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Identifying areas of optimal multispecies conservation value by accounting for incompatibilities between species



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ABSTRACT

Conservation planning is designed to optimize conservation actions when only limited resources are available for managing habitats and mitigating threats, and excels at selecting reserve networks that protect the largest number of species. However, the spatial optimization of the protection of multiple species can be complicated by interactions among those species and incompatibilities in their habitat needs. The challenge is to identify an optimal solution when two species with similar habitat needs cannot co-occur. We propose here a new approach to find the optimal conservation planning solution in cases of species incompatibilities, and demonstrate this solution for a 144 km² area (a 160,000-cell grid) in northern Wisconsin. Specifically, our study objectives were to simultaneously (a) identify the smallest area needed to meet minimum habitat requirements for every species considered, (b) maximize the compactness of that area, and (c) avoid any overlap between species with incompatible habitat requirements. We found an optimized solution based on potential habitat models for 19 bird species using a novel application of mixed integer linear programming, with a clustering approach suited for large cell arrays. Under this solution, 9.9% of the study plot was sufficient to meet the minimum requirements for every species considered, maximize the compactness of that area, and avoid any overlap between species with incompatible habitat requirements. Our results are useful to assist managers in providing well-connected, sufficient habitat to at-risk species while minimizing costs and land use conflicts.

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1. Introduction

Land use is the single most important driver of terrestrial biodiversity loss (Wilcove et al., 1998), and it is forecasted to remain so for at least the next 100 years (Sala et al., 2005). To protect biodiversity, managers are tasked with improving the conservation value of protected land and areas with residential, recreational, or extractive use (e.g., logging). At the landscape scale, there are wide spatial variations in conservation value over the landscape. When faced with limited resources for managing habitats and mitigating threats, conservation planning efforts help identify opportunities for managing at-risk species (Groves et al., 2002).

Conservation planning is a process that originated in the context of systematic reserve selection (Shaffer, 1999; Margules and Pressey, 2000). Systematic reserve selection has direct applications

for conservation planning of protected areas and in multiple-use landscapes. Conservation planning often involves trade-offs between conservation on one hand, and land use, or economic goals on the other, making it necessary to optimize the area designated for conservation. The approaches that have been developed for such an optimization can be classified in two groups. Heuristic algorithms are logical iterative processes that use stepwise rules where the progress toward certain goals is checked at each step, such as the addition or removal of a new site (Pressey et al., 1997). Heuristic methods can provide near-optimum solutions for problems with large numbers of variables and spatial units, and have been successfully applied to conduct multispecies analyses of large landscapes (Kremen et al., 2008), guide reserve selection (Leathwick et al., 2008), address both economic and biodiversity objectives via different land use configurations (Polasky et al., 2008), and identify priority areas under different management goals within and outside reserves (Chan et al., 2006). A major advantage of heuristic approaches such as simulated annealing (Possingham et al., 2000) or hierarchical prioritizing (Moilanen et al., 2009) is that they can be applied at broad spatial extents (e.g., 5.9×10^5 km² extent,

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30 arc-second resolution in Madagascar, Kremen et al. (2008) or 1.7×10^6 km² extent, ~ 4.8 km² resolution for parts of Central and South America, Sarkar et al. (2009)) because heuristic approaches are flexible and computationally less demanding. However, the drawback of heuristic approaches is that they can yield sub-optimal solutions (Underhill, 1994; Rodrigues and Gaston, 2002).

The second group of approaches that assess trade-offs in conservation planning consists of mathematical optimization algorithms, which precisely identify the optimal solution set, and typically employ linear programming techniques (Vanderkam et al., 2007). For example, mixed integer programming has been used to optimize the restoration of 55 tidal wetlands for bird species organized in nine functional groups (Stralberg et al., 2009). The drawback of these optimal algorithms is that they have much higher computational demands, which is why they have generally been limited to small problem sets, but increasing computational capacities provide new opportunities to optimally solve larger problems (Vanderkam et al., 2007).

Current heuristic or optimal approaches to conservation do not take explicitly into account incompatibilities among species. The challenge is to identify an optimal solution when two species that otherwise share habitat cannot co-occur. Reasons for incompatibilities can be, for example, competition (e.g., blue-winged [Vermivora pinus] and golden-winged [Vermivora chrysoptera] warblers, Buehler et al., 2007), or the transmission of parasites between two species, (e.g., white-tailed deer [Odocoileus virginianus] out-competing moose [Alces alces] via differential resistance to a parasite; Anderson, 1972). Another major cause of incompatibilities occurs when potential habitat models or potential distribution maps are used for conservation planning (Beaudry et al., 2011). Potential habitat models identify locations where habitat elements needed by a species may be present, and a species may occur, but potential habitat models do not automatically imply occupancy which could also be affected by other factors (e.g., Braunisch and Suchant, 2007; McComb et al., 2009). This means that potential habitat maps for different species may overlap, but the actual occupancy of one species may be dependent on conditions that would make the area unsuitable for another species. For example, both golden-winged warblers and wood thrush (*Hylocichla mustelina*) can occupy the same deciduous forest stand but the former will only be present when the trees are young while the latter will use the stand when the trees are more mature (Beaudry et al., 2010).

