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Optimizing regional conservation planning for forest birds

Frederic Beaudry[1]*, Anna M. Pidgeon[1], David J. Mladenoff[1], Robert W. Howe[2], Gerald A. Bartelt[3] and Volker C. Radeloff[1]

[1]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA 53706; [2]Department of Natural and Applied Sciences, University of Wisconsin-Green Bay, Green Bay, WI, USA 54311; and [3]Wisconsin Department of Natural Resources, Science Operation Center, Madison, WI, USA 53716

Summary

1. Habitat conservation, particularly for large, multiple use areas, must account for the needs of multiple species. However, an unresolved issue is how to manage habitat when the needs of resident species conflict and when the habitat can only be modelled at a coarse scale. Here, we illustrate an approach to optimizing habitat management using an example of a community of forest-breeding birds.

2. We used potential habitat maps for 20 bird species in northern Wisconsin and identified a spatial arrangement that maximizes conservation value for multiple species, maximizes connectivity and minimizes the area needed for conservation. To do this, we ranked each cell of the study area using a nested percentage value, with for example the highest-ranking 1% holding lands of highest conservation value.

3. As we progressively increased the portion of landscape considered, starting with the highest-ranking habitat first, the number of species for which the minimum habitat requirements were met reached plateaux at 3% and 20% of the landscape. To provide enough area to meet the minimum habitat requirements for all but two species, an estimated 20% of the habitat with the highest conservation value, *c*. 1 million hectares, would need to be maintained. Of that 20% highest-ranking area, 42% was on public lands, compared with 28% for the study area.

4. Tribal lands held a disproportionally large amount of area estimated to be of high conservation value: within the highest-ranking 1% of land, 14% consisted of tribal lands, while these lands held only 5% of the entire study area's forests.

5. *Synthesis and applications*. Hierarchical prioritization provided an efficient mapping approach and the regional perspective necessary to identify management opportunities for a wide range of species. However, it could not explicitly address conflicts among species with overlapping potential habitat but incompatible fine-scale habitat needs. Ignoring this issue may lead to a failure to meet conservation objectives. This issue of habitat mischaracterization needs to be recognized in conservation planning objectives, preferably integrated in an optimization strategy, and can only be partly addressed with a *post hoc*, stepwise heuristic approach.

Key-words: hierarchical prioritization, optimization, potential habitat models, public land, tribal land, Wisconsin, Zonation

Introduction

Habitat loss and degradation are primary causes of biodiversity loss (Wilcove *et al*. 1998; Sala *et al*. 2000). Consequently, maintaining viable populations of at-risk species often requires protecting or managing for high-quality habitat. Managing for habitat can be difficult though. On public lands, habitat management can be costly and may conflict with other land uses such as logging or recreation, and on private lands, mechanisms to coordinate conservation efforts are often lacking. Given the potentially numerous competing management goals for a given area, efficiency at maintaining or creating

*Correspondence author. Environmental Studies and Geology Division, Alfred University, 1 Saxon Drive, Alfred, NY 14802, USA. E-mail: beaudry@alfred.edu

high-quality habitat can be maximized by considering multiple species and identifying high conservation value areas where they can be managed for simultaneously (Root, Akçakaya & Ginzberg 2003). Additionally, conservation management is most effective when conducted at a broad spatial scale, so that the ecological context within which habitat occurs can be considered (Noss 1983; Margules & Pressey 2000). Planning at broad spatial scales (e.g. region-wide, or state/province-wide) facilitates coherence between conservation actions at the local scale and objectives set at broader levels.

Conservation planning, which can assist managing for at-risk species with limited resources, originated in the context of reserve selection (Shaffer 1999; Margules & Pressey 2000). In general, conservation planning assesses trade-offs and opportunities between conservation and economic values, or between alternative conservation goals. For example, conflicts between conservation and other land uses can be most severe on private lands, where economic returns and conservation value can both be high because many at-risk species depend on private lands for the majority of their habitat requirements (Groves *et al.* 2000). Public lands are often more explicitly managed for conservation goals, but they sometimes lack representativeness in land cover and biodiversity (Scott *et al.* 2001). Conservation planning seeks to find optimal solutions that simultaneously maximize competing objectives (Haight 1995; Moilanen *et al.* 2005), allowing planners to assess the relative importance and potential contributions of public and private lands in conserving species and their habitat.

