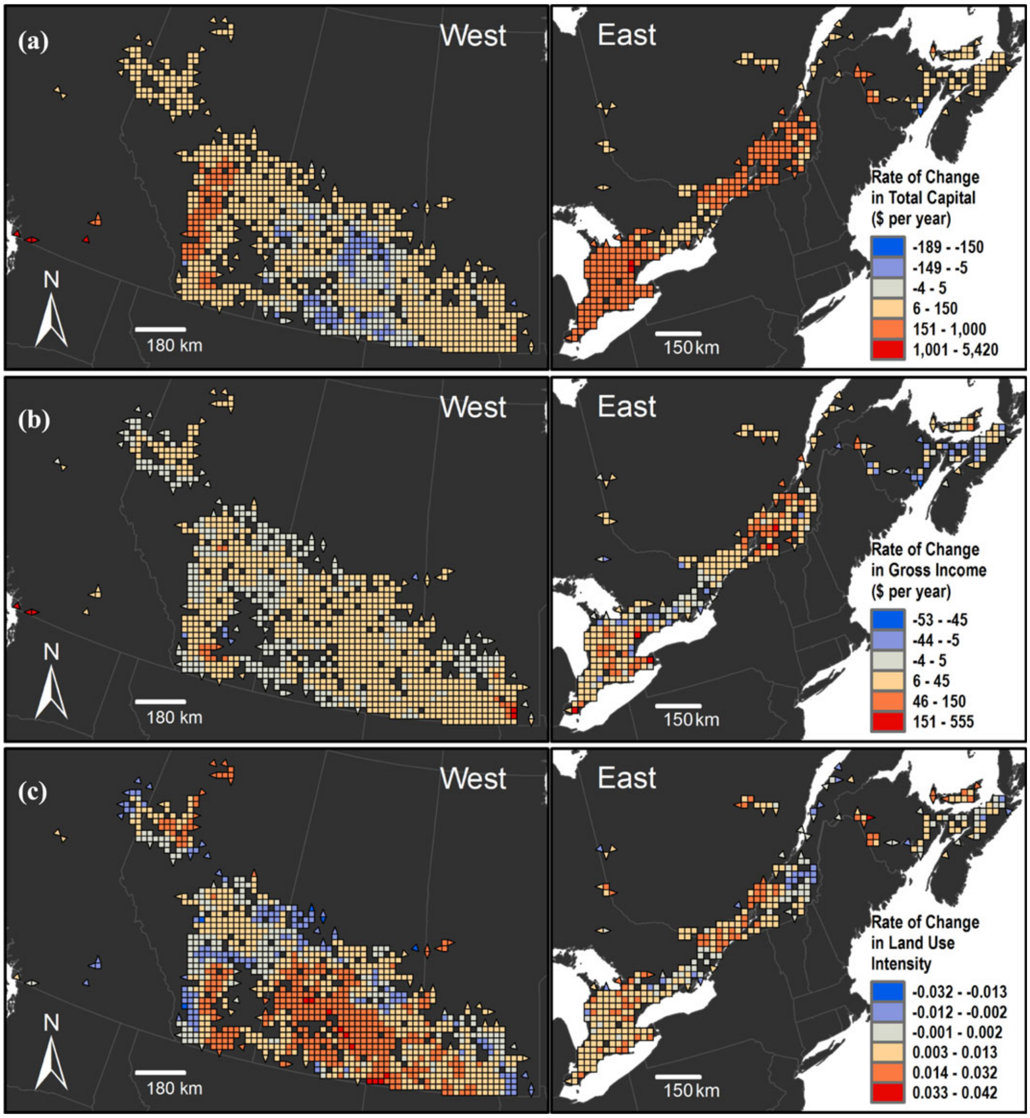

Figure 1. Rate of change in (a) total capital (mean per-hectare value of the land's capital) and (b) gross income (mean annual per-hectare gross receipts from farming) in 2011 constant dollars, and (c) land-use intensity (estimate of relative cost to restore land for species at risk) within the satellite-derived extent of farmland in Canada, as calculated from Census of Agriculture data. Rates of total capital and land-use intensity are for 1986–2011 (measured as the slope of the regression line through values at 5-year intervals [1986, 1991, etc.]). Gross income rates are for 1991–2011 (measured as the slope of the regression line through values at 10-year intervals [1991, 2001, and 2011]).

ranges for these sets 19–82% smaller (Supporting Information) than the ranges for sets ignoring explicit land prices.