Habitat incompatibility issues among species are not uncommon (Beaudry et al., 2011), and they arise when habitat is modeled for multiple species and at broad spatial scales. These species conflicts are usually ignored, which may lead to conservation reserves that offer habitat which will not be occupied or will produce depressed fitness outcomes, and ultimately unmet conservation objectives. Habitat incompatibilities need to be addressed in multi-species conservation planning efforts and preferably integrated in an optimization strategy. Incompatibility issues could potentially be addressed through a heuristic approach, for example, by dividing the contested areas and distributing them among the conflicting species, and this may be valid in cases where full optimization is superfluous. For example, if the contested areas were small enough to be nested within the boundaries of publicly managed property, managers could just divide the area and allocate different forest stands to the exclusive management of either species. However, even in that situation there would be no guarantee that other objectives, such as connectivity, were optimized. Additionally, an ad-hoc solution to addressing incompatibilities becomes quickly intractable as more species, habitat patches, and potential habitat overlaps are involved. Heuristic methods could be used to find an optimal solution when partitioning and managing habitat for conflicting species, and a somewhat related example for this is the optimal partition and allocation of grazing intensity in a

grassland (Holzkämper et al., 2006; van Teeffelen et al., 2008). These solutions are designed for landscapes with elements which can readily be managed into the best possible arrangement. However, there remains a need for methods that can address incompatibilities where the goal is to use landscape features that are already in place to provide the best conditions for all species under consideration; in other words, when the area considered is not a blank slate that can be managed outright to meet goals.

Our goal here was to develop a new approach to find the optimal solution to multispecies conservation planning problems involving incompatibilities between conflicting species. We tested our new approach and identified areas of greatest conservation value over a forested landscape in northern Wisconsin, U.S.A., for a set of forest birds of conservation concern, while solving habitat incompatibility conflicts. Specifically, our study objectives were to simultaneously meet minimum habitat requirements for every species using a function favoring a solution which (a) minimizes area, (b) favors compactness, and (c) avoid spatial overlap between species with incompatible habitat requirements.

2. Methods

2.1. Study area

Our study area was located in Forest and Oneida Counties, northern Wisconsin (U.S.A.), part of the Laurentian Mixed Forest Ecoregion (Bailey, 1995; Fig. 1). Totaling 14,400 ha in size (12×12 km), it encompassed a portion of the Chequamegon-Nicolet National Forest and adjacent private land, and was part of a larger study area where we documented many species with incompatibilities (Beaudry et al., 2010), and ranked conservation value for 4.6 million ha of forest land (Beaudry et al., 2011). We chose this study area because it included many incompatibilities, and because we were familiar with the area, facilitating our interpretation of the results. Spatial resolution was 30 m (0.09 ha), for a 160,000 cell grid. Extensively logged in the first half of the 20th century, this region has since largely reverted to forests that have re-grown on former clear-cuts and abandoned fields (Radeloff et al., 2005). During our study, common land uses included forestry and outdoor recreation.

2.2. Habitat models

As a strategic approach to encourage regional conservation planning, the U.S. Congress mandated development of a Wildlife Action Plan by each state and territory. In Wisconsin, the State Wildlife Action Plan identified 152 vertebrate Species of Greatest Conservation Need, with the goal of conserving these species and their habitat before they become rare and need more costly protection (Wisconsin Department of Natural Resources [WIDNR], 2005). Of Wisconsin's 152 Species of Greatest Conservation Need, 20 are birds that regularly breed in the state's northern forests (Table 1), and we included habitat models for the 19 species that occurred in our study area (Fig. 2; Beaudry et al., 2010). Fourteen of the focal species are migratory, and five are year-round residents (Table 1).

Our modeling approach consisted of three nested habitat components reflecting different levels of specificity, category resolution, and data availability: (1) habitat groups, defined as broad vegetation types based on the classes of the 2001 NLCD National Land Cover Database (NLCD; Multi-Resolution Land Characteristics Consortium, <http://www.epa.gov/mrlc/nlcd-2001.html>) and land cover classes from the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND, <http://www.sco.wisc.edu/wiscland>), (2) constraints, defined as species-specific modifiers to the habitat groups (e.g., edge- or area-sensitivity,

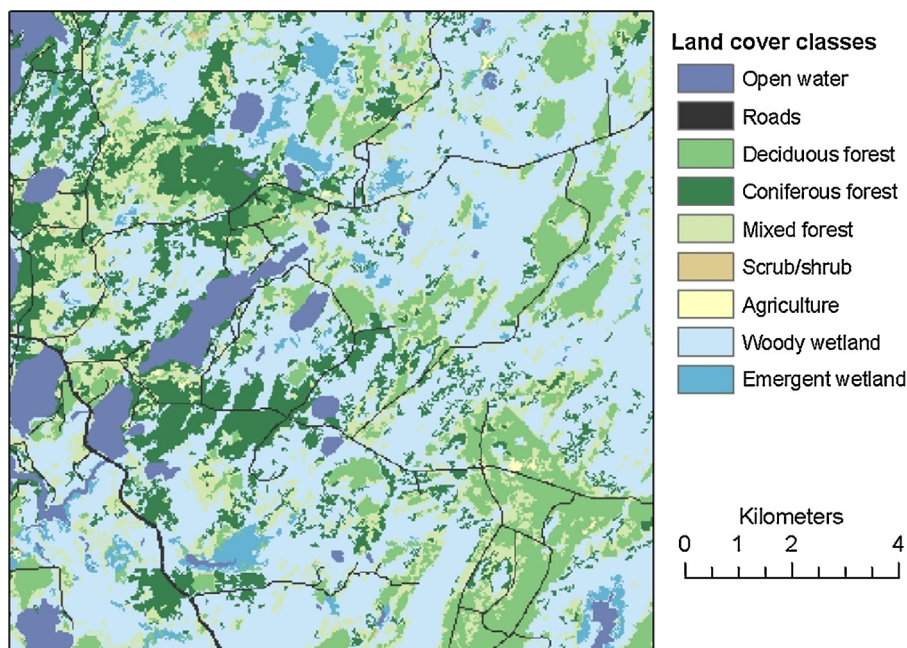


Fig. 1. Study plot in northern Wisconsin, USA, with land cover classes based on National Land Cover Database (NLCD) classes. Grassland, herbaceous, pasture, hay, and cultivated crops were collapsed into an agriculture class. The developed land NLCD class was only represented by roads in our study, and was therefore labeled as such.