Any optimization approach requires good input data and challenges arise when detailed data on habitat ecology are not available for every species of concern. Habitat models that rely on inductive reasoning to generalize habitat relationships based on a sample of observations, for example habitat selection and habitat distribution models, are highly dependent on the availability of distributional data. In all but the longest field studies, fluctuations in population size, population cycles or metapopulation dynamics can lead to habitat models built from an unrepresentative snapshot of the population (Hobbs & Hanley 1990; Heglund 2001). In addition, an inductive habitat model may successfully predict a species' habitat when it is fully occupied, but the model may perform relatively poorly when the species occupies only a portion of available habitat and is spreading into unoccupied habitat (Hirzel, Helfer & Metral 2001). Alternatives to data-hungry habitat models include deductive models that integrate information from published literature or expert opinion. The most common deductive models are habitat suitability index (HSI) models, but it is difficult to determine appropriate suitability functions over broad areas for HSI models (Roloff & Kernohan 1999). Managers have to contend with species with varying amounts of available information, and there is a clear need for methods that can accommodate these species.

Broad-scale habitat modelling, especially when developed with less than perfect empirical data sets, often results in habitat models with coarse spatial resolution displaying coarse patterns of habitat selection, leading to the unresolved issue of predicted co-occurrence of two or more species with incompatible habitat needs. This occurs when habitat characteristics are common for a pair of species, but un-mapped habitat requirements conflict (e.g. two species requiring the same forest composition but different stand ages). Co-occurrence of incompatible species predicted by overlapping habitat models results in incorrect habitat assessments and thus poorly informed management efforts. We lack an approach that incorporates what is known for all species of conservation concern, not just for the best-studied species, and that can explicitly address the issue of overlapping habitat predictions for incompatible species.

Our goal here was to develop an approach for spatially explicit conservation planning to maintain populations of at-risk forest-breeding birds in northern Wisconsin. Our approach integrated previously published regional-scale potential habitat models for forest-breeding birds in northern Wisconsin (Beaudry *et al.* 2010) into a heuristic optimization algorithm. The objectives were to find a spatial arrangement that maximizes habitat availability for multiple bird species, maximizes connectivity and minimizes the area needed for conservation. The spatial arrangement of these conservation opportunities had to take into account and avoid conflicts among species with overlapping potential habitat but incompatible fine-scale habitat needs. Finally, the spatially explicit solution obtained was analysed to compare the respective conservation contribution provided by public, private and tribal lands.

Materials and methods

STUDY AREA AND STUDY SPECIES

Our study area covered most of northern Wisconsin, USA, and was part of the Laurentian Mixed Forest Ecoregion (Bailey 1995; Fig. 1). This landscape encompassed 7 million ha, 4·6 million of which were classified as forest in the 2001 National Land Cover Database (NLCD; Multi-Resolution Land Characteristics Consortium, http://www.epa.gov/mrlc/nlcd-2001.html). Extensively logged in the first half of the twentieth century, the study area has since largely reverted

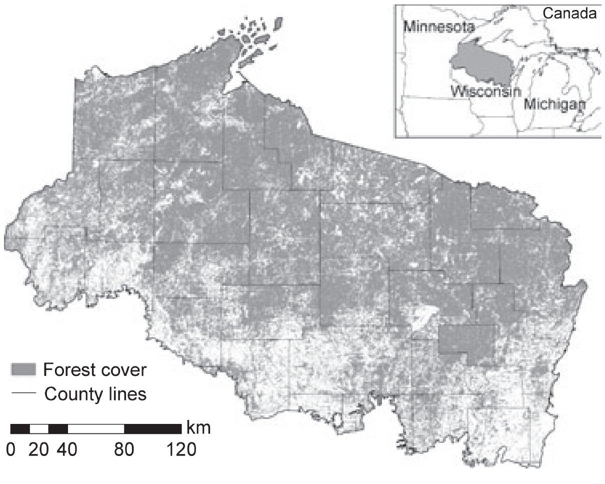

Fig. 1. Study area: northern Wisconsin Laurentian Mixed Forest Ecoregion.

to forests that have re-grown on former clear-cuts and abandoned fields (Radeloff, Hammer & Stewart 2005). Common land uses included forestry, recreation, small private woodlots and agriculture on the best soils. A substantial portion (35%) of the study area's forested land was publicly owned, 5% was owned by American Indian tribes, and the rest (60%) was non-tribal, private properties. On these private lands, second-home building has flourished since the 1950s, with development concentrated along lakeshores and resulting in substantial forest fragmentation (Radeloff, Hammer & Stewart 2005).