For all scenarios, agreement between the distribution of selection frequencies among sites in the first versus subsequent years remained high through time (Table 3). Although statistically significant declines in agreement were detected for land-use intensity and total capital, these declines for all cost types were low, losses of <5% in the similarity of the final distribution of values relative to the distribution in the first year.

For both types of land acquisition cost at all target levels, total costs of the best reserve set increased through time (Figs. 2a–c for 4-occurrence target results). This trend was also generally present for reserve sets based on land-use intensity. Most yearly increases in cost were greater than variability in solution costs within a year. Although in some total-capital and gross-income scenarios, cost increases in a few sites strongly affected total cost of plans across all sites, excluding these sites from the analysis revealed similar trends toward increasing costs through time (Supporting Information).

The capacity of fixed budgets to accomplish representation goals, even after adjusting for inflation, eroded through time. For all cost types and target levels, using the median cost of the optimal 1986 solution as a budgetary constraint in future years generally led to species losses from reserve sets and fewer occurrences of remaining species (Figs. 2d–f). In the scenario 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. The trends of change in cost and capacity to accomplish representation goals through time did not differ among target levels for a given cost type.

Discussion

This study is intended as a starting point from which conservationists can further explore how past changes in the spatial patterns of land value and land-use intensity through time have affected the cost-efficiency of conservation planning. Trends were broadly similar among approaches that employed different cost metrics and different levels of conservation effort. The spatial arrangement of the most optimal conservation plans remained stable, despite heterogeneous cost changes within the planning region and an erosion of return on conservation investment through time.

It is perhaps intuitive that land costs would increase through time and thus increase the cost of conservation plans in our analysis. Many sites chosen for our optimized plans were in Southern Ontario and the St. Lawrence Lowlands, where farmland exists among multiple urban centers and urban and suburban populations have increased, which has increased development pressure on adjacent lands (Bowler 2014). Given that urbanization will likely continue (Theobald 2010; Bowler 2014), costs reported here are likely to rise in the future. It is less intuitive that despite heterogeneous rates of cost change across the planning region, the array of sites required for recovery of target species in this study remained stable. This stability may reflect range restriction among species at risk in southern Canada: More than half of the study's target species had historical ranges overlapping fewer than 9 sites. Such range restrictions constrained conservation solutions, especially in scenarios with ambitious species representation targets (4 or 7 occurrences). This stability provides a strong geographical focus for conservation and restoration. Conversely, our results highlight the risk of continued land-use intensification in areas that emerge consistently as high-priority areas for restoration.

The diminishing rate of return on funds applied to conservation plans for a given target through time is a concern when viewed in the context of existing funds for similar initiatives. For example, assuming an area of approximately 7.7 km^2 per site acquired, we found that in 1986 conservation plans that secured habitat for at least one occurrence each of all 91 target species could be accomplished for approximately \$181.7 million in 2011 constant dollars (the cost of replacing all farm capital). This is the most expensive cost type we considered, yet this amount is less than the 2007 federal grant to Nature Conservancy of Canada for the Natural Areas Conservation Program (\$225 million [approximately \$241 million in 2011 constant dollars] [Department of Finance Canada 2007]). By 2006, the same conservation goal would cost about \$347.4 million, and in 2011 it would cost approximately \$461.8 million, almost two-thirds of all funds raised for the program to date (Nature Conservancy of Canada 2017).

The rate at which conservation costs change in the future will necessarily be subject to uncertainty (Carwardine et al. 2010; Barraquand & Martinet 2011). Analyses of how those costs have shifted through the recent past, as performed here, can inform such complex predictions and help predict the shelf life of new conservation plans. As demonstrated, economic costs can be estimated based on outright purchase or income replacement, but costs can also be measured relative to land-use intensity and subsequent restoration requirements. We focused on agricultural landscapes, subject to a particular array of land-use practices, and where land prices at a given time depend on both current uses and the complexities of international commodities markets. While our findings may be particular to our own study region, our analytical approach can be repeated anywhere there is detailed cost and species distribution data, to inform planning in other regions. Such analyses are not possible without regularly collected data. In the Canadian context, it is important to stress the need to continue monitoring land uses and farm economic activity, through vehicles such as the Canadian Census of Agriculture, at a time when the nation's ability to collect such data has been in flux (Nature Editorial Board 2012; Walton-Roberts et al. 2014). This need applies internationally. Accurate, timely records of economic and land-use patterns are indispensable in conservation planning.