minimum distance to water), and (3) intrinsic elements, i.e., fine-scale habitat selection requirements that are important for a given species, but infeasible to map across large areas. The reason to include intrinsic elements, even though they cannot be used to inform maps of potential habitat, is that many intrinsic elements (e.g., snags, understory vegetation) can be managed for. We combined the habitat groups and habitat constraints into habitat distribution models to identify potential habitat which can support the species of conservation concern if the necessary intrinsic elements are present. Independently acquired empirical data was used for model training (breeding bird atlas data) and model evaluation (point-count survey data). Full occupancy of the resulting areas mapped as potential habitat should not be expected: our model structure, unlike habitat models relying on correlation between habitat variables and animal occupancy or abundance, allows for distributions that vary due to environmental conditions or metapopulation dynamics (O'Connor, 2002; Early et al., 2008).

Further details concerning model development and evaluation are available in Beaudry et al. (2010).

We needed to establish the minimum habitat required for each species in the study area. To do this we used values obtained for the entire northern Wisconsin region (Beaudry et al., 2010). Habitat objectives were based on Partners in Flight population estimates and objectives for Wisconsin (Panjabi et al., 2005) translated as a percentage of potential habitat (Table 1; Beaudry et al., 2010). The minimum habitat requirements were used for demonstration purposes, as they originally were estimated at the regional scale and not for this study area.

2.3. Optimization

Conceptually, the principal concern is to assign cells (x,y) to be managed for a species s , which we modeled as a binary variable $m(s,x,y)$. The remaining model variables are described in Table 2.

Table 1
Study species name and migratory status, with minimum habitat requirement used as a constraint in the analysis.

Species	Scientific name	Migratory status	Minimum habitat requirement (%) ^a	
Black-backed Woodpecker	BBWO	<i>Picoides arcticus</i>	Resident	1.50
Black-billed Cuckoo	BBCU	<i>Coccyzus erythrophthalmus</i>	Neotropical	10.00
Black-throated Blue Warbler	BTBW	<i>Dendroica caerulescens</i>	Neotropical	6.30
Blue-winged Warbler	BWWA	<i>Vermivora pinus</i>	Neotropical	1.60
Boreal Chickadee	BOCH	<i>Poecile hudsonica</i>	Resident	4.20
Brown Thrasher	BRTH	<i>Toxostoma rufum</i>	Short-distance	63.70
Canada Warbler	CAWA	<i>Wilsonia canadensis</i>	Neotropical	2.30
Cerulean Warbler	CEWA	<i>Dendroica cerulea</i>	Neotropical	10.00
Connecticut Warbler	CONW	<i>Oporornis agilis</i>	Neotropical	0.50
Golden-winged Warbler	GWWA	<i>Vermivora chrysoptera</i>	Neotropical	0.80
Least Flycatcher	LEFL	<i>Empidonax minimus</i>	Neotropical	2.30
Northern Goshawk	NOGO	<i>Accipiter gentilis</i>	Resident	100.00
Olive-sided Flycatcher	OSFL	<i>Contopus cooperi</i>	Neotropical	3.30
Red Crossbill	RECR	<i>Loxia curvirostra</i>	Resident	10.00
Spruce Grouse	SPGR	<i>Falciennis canadensis</i>	Resident	10.00
Veery	VEER	<i>Catharus fuscescens</i>	Neotropical	17.90
Whip-poor-will	WHIP	<i>Caprimulgus vociferus</i>	Neotropical	10.00
Wood Thrush	WOTH	<i>Hylocichla mustelina</i>	Neotropical	10.00
Yellow-billed Cuckoo	YBCU	<i>Coccyzus americanus</i>	Neotropical	10.00

^a As a percentage of available potential habitat in the study area. See Beaudry et al. (2010).