As a strategic approach to encourage regional conservation planning, the US Congress mandated in 2001 the development of a Wildlife Action Plan by each US state and territory. In Wisconsin, the State Wildlife Action Plan identified 152 vertebrate species of greatest conservation need, 84 of which were birds, with the goal of conserving these species and their habitat before they become rare and require more costly protection (Wisconsin Department of Natural Resources 2005). Of the 84 avian species of greatest conservation need in Wisconsin, 20 regularly breed in northern forests (Table 1). We developed potential habitat models and maps for these 20 species (Beaudry *et al.* 2010), 13 of which are neotropical migrants, two short-distance migrants, and five year-long residents.

ANALYSIS

We obtained general habitat requirements of forest-breeding, northern Wisconsin avian species of greatest conservation need from published studies, breeding bird atlases and species accounts. Our modelling approach consisted of three nested habitat components that reflect levels of specificity, category resolution and data availability (Beaudry *et al.* 2010):

1. *Habitat groups* are our main modelling unit. These are broad vegetation cover types (e.g. deciduous, mixed or coniferous forest) that capture the general habitat requirements for a given species. A species may rely on more than one habitat group. Habitat groups' distributions are well mapped at the regional scale.

2. *Constraints* are species-specific modifiers to the habitat groups. They refine habitat requirements by taking into account the more specific conditions needed by birds (e.g. edge-sensitivity, exclusion of some stand types, proximity to water). Constraints allow us to refine the habitat models using parameters that are mapped at broad spatial scales.

3. *Intrinsic elements* are fine-scale habitat selection requirements. These elements are not usually mapped at the regional scale, but most can be maintained within habitat groups under appropriate management (e.g. snags, understorey vegetation).

We combined habitat groups and habitat constraints into habitat distribution models that identified potential habitat. Potential habitat can support species of conservation concern if land management provides the intrinsic elements. We identified intrinsic elements from studies completed in the study region when available, and from a statewide bird conservation plan that synthesizes the requirements and recommendations for all species of greatest conservation need (Kreitinger & Paulios 2007).

We developed potential habitat models based on a 30-m resolution grid. The first step was to associate each species with one or more habitat groups, which corresponded to the classes of the 2001 NLCD (Multi-Resolution Land Characteristics Consortium, http://www.epa.gov/mrlc/nlcd-2001.html) and to map all areas with the identified vegetation cover. We then extracted areas satisfying the habitat constraints that we had identified in the literature. Depending on the species, constraints could include area sensitivity and edge effects, modelled using morphological image processing applied to the 2001 NLCD image classification (Vogt *et al.* 2007). For some species, we used tree species composition to extract tree species from the broader habitat groups. Tree species composition was obtained from the Wisconsin Initiative for Statewide Cooperation on Landscape Analy-

Table 1. Forest-breeding avian Species of Greatest Conservation Need for northern Wisconsin, with amount of potential habitat in the 20% highest-ranking fraction of the landscape in terms of conservation value, and the portion of that potential habitat located on public lands