Although using Canada-wide species representation goals resulted in a coarse analysis, national-scale systematic conservation plans have been shown to cost less overall than a series of regional plans (Strange et al. 2006). Although exercises such as those we conducted identify solutions, no modeling scenario provides a single, definitive solution for how conservation planning must proceed. Other factors make site selection less straightforward. For example, we could not account for possible range shifts among target species following climate change (Kujala et al. 2011; Coristine & Kerr 2015; Robillard et al. 2015). However, because 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

Table 1. Mean cost across all farmland sites within the planning region of mean per-hectare value of the land's capital (total capital), mean annual per-hectare gross receipts from farming operations (gross income), and relative effort required to restore land (land-use intensity) over time.

	Mean cost across sites					
Variable	*1986*	*1991*	*1996*	*2001*	*2006*	*2011*
Land acquisition total capital ($)	3259	3370	3522	4085	4654	5814
gross income ($)	–	634.6	–	811.4	–	917.1
Agricultural intensity land-use intensity (unitless)	0.763	0.695	0.793	0.827	0.841	0.949

Table 2. Differences between the mean total implementation costs of conservation plans generated while accounting for variation in the price of conservation sites and the realized mean total cost of plans generated while ignoring price variation.[a]

Scenario[b]		*Mean cost*				
		costs considered	*costs ignored*	*Difference*	*Percent difference*	*Difference for 7.7-km² sites*
Total capital ($)	1986, 1 occurrence	2.403×10^5	2.558×10^5	1.551×10^4	6.46	1.194×10^7
	1991, 7 occurrences	1.027×10^6	1.044×10^6	1.774×10^4	1.73	1.366×10^7
Gross income ($)	2011, 1 occurrence	9.128×10^4	1.040×10^5	1.269×10^4	13.9	9.772×10^6
	1991, 7 occurrences	2.079×10^5	2.124×10^5	4.509×10^3	2.17	3.472×10^6

[a] *For all t-test comparisons, $p \ll 0.001$.*
[b] *Occurrences refer to the number of different sites containing a given target species that must be included in a conservation plan. Scenarios are defined in Methods.*

Table 3. Amount of agreement* in mean selection frequency of all sites in the planning region between the first year and subsequent years measured using Spearman's rank correlation coefficient and the linear rate of change in agreement over time.

	Agreement in mean selection frequency of all sites with initial values							
Cost type	*1986*	*1991*	*1996*	*2001*	*2006*	*2011*	*Slope*	*p*
Total capital	1	0.91	0.88	0.86	0.85	0.84	-1.45×10^{-03}	0.009
Gross income	–	1	–	0.92	–	0.91	-1.67×10^{-03}	0.137
Land-use intensity	1	0.89	0.90	0.92	0.88	0.90	-1.39×10^{-03}	0.030

**Value of 1 represents perfect agreement.*

recovery should increase these species' ability to endure challenges associated with climate change (Olson & Lindsay 2009; Robillard et al. 2015). Possible landscape effects of converting farmland to nature reserves (e.g., increased intensity in adjacent farms), are also an important consideration, although such effects are minimized within a voluntary program targeting less valuable farmland.

There are also uncertainties inherent in our data that could not be fully addressed here, despite using the best data available. First, we found modest cost savings in accounting for land-price variation during site prioritization. However, in the most modest cost-saving scenarios (e.g., 2% savings, Table 2), the calculated savings were smaller than likely variability of farm prices within a grid cell, which could not be calculated due to aggregation of prices by the census within a CCS. Second, although we believe our land-use-intensity metric is a useful proxy for restoration costs, there is no straightforward way to precisely predict such costs across Canada without rigorous field testing. Third, we assumed all sites contained some land parcels where landowner cooperation would be achievable. 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 measurements exist nationally that would have permitted our assessment of this issue. Our sites were large relative to farm sizes, making it likely that one or more landowners within a site would be willing to participate. In a hypothetical situation where this is not the case for some sites, alternative solutions of the 1000 generated by Marxan could be explored that exclude the sites where no land is available. Finally, our historical species distributions are inherently uncertain. It is important to consider, wherever possible, the robustness of conservation plans to uncertainty in target-species distributions or habitat availability because the optimal solution may not always be the most certain solution to accomplish the representation target (Moilanen et al. 2006). Such analyses cannot be completed for Canada's species at risk without substantial, comprehensive improvements in understanding of species' distributions and habitat requirements. Filling these data gaps is critical for southern Canada's cost-effective conservation of species at risk.