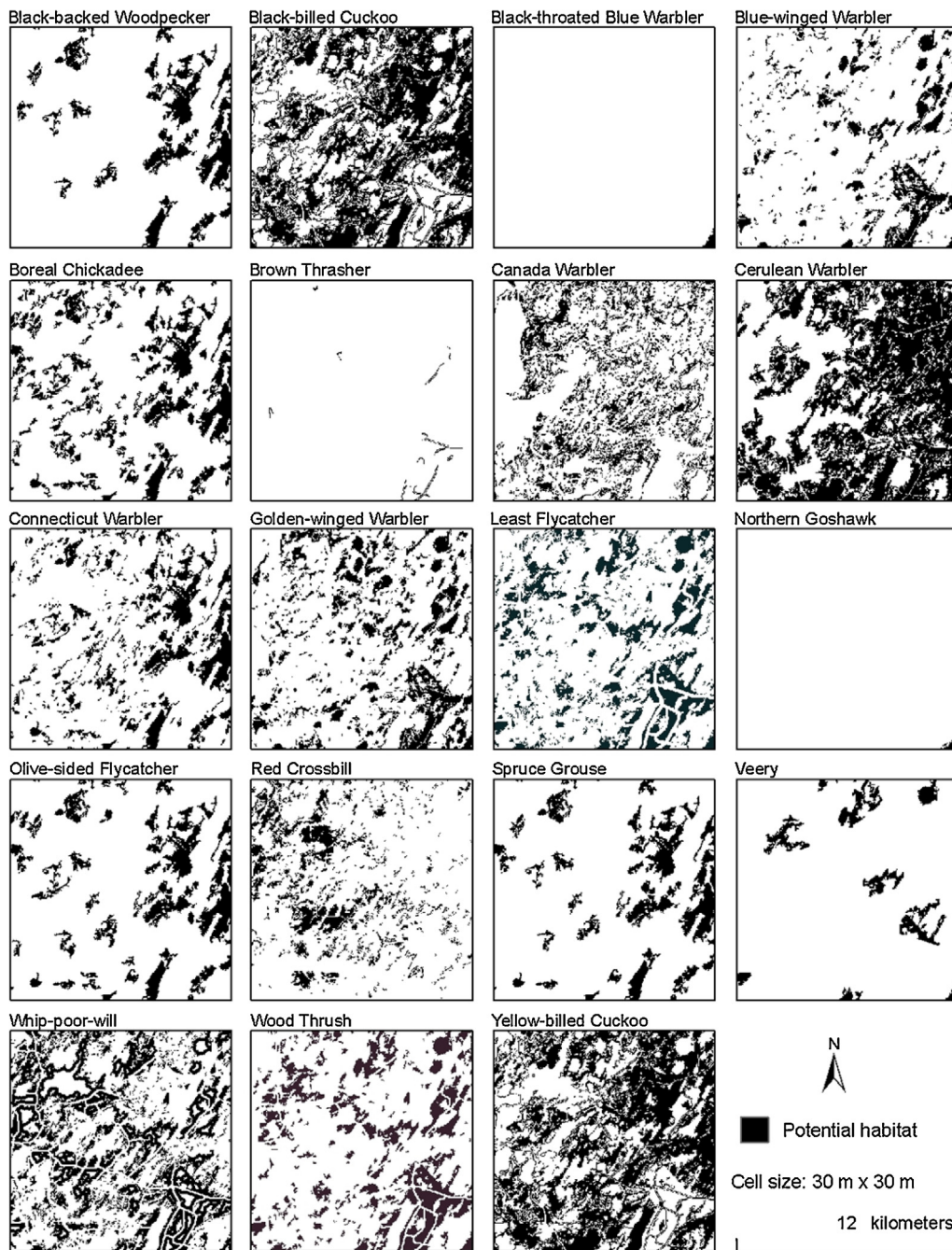


Fig. 2. Potential habitat models for 19 forest-breeding bird species used in the optimization algorithm for conservation planning in northern Wisconsin, USA.

Valid solutions to this problem are limited by two constraints. First, to meet management objectives minimum habitat area requirements for each species must be satisfied:

$$\sum_{(x,y):(s,x,y) \in P} m(s, x, y) \geq n(s), \quad \forall s \in S$$

Second, incompatibilities between species, in our case stemming from the use of potential habitat models, must be avoided by taking all pairs of species (s, t) from a set of (incompatible) species I , and enforcing a constraint that only one of them is present at location (x, y) :

$$m(s, x, y) + m(t, x, y) \leq 1, \quad \forall (s, t) \in I : (s, x, y) \in P, (t, x, y) \in P$$

The key objective of the problem is to minimize the total number of cells while establishing a number of (compact) habitat clusters for each species. It is difficult to define the notion of compactness of a cluster. Several alternatives (minimizing total cluster perimeter length, total number of rows and columns used in a cluster, total inter-cluster Euclidean distances, etc.) were experimented with in this project, but all of them led to optimization approaches that were computationally intractable, mainly due to the large number of grid cells upon which we had to make management decisions for each species (i.e. the number of binary variables $m(s, x, y)$ is too large when coupled with the above objectives).

Instead, we reduced the size of our problem to consider “collections of grid cells” organized into connected clusters, and formed an optimization problem to determine which clusters to manage for each species. It is possible to use clustering algorithms from

Table 2
Problem data and variables to describe and optimize conservation planning for forest birds in northern Wisconsin, USA.

Problem data and variables	Definitions
S	Set of species
I	Set of pairs of species (s_1, s_2) that are incompatible
G	Set of grid cells ((x, y) pairs for example)
$n(s)$	Vector, indexed by species, that gives the required number of cells for each species
$P = \{(s, x, y) \in S \times G: s \text{ can live at } (x, y)\}$	Set of possible habitat locations on the grid for each species
$m(s, x, y)$	Binary variable, with value 1 if (x, y) is maintained for s , otherwise 0
$u(x, y)$	Binary variable, with value 1 if (x, y) is maintained for some species s , otherwise 0
$r(x, y)$	Binary variable, with value 1 if the assignment $m(s, x, y) = 1$ for some y , otherwise 0
$c(s, y)$	Binary variable, with value 1 if the assignment $m(s, x, y) = 1$ for some x , otherwise 0

machine learning (such as k-means and its generalizations) as a data preprocessing to identify these groupings of grid cells, and our approach can utilize any collection of clusters as its data. Formally, to cluster grid cells into connected components we defined a graph whose vertices correspond to the grid cells (x, y) . For each species s , a pair of grid cells (x, y) and (x', y') were connected by an edge if $(s, x, y) \in P$, $(s, x', y') \in P$ and either $\|x - x'\| \leq 1$ and $y = y'$ or $x = x'$ and $\|y - y'\| \leq 1$. As elements of graph theory, a path was defined as a sequence of vertices connected by edges. A graph is connected if there is a path of edges from any vertex to any other vertex. If a graph is not connected, then it can be partitioned into a set of connected components using depth-first search. These connected components (clusters) can be ordered by size, and for each species we selected a collection of clusters, rather than individual cells, to make the optimization problem smaller. To determine a good set of clusters to consider for each species, we used a Markov Cluster (MCL) algorithm (<http://micans.org/mcl>) for graphs because it is efficient for large-scale problems, such as protein clustering (Enright et al., 2002). MCL has a number of options that allow the user to specify different properties for the clusters. We selected forced connectivity and used an index parameter $l = 1.2$.