Species	Code	Scientific name	Migratory status	Potential habitat (ha)	Area on public lands	
					(ha)	(%)
Black-backed Woodpecker	BBWO	*Picoides arcticus*	Resident	198 097	91 738	46
Black-billed Cuckoo	BBCU	*Coccyzus erythropthalmus*	Neotropical	367 425	124 331	34
Black-throated Blue Warbler	BTBW	*Dendroica caerulescens*	Neotropical	231 878	126 945	55
Blue-winged Warbler	BWWA	*Vermivora pinus*	Neotropical	455 335	175 840	39
Boreal Chickadee	BOCH	*Poecile hudsonica*	Resident	130 249	63 952	49
Brown Thrasher	BRTH	*Toxostoma rufum*	Short-distance	231 803	50 793	22
Canada Warbler	CAWA	*Wilsonia canadensis*	Neotropical	231 865	115 135	50
Cerulean Warbler	CEWA	*Dendroica cerulea*	Neotropical	231 851	74 737	32
Connecticut Warbler	CONW	*Oporornis agilis*	Neotropical	231 822	103 861	45
Golden-winged Warbler	GWWA	*Vermivora chrysoptera*	Neotropical	348 945	157 923	45
Least Flycatcher	LEFL	*Empidonax minimus*	Neotropical	356 240	180 831	51
Northern Goshawk	NOGO	*Accipiter gentilis*	Resident	465 556	240 641	52
Olive-sided Flycatcher	OSFL	*Contopus cooperi*	Neotropical	240 106	110 797	46
Red Crossbill	RECR	*Loxia curvirostra*	Resident	231 865	111 502	48
Red-shouldered Hawk	RSHA	*Buteo lineatus*	Short-distance	231 883	119 266	51
Spruce Grouse	SPGR	*Falcipennis canadensis*	Resident	155 527	75 742	49
Veery	VEER	*Catharus fuscescens*	Neotropical	316 188	168 222	53
Whip-poor-will	WHIP	*Caprimulgus vociferus*	Neotropical	411 229	192 892	47
Wood Thrush	WOTH	*Hylocichla mustelina*	Neotropical	416 911	198 588	48
Yellow-billed Cuckoo	YBCU	*Coccyzus americanus*	Neotropical	367 425	124 331	34

sis and Data (WISCLAND, http://www.sco.wisc.edu/wiscland) and the US Forest Service Forest Inventory Analysis data (Miles *et al.* 2001).

Full occupancy of the resulting mapped potential habitat was not and should not be expected. Our model structure focused on potential habitat and was not affected by variations in bird distributions because of such factors as weather variations or metapopulation dynamics, unlike habitat models relying on correlations between habitat variables and animal occupancy or abundance data (O'Connor 2002; Early, Anderson & Thomas 2008). However, independently acquired empirical data were used in both model training (breeding bird atlas data) and evaluation (point-count survey data). Territory size and density data plus Partners in Flight bird population estimates and objectives (Panjabi *et al.* 2005) provided habitat objectives for northern Wisconsin. Further details concerning model development and evaluation are available in Beaudry *et al.* (2010).

We used the potential habitat models to identify the optimal spatial configuration of habitat that has conservation value for all 20 species simultaneously. We conducted an optimization process for all species using Zonation v.2, a heuristic conservation planning tool (Moilanen *et al.* 2005, http://www.helsinki.fi/bioscience/consplan/software/Zonation/). We used the basic core-area cell removal algorithm in Zonation, which handled our objectives by iteratively removing the least important pixels of multispecies distribution maps. Cell importance was determined by calculating the number of species (all weighed equally) for which the cell is potential habitat and by giving an increasingly higher value to cells progressively further away from edges, integrating a connectivity estimate into each cell's conservation value. This produced a hierarchically prioritized landscape, or solution map, based on value for multiple species (Moilanen *et al.* 2005).

Zonation thus provided a hierarchical prioritization of each cell in the study area, and we identified the cells that were part of specific percentages of the highest-ranking portion of the landscape (top 1%, 2%, 3%, etc.). The output files were imported and analysed in ArcGIS v. 9.3 (ESRI Inc., Redlands, California, USA). For each species, we determined the amount of potential habitat included within each 1% incremental fraction of the landscape and compared that value to the minimal amount of potential habitat needed to meet PIF objectives for that species in Wisconsin (Beaudry *et al.* 2010). Of the 20 species used in this analysis, 16 had known minimum habitat requirements. We could not determine the minimum habitat requirements for black-billed cuckoo *Coccyzus erythropthalmus*, red crossbill *Loxia curvirostra*, spruce grouse *Falcipennis canadensis* and whip-poor-will *Caprimulgus vociferus* because no data on territory size or density were available to translate population objectives into habitat objectives.

The potential habitat models used here sometimes identify the same area as potential habitat for two species that had incompatible fine-scale habitat needs because the data on these fine-scale variables are presently not available. Currently, optimization algorithms cannot solve these incompatibility conflicts at the regional scale for the level of resolution we used. We therefore distributed potential habitat for incompatible species by allocating different areas to each member of the pair following a heuristic stepwise approach. During this process, the species with the largest amount of habitat needed has the greatest influence on the total area that needs to be managed for all species; we assume that this species' entire potential habitat must have intrinsic elements in suitable conditions in order to have minimum habitat needs met. Then, we evaluated species with conflicting needs individually to allocate their minimum habitat requirements. This is done while maximizing efficiencies by intersecting potential habitats of compatible species.