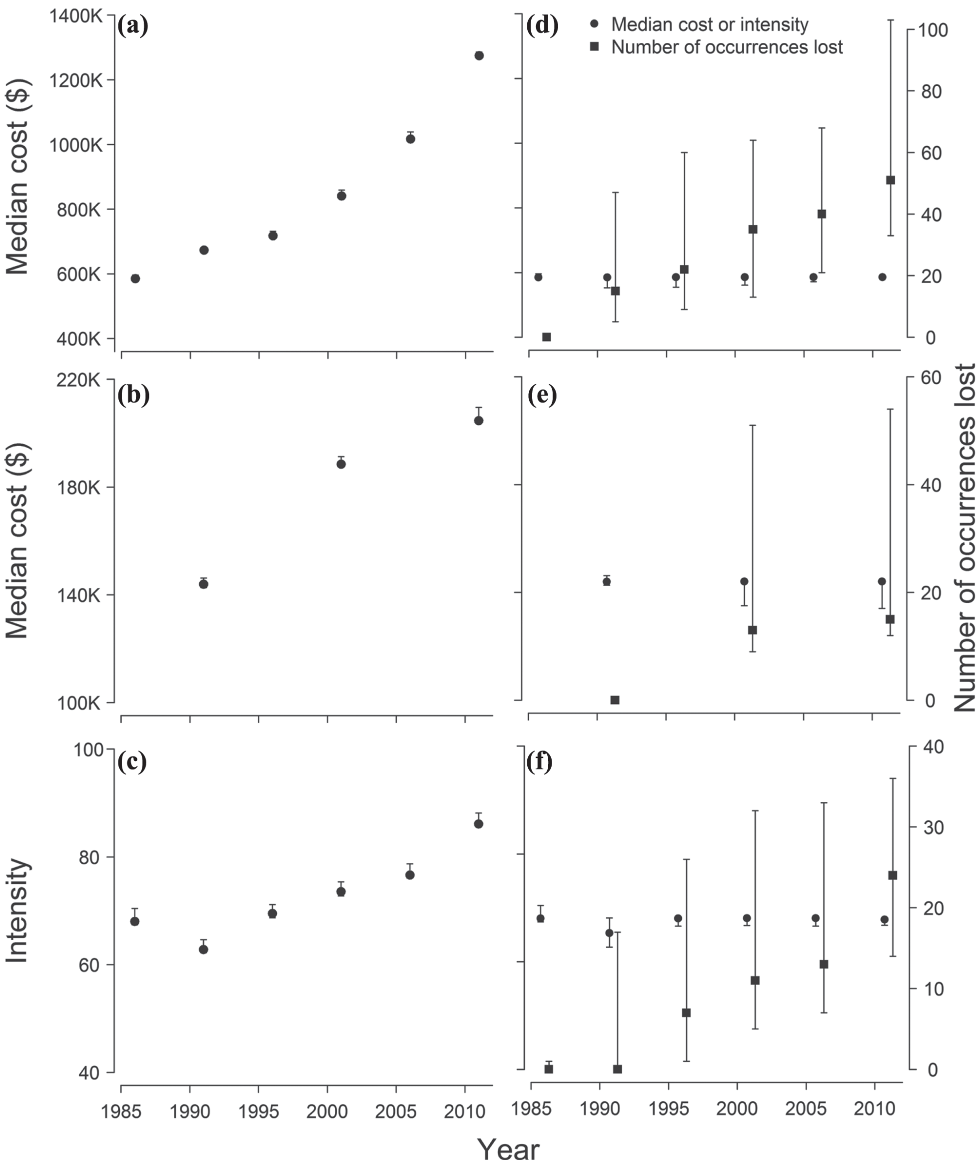

Figure 2. (a–c) Median cost of 1000 conservation solutions generated in Marxan based on (a) total capital, (b) gross income, and (c) land-use intensity (terms defined in legend of Fig. 1) that include 4 occurrences of each of our 91 target species at risk within the study's planning region, and (d–f) cost of solution (circles) based on (d) total capital, (e) gross income, and (f) land-use intensity (unitless) and number of species occurrences lost from a solution (squares) when solution cost is constrained based on the minimum cost in the initial year (bars, minimum to maximum observed values; cost and intensity axes are truncated to magnify the data while preserving comparability of trends). See Supporting Information for a similar plot based on the 7-occurrence target and for plots of number of species lost entirely from the reserve set.

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Supporting Information

Details of study methods (Appendix S1) (including the construction of the land-use intensity variable, descriptions of Marxan parameters, and a target-species list) and results (Appendix S2) (including cost-richness correlations, mapped Marxan solution examples, and plotted results for 1- and 7-occurrence targets) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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