This particular code can generate lots of very small clusters that are not good candidates for selection, so we only used the subset of the largest clusters generated by the MCL code, determined so that the total number of possible grid cells under consideration for each species is at least twice the minimum habitat required in the study area for that species (as defined in Section 2.2).

The optimization model we solve relies on the following data: a set S that gives the species considered, a set C containing a list of clusters (generated as described above for example). We determine the number of cells in each cluster $c \in C$ that are appropriate habitat for species $s \in S$, $N(s, c)$. For two pairs (s_1, c_1) and (s_2, c_2) we determine the number of cells that overlap, and whether they are compatible (g) or incompatible (b).

The model involves the binary variables $use(s, c)$ (that indicate whether cluster c was used for species s or not) and $inboth(s_1, c_1, s_2, c_2)$ (that indicate if species s_1 used cluster c_1 and species s_2 used cluster c_2) and the continuous variables $usedcells(s)$, representing the number of cells allocated to species s .

$$\min \sum_s usedcells(s) + 0.05 * \sum_b overlap(b)inboth(b) + 0.01 * \sum_g overlap(g) * (1 - inboth(g))$$

Subject to:

$$usedcells(s) = \sum_{s,c} N(s, c) * use(s, c), \quad \forall s$$

$$inboth(s_1, c_1, s_2, c_2) + inboth(s_2, c_2, s_1, c_1) = 1, \quad \forall (s_1, c_1, s_2, c_2) \in g \cup b, s_1 < s_2$$

$$inboth(s_1, c_1, s_2, c_2) \leq use(s_1, c_1), \quad \forall (s_1, c_1, s_2, c_2) \in g \cup b$$

$$inboth(s_1, c_1, s_2, c_2) \leq use(s_2, c_2), \quad \forall (s_1, c_1, s_2, c_2) \in g \cup b$$

These three terms ($use(s, c)$, $inboth(s_1, c_1, s_2, c_2)$, and $usedcells(s)$) were weighted and combined in an objective function. We applied a larger weight (penalty) to the incompatibility. To enforce the satisfaction of incompatibility constraints, we modified the clusters chosen. We considered all variables $inboth(s_1, c_1, s_2, c_2) = 1$ which had overlap and for which $(s_1, s_2) \in I$. For each of these, we chose the species with the largest excess number of grid cells used, and removed from the corresponding cluster all grid cells in the overlap. Having done this, we solved the model once again to determine a modified solution that was more likely to satisfy all incompatibility constraints. In practice, we never had to repeat this process more than once.

This problem is a mixed integer linear programming (MILP; i.e. a problem with binary variables, with a linear objective function and inequality constraints that are linear in the variables). MILP problems are difficult to solve; they are non-deterministic polynomial-time (NP) hard from a complexity viewpoint (Papadimitriou, 1981), but much progress has been made over the past few decades in solving these problems by applying some combination of branch-and-bound, branch-and-cut, and heuristic approaches to generate feasible solutions (Nemhauser and Wolsey, 1988; Achterberg, 2009). The implementations of the methods we used here are characterized by their ability to provide an optimality gap, i.e., a feasible solution that satisfies the constraints of the problem whose objective value is guaranteed to be within some (small) fraction of the best possible solution:

$$|o_{bp} - o_{bf}| < optol |o_{bp}|$$

where O_{bp} is defined as best objective possible, O_{bf} as best objective found, and $optol$ is a given optimality tolerance. The best known implementations of methods of this type are currently CPLEX (URL: <http://www-01.ibm.com/software/integration/optimization/cplex-optimizer>), Xpress (URL: <http://www.fico.com/en/Products/DMTools/Pages/FICO-Xpress-Optimization-Suite.aspx>) and Gurobi (URL: <http://www.gurobi.com>).

The solution of this optimization problem was termed the raw optimization solution (Fig. 3). It consists of a collection of clusters for each species that satisfied both the incompatibility constraints and the threshold constraints. To improve this solution further, we applied two “post-optimality” steps. The first step was based on the observation that certain cells included in the raw solution provided additional cells for other (compatible) species, essentially at no extra cost. We therefore solved an additional optimization problem (termed opportunity-optimization) that maximized the total number of cells managed for all species (the sum of $m(s, i, j)$) subject to the incompatibility constraints, allowing only the use of raw-solution managed cells, and forcing currently managed species/cell combinations $m(s, i, j)$ to remain in place.