The results were examined in terms of land ownership types. We used three main categories: public (county, state and federally owned land), tribal and private (non-tribal, non-public). Land ownership was identified using a Wisconsin Department of Natural Resources database. We calculated the proportion of each ownership type for the highest-priority areas and for each species' potential habitat. We also examined the representation of each ownership type in areas with a range of conservation value and contrasting the results with the proportion of the study area's forest lands belonging to each ownership type.

To evaluate the robustness of the solution maps, we conducted two tests. The potential habitat models were built at 30-m resolution, corresponding to the resolution of the NLCD. We resampled the grids at a 100-m resolution to accommodate Zonation's memory limits (a model contained 7×10^6 pixels at 100-m resolution). To test for differences between both resolutions, we compared results for a 100-km^2 test area. Also, potential habitat models for six of the species could not be evaluated with empirical data owing to a paucity of data (Beaudry *et al.* 2010). In these cases, potential habitat models were built on literature-based, more general habitat associations (e.g. all areas classified as coniferous forests in NLCD were identified as potential habitat for red crossbills). We thus compared the solution incorporating all habitat models with the solution based on only those habitat models that evaluated well in a previous analysis [i.e. those with a significant correlation coefficient between the amount of habitat predicted by the model and the density of point-count detections (Beaudry *et al.* 2010)]. To do this, we calculated the kappa coefficient as implemented in Map Comparison kit v.3 (Research Institute for Knowledge Systems, Maastricht, Limburg, Netherlands) to compare the best-models-only-map with the all-models-map. The kappa coefficient can range from 0 to 1, with 0–0·6 indicating poor to moderate agreement, 0·6–0·8 indicating good agreement and 0·8–1·0 suggesting very good agreement (Cohen 1960; Altman 1991).

Results

Land conservation value for forest-breeding birds was clearly unevenly distributed in northern Wisconsin, with some areas simultaneously providing potential habitat for a greater number of species and more habitat connectivity (Fig. 2). The highest conservation value areas for the 20 bird species that we modelled were concentrated within the Chequamegon-Nicolet National Forest, Rusk County Forest, the Lac Courte Oreilles Band of Ojibwe reservation, the Menominee Indian Tribe reservation, and Apostle Islands National Lakeshore (Fig. 2). As we progressively included greater proportions of the landscape, starting with the highest conservation value areas, the number of species for which the minimum habitat requirements were met increased nonlinearly, with plateaux starting at the highest-ranked 3% and 20% of the landscape (Fig. 3). While four species had no published population objective and therefore no known minimum habitat requirements, we estimated that 15 species would have their minimum requirements met in the 20% highest-ranked fraction of the landscape, provided that suitable conditions of intrinsic elements are present. To provide habitat for the 16th species, the northern goshawk *Accipiter gentilis*, the fraction of the landscape required jumped to 92% or $> 3 \times 10^6$ ha. We therefore used the 20% highest-