The opportunity optimization problem requires data including the set S of species, the set of grid cells G identified as used in the raw solution, the species incompatibility matrix I , the species habitat location maps $P(s, i, j)$, and the threshold values $n(s)$. The binary variables of this problem are $m(s, i, j)$ that determine if a cell $(i, j) \in G$ is used for a species $s \in S$. Before solving the problem, we fix the values of $m(s, i, j)$ to 1 that are identified as managing (i, j) for species

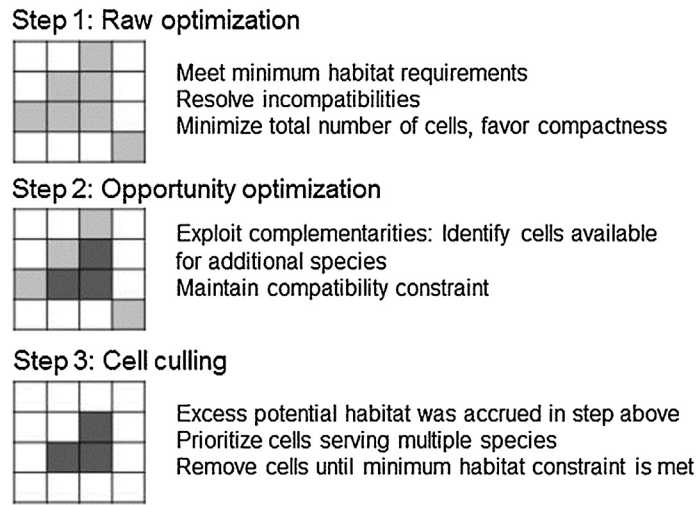


Fig. 3. Illustration summarizing the three main optimization steps. The grids conceptualize each step. Light gray cells represent potential habitat for a single species, while the dark gray cells denote the identification of potential habitat for multiple species.

s and simply adjust the other possible variables using the following MILP:

$$\max \sum_{(s,i,j) \in P} m(s, i, j)$$

Subject to:

$$\sum_{(s,i,j) \in P} m(s, i, j) \geq n(s), \quad \forall s \in S$$

$$m(s_1, i, j) + m(s_2, i, j) \leq 1, \quad \forall (s_1, s_2) \in I : (s_1, i, j) \in P, (s_2, i, j) \in P$$

This resulted in a significant increase in the number of cells available for each species. Given this excess of cells, we performed a culling (the cell-culling step), starting with those that were only used for one species and proceeding with increased numbers of species. We culled cells whose removal did not result in a violation of the threshold constraints for any species. Since these problems only considered the subset of grid cells that had been selected as possibilities from the previous models, the optimization problems were much smaller and hence processed quickly.

The optimization was written and processed in CPLEX (ILOG, Sunnyvale, California, USA) implemented in GAMS (Brooke et al., 2001; GAMS Development Corp., Washington, DC, USA). Input habitat models and output solutions were processed and visualized in ArcGIS v.9.3 (ESRI Inc., Redlands, California, USA).

3. Results

As described above, our study built upon a prior analysis of habitat for species of greatest conservation concern across northern Wisconsin. That prior analysis identified about 1 million ha as potential habitat. We examined those data and found that there were 131 spatial overlaps of potential habitat. Among these overlaps, 30 species pairs (23% of the interactions) had conflicting habitat requirements. If we consider only those pairs that overlapped in at least 5% of the total, there were 98 potential habitat overlaps, 27 of which (28%) were between species with conflicting habitat requirements (Table 3). Incompatibilities encompassed large areas in the entire northern Wisconsin study area: for example, 316,000 ha of potential habitat would be in conflicted between Blue-winged Warbler and Wood Thrush, and 304,000 ha between Blue-winged and Golden-winged Warblers. For conflicting pairs, the intrinsic habitat elements were mutually exclusive, restricting management to a single member of the pair in a given location.

Incompatibilities were common between late successional deciduous forest species (e.g., Wood Thrush, Least Flycatcher) versus early successional deciduous species (e.g., Blue-winged Warbler). Another common source of conflict was deciduous forest species that have a requirement for open understory (e.g., Red-shouldered Hawk) versus those with a need for thicker ground or shrub vegetation (e.g., Veery, Black-throated Blue Warbler).

For the smaller, 14,400 ha study area for which we conducted the optimization, potential habitat for the 19 species covered 13,198 ha (92%) of the plot. After the raw optimization process, a total of 2118 ha (14.7% of the study plot) was identified as the best solution to meet the potential habitat requirements for the study species (Fig. 4a). The opportunity optimization maintained the same amount of area (Fig. 4b), but once excess cells beyond each species' minimum threshold were culled, only 1425 ha (9.9% of the study area) were retained (Fig. 4c). This area represents the area needed to meet minimum habitat requirements for every species considered, with maximum compactness, and without any overlap between species with incompatible habitat requirements.

In contrast, habitat overlap between incompatible species was greater than 12% of the 14,400 ha for seven pairs of species (Table 4). These incompatibilities exceed the 9.9% optimization solution. Most conflicting were Olive-sided Flycatcher and Spruce Grouse (coniferous forests that are more open versus dense, early successional stands) and deciduous forest species exhibiting late versus early successional conflict as described earlier.

The most suitable clusters of cells (the largest clusters with the most species overlapping) were in the northwestern and western parts of the study plot (Fig. 4c). These clusters included potential habitat for seven species, with some cells representing potential habitat for eight (31 cells; 2.8 ha) or nine (4 cells; 0.36 ha) species.

The effects of the opportunistic optimization on the distribution of species' habitat overlap became clear when comparing the selection after the opportunistic optimization to that of the raw optimization: the opportunistic optimization solution showed a greater number of hectares with three or more species overlapping, notably with modes at three and seven species (Fig. 5). The cell culling process then reduced the total number of hectares that were part of the solution, with more species overlap (Fig. 5).

4. Discussion

The new multi-step optimization approach developed and presented here allowed us to simultaneously identify the smallest area

Table 3
Overlap between pairs of species' potential habitat, in proportion of the highest conservation value area (the 20% highest ranking fraction of the landscape, 1,019,000 hectares, for the northern Wisconsin study area – see Beaudry et al., 2011 for details). Values in parentheses represent overlap between species with incompatible habitat requirements. Blank cells mean there was no potential habitat overlap. Only overlaps with $\geq 5\%$ were retained. Species codes are defined in Table 1.