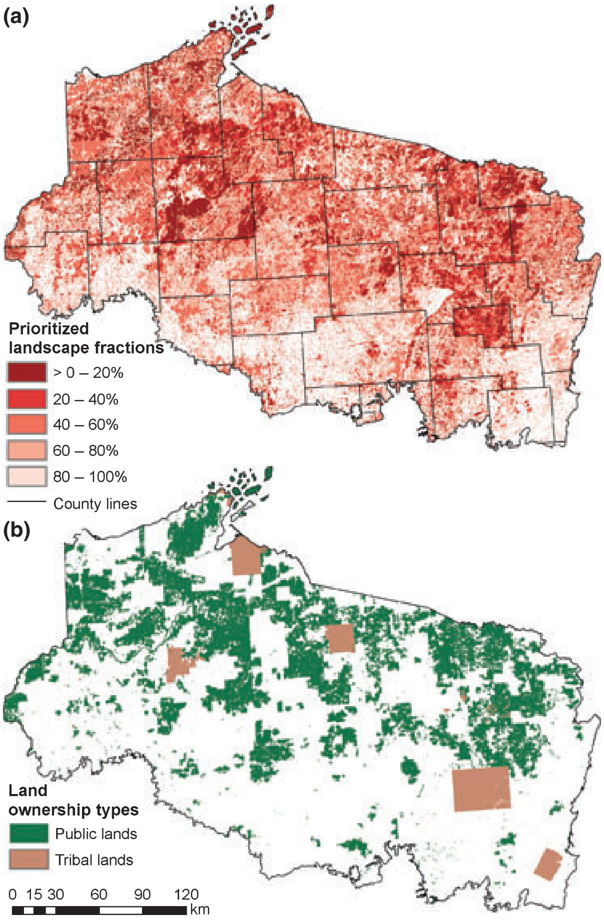

Fig. 2. Map of optimized, hierarchical multispecies habitat prioritization (a) and land ownership types (b). Prioritized landscape fractions are areas ranked on the basis of their ability to simultaneously maximize potential habitat overlap for multiple species and maximum connectivity (the best areas are in >0–20% fractions).

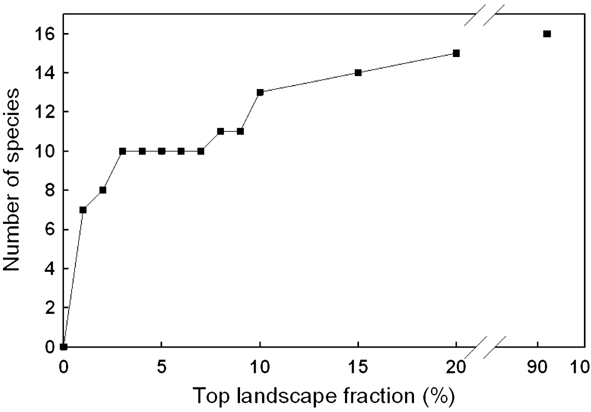

Fig. 3. The number species for which the minimum habitat requirements are met as top fractions of the landscape were progressively included, with the highest-ranking areas first (based on conservation value from a Zonation analysis). The 16th species added is northern goshawk, for which habitat requirement is equal to 92% of the entire study area.

ranked fraction of the landscape (1 019 000 ha) as the selected optimal area to be managed for all but one (northern goshawk) of the 16 species for which minimum habitat requirements were known. The 20% cut-off would also provide considerable potential habitat for those species whose minimum habitat requirements could not be determined: black-billed cuckoo (332 000 ha), red crossbill (232 000 ha), spruce grouse (156 000 ha) and whip-poor-will (436 000 ha).

The amount of potential habitat accrued rapidly beyond the minimum amount needed for many species. When the 1% highest-ranked fraction was considered, minimum requirements for seven species were met (Fig. 4). For every species, the rapid rise in potential habitat needed eventually flattened as its entire potential habitat was included. For northern goshawk, the minimum potential habitat needed was very close to the entire landscape, but when only the 20% highest-ranked fraction of the landscape was considered, less than a quarter (23·9%) of the minimum habitat required was included (Fig. 4).

Of 125 spatial overlaps in the potential habitat models, 30 overlaps occurred between species with conflicting habitat requirements (Table 2). For those species, the intrinsic habitat elements were not compatible, and only one species can be managed for in a given location. The species with the largest amount of habitat needed was veery *Catharus fuscescens* (Fig. 4) – potential habitat shared between veery and other species cannot be managed in ways that would exclude veery. We therefore assigned separate areas for blue-winged warbler *Vermivora pinus* and golden-winged warbler *Vermivora chrysoptera* so that their incompatible habitat needs did not overlap with veery habitat. Potential habitat for wood thrush *Hylocichla mustelina*, least flycatcher *Empidonax minimus*, cerulean warbler *Dendroica cerulea* and Canada warbler *Wilsonia canadensis* also overlapped with veery potential habitat, but they are late successional species that cannot co-occur with early-successional blue-winged and golden-winged warbler. Therefore, once the veery's and the late successional species' minimal habitat requirements were met, early-successional species' habitat was attributed.