Species	BBWO	BBCU	BTBW	BWWA	BOCH	BRTH	CAWA	CEWA	CONW	GWWA	LEFL	NOGO	OSFL	RECR	RSHA	SPGR	VEER	WHIP	WOTH
YBCU	0.09	0.33		0.11	0.07	0.08		0.07	0.15	0.07		0.05	0.11			0.09		0.03	
WOTH			0.21	(0.31)			(0.07)	0.14		(0.23)	0.32	0.27			0.19		0.29	0.24	NA
WHIP	0.06		(0.13)	(0.22)			(0.14)	0.09	0.06	(0.16)	0.21	0.26	0.08	0.15	0.13		(0.19)	NA	
VEER			(0.22)	(0.25)			0.06	(0.12)		(0.19)	0.30	0.23			(0.18)		NA		
SPGR	0.14	0.09			0.07		(0.05)		0.11				(0.15)	(0.05)		NA			
RSHA			(0.13)	(0.19)				0.06		(0.15)	0.18	0.17			NA				
RECR	0.09						0.12					0.14	0.11	NA					
OSFL	0.19	0.11			0.09		0.07		0.14			0.08	NA						
NOGO	0.06		0.18	(0.27)		0.05	0.12	0.11		(0.22)	0.25	NA							
LEFL			0.22	(0.28)			0.07	0.13		(0.21)	NA								
GWWA		0.07	(0.15)	(0.30)		0.07		(0.11)		NA									
CONW	0.11	0.15			0.08				NA										
CEWA		0.07	0.07	(0.17)				NA											
CAWA	0.06						NA												
BRTH		0.08		0.10		NA													
BOCH	0.07	0.07			NA														
BWWA		0.11	0.18	NA															
BTBW			NA																
BBCU	0.09	NA																	

needed to meet minimum habitat requirements for every species considered, encourage a solution as compact as possible, and avoid any overlap between species with incompatible habitat requirements. The approach identified optimal solutions that were found in computational times that are orders of magnitude shorter than competing approaches such as quadratic assignment or genetic

algorithms. Taking habitat incompatibilities into account is often necessary when working across large areas, whether incompatibilities are arising from ecological reasons (for example predation or competition) or from potential habitat models where actual occupancy depends on management for specific intrinsic elements. Incompatibility issue can have important consequences when

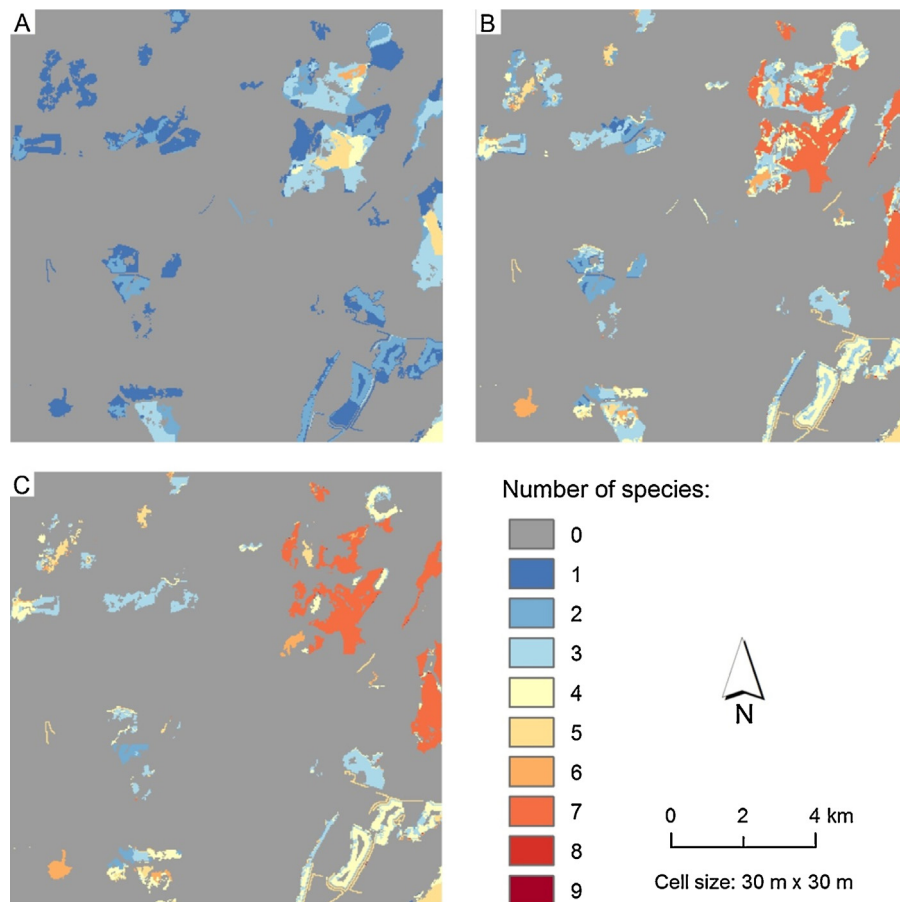


Fig. 4. Solutions for forest bird conservation planning, with (a) the output of the raw optimization process, then (b) the opportunity optimization where complementarities are exploited and species with overlapping potential habitat are added to patches identified in the previous panel, and (c) the output of the cell culling step where the excess potential habitat accrued in the previous step is reduced.

Table 4

Overlap of potential habitat, in hectares, for pairs of incompatible species within the 14,400 ha study area. Values in parentheses are the percentage of the study area. Blank cells mean there was no conflicting potential habitat overlap. Species codes are defined in Table 1.