Another conflict appeared between red-shouldered hawk *Buteo lineatus* and veery, which cannot co-occur because the veery needs thick ground and shrub vegetation (Bevier, Poole & Moskoff 2004) while red-shouldered hawks occupy forests with an open understorey (Dykstra, Hays & Crocoll 2008). After allocating the entire veery minimum habitat, only 55 378 ha of potential red-shouldered hawk habitat remained to meet its minimum requirement of 114 911 ha (48% of minimum requirement). Allocating the red-shouldered hawk, its entire required habitat would leave the veery closer to its objective of 201 277 ha, corresponding to 65% of its minimum requirements. In other words, while minimal habitat requirements were ostensibly met for both these species after the hierarchical prioritization, accounting for habitat incompatibilities meant red-shouldered hawk (or alternatively, veery) had to be left with unmet minimum habitat needs.

Of the 20% highest-ranked fraction of the landscape, 42% was on public lands (i.e. county, state or federal land), representing 24% of northern Wisconsin's public lands (Fig. 2b). If the minimum habitat objectives for all species of greatest conservation need (except for northern goshawk, discussed below)

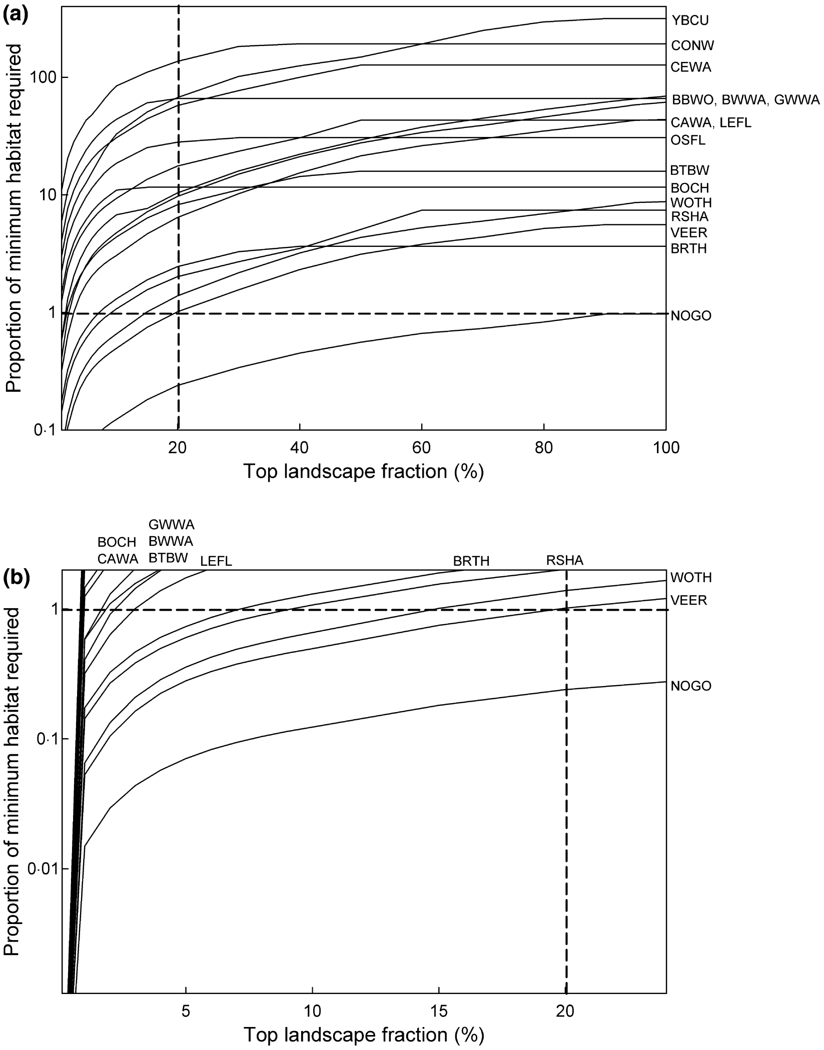

Fig. 4. Potential habitat accumulation curves by species (log scale), with increasing fraction of the landscape considered for (a) the entire curve range and (b) the 20% highest-ranked landscape fraction only. The horizontal dashed line represents the minimum habitat required, and the vertical dashed line the top fraction needed to meet the minimum habitat required for all but one species (NOGO). For species codes, see Table 1.

had to be met on public lands only, the 37% highest-ranked fraction would need to be managed, instead of 20%, corresponding to 41% of all public lands. When analysed by species, the proportion of potential habitat on public land was highest for black-throated blue warbler *Dendroica caerulescens*, veery, northern goshawk and least flycatcher (55%, 53%, 52% and 51%, respectively), and lowest for brown thrasher *Toxostoma rufum*, cerulean warbler, black-billed cuckoo and yellow-billed cuckoo *Coccyzus americanus* (22%, 32%, 33% and 34%, respectively; Table 1).