Species	BWWA	CAWA	GWWA	OSFL	RECR	SPGR	VEER
YBCU			945 (7%)				
WOTH	1698 (12%)	1048 (7%)					
WHIP	1659 (12%)	2335 (16%)	1812 (13%)			418 (3%)	774 (5%)
VEER	521 (4%)		534 (4%)				
SPGR		56 (<1%)		2142 (15%)	424 (3%)		
LEFL	1661 (12%)		1766 (12%)				

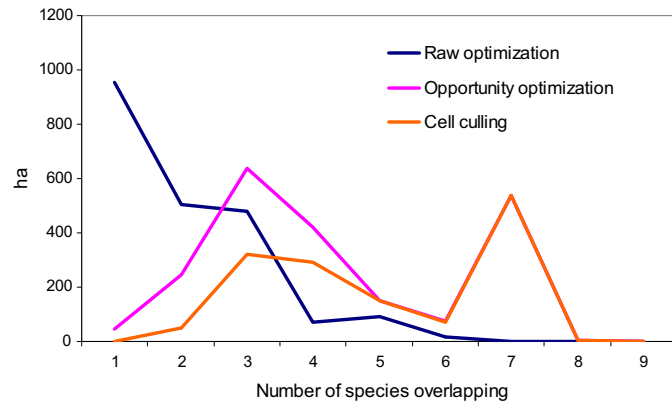


Fig. 5. Portions of the total area with varying potential habitat overlap (by species) for the three main analysis stages: raw optimization, opportunity optimization where complementarities are exploited where potential habitat for different species overlap, and after the cell culling step where the excess potential habitat is reduced and the total area of the solution is minimized.

conducting multispecies conservation planning and management, because such efforts are most effective when performed at broad spatial scales (Noss, 1983), so that the ecological context within which habitat occurs can be considered (Margules and Pressey, 2000). We found habitat conflicts between our study species easy to identify, as they are associated with well-known competitive relationships or discernably contrasting habitat requirements (e.g. early- versus late-successional). Such incompatibilities are relatively simple to anticipate for well-known ecological communities, but they will be more obscure for understudied communities or cryptic taxa. An incomplete understanding of exclusionary relationships among species should not preclude the use of the method we propose here, though, as the set of incompatible species pairs does not need to be exhaustive.

The combined use of algorithms maximizing compactness and identifying large cell clusters favored highly connected solutions. Landscape connectivity is key to maintaining ecosystem level integrity (Taylor et al., 1993; With et al., 1997) as well as species' dispersal ability and persistence (Fahrig and Merriam, 1985; Kramer-Schadt et al., 2004). We used an operational definition of graphs to identify cell clusters. Our approach is related to graph theory, which has made important contribution to measurements of landscape connectivity (Urban and Keitt, 2001), and has been successfully applied in the selection of important habitat patches (e.g., Minor and Urban, 2007; Ziolkowska et al., 2012). In our approach, graph theory provides an efficient way to detect spatial relationships among habitat cells and allows for a computationally rapid identification solution for a large landscape.

Only few solutions to the incompatibility problem had been proposed previously. Holzkämper et al. (2006) used a genetic algorithm to estimate an optimal landscape configuration with the goal to maximize habitat suitability values for three bird species that have contrasting habitat requirements. Their solution identifies the

optimal amount and placement of grasslands, forests, and edges in their study area. Similarly, a forward stepwise heuristic algorithm was used to identify optimal grazing regimes for grassland species with incompatible habitat requirements (van Teeffelen et al., 2008). These optimization approaches determine the optimal composition and arrangement of a landscape to simultaneously benefit all species and are a useful approach, for example, for restoration projects. The problem that we tackled is conceptually different though, and we argue more common in multiple-ownership and multiple-use (recreation, logging, conservation) landscapes. Instead of a “blank slate” that can be managed exactly for the needs of certain species, managers are typically faced with a mosaic of land covers in a range of conditions and arrangements due to various land uses. Instead of having to find the optimal way to shape the landscape into target species' habitat, our goal was to identify those areas that can currently best support the target species.

In terms of management applications, our optimal solution identified large habitat clusters in the northeastern quadrant and at the eastern edge of the study plot, where up to nine species' potential habitats overlap. This area is part of the Chequamegon-Nicolet National Forest, and a large, undisturbed lowland conifer area protected as a Wilderness area under the 1964 Wilderness Act. Another noticeable pattern is that linear arrangements of cells are visible in the solutions, especially in the southeast corner of the plot. These features are associated with potential habitat for the Brown Thrasher, which includes forest edge vegetation such as that found alongside roads (Cavitt and Haas, 2000).

For our analysis we assumed that none of the species considered are area-sensitive, i.e., that they do not require a minimum patch size. However, some of the bird species modeled are area-sensitive (e.g., Black-throated Blue Warbler, Canada Warbler; Robbins et al., 1989), but their minimum patch size is comparatively large, and patch size calculations were confounded by patches being cut at the edges of the study area. Area sensitivity could be added as a constraint to further refine the models for larger study areas though.

The method that we developed allowed identifying areas of greatest conservation value for nineteen bird species, among which there were twenty-two habitat incompatibility conflicts. Our algorithms identified the smallest area needed to meet minimum habitat requirements for every species considered, while maximizing the compactness of that area, and avoiding any overlap between species with incompatible habitat requirements. In practice, these results are useful to managers aiming to provide well-connected, sufficient habitat to all at-risk species over a small area in order to minimize costs and land use conflicts.

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