Non-public lands played a considerable role in providing habitat to Wisconsin's species of greatest conservation need. Of the 20% highest-ranked fraction of the landscape, 52% was on private land and 6% on tribal land (Fig. 2b). When observing the nested, highest-ranked landscape fraction, the ownership distribution changed at the very highest fractions (the top 1–3% highest-landscape fraction, Fig. 5). Within the landscape with the very highest conservation value, the portion that is publicly owned dips, offset by a large increase in tribal lands and a proportionally smaller increase in private land (Fig. 5). Within the top 1% portion of the landscape, close to 14% was on tribal lands, while they held only 5% of the study area's forested land.

The correspondence between the results obtained from models with resolutions of 30 vs. 100 m was very high ($r^2 > 0{\cdot}98$), justifying the use of 100-m resolution potential habitat models. When comparing the all-species optimal solution with the solution excluding the literature-based models, we found a kappa coefficient of 0·87, indicating very good agreement in terms of the number of cells allocated to the same category for both solutions, and the spatial arrangement of those cells. We thus conducted all analyses with the full set of species (Table 1).

Discussion

Hierarchical prioritization of the landscape allowed us to identify the 20% highest-ranking fraction of the landscape where habitat for all but one species of greatest conservation need could be managed simultaneously while maximizing connectivity among patches. Matching the prioritization approach with habitat potential models that accommodate lesser-known species provided guidance for habitat management within a

Table 2. Overlap, in hectares, between pairs of species' potential habitat within the 20% highest-ranking fraction of the landscape. Values in parentheses represent overlap between species with incompatible habitat requirements

Species	BBWO	BBCU	BTBW	BWWA	BOCH	BRTH	CAWA	CEWA	CONW	GWWA
YBCU	96 204	332 010	NA[1]	115 661	70 372	83 836	23 941	73 821	153 196	74 642
WOTH	NA	42 945	218 955	(316 086)	NA	31 937	(76 128)	147 430	NA	(235 815)
WHIP	63 669	30 443	(137 184)	(222 611)	36 291	23 330	(140 484)	94 146	56 185	(166 989)
VEER	NA	NA	(228 289)	(252 508)	NA	NA	58 047	(117 981)	14 201	(194 947)
SPGR	143 163	95 118	NA	NA	74 863	NA	(47 253)	NA	111 002	NA
RSHA	NA	29 832	(130 425)	(193 245)	NA	18 733	(29 262)	62 751	NA	(149 132)
RECR	91 572	14 056	NA	NA	43 655	13 502	124 292	NA	33 827	NA
OSFL	198 097	116 734	NA	NA	91 767	5 784	76 227	NA	142 181	NA
NOGO	65 869	55 813	181 492	(275 587)	28 926	51 254	125 133	110 958	41 738	(222 601)
LEFL	NA	13 890	228 289	(289 200)	NA	10 630	68 112	133 751	NA	(215 422)
GWWA	NA	74 642	(150 720)	(304 893)	NA	69 059	NA	(116 853)	NA	–
CONW	115 490	153 196	NA	27 365	83 347	44 661	21 821	NA	–	
CEWA	NA	73 821	69 023	(170 783)	NA	19 992	NA	–		
CAWA	61 646	23 941	41 050	10 914	41 425	NA	–			
BRTH	NA	83 836	NA	106 556	NA	–				
BOCH	69 315	70 372	NA	NA	–					
BWWA	NA	115 661	187 507	–						
BTBW	NA	NA	–							
BBCU	96 204	–								
Total[2]	198 097	1 721 958	446 221	2 879 657	130 474	344 630	570 187	511 537	326 752	2 413 886
Minimum[3]	3 000	Unk	28 125	46 940	11 250	94 462	13 191	4 030	1 697	33 551

	LEFL	NOGO	OSFL	RECR	RSHA	SPGR	VEER	WHIP	WOTH	YBCU
YBCU	NA	55 813	116 734	14 056	29 832	95 118	NA	30 443	42 945	–
WOTH	323 755	277 734	NA	NA	195 604	NA	293 346	247 748	–	
WHIP	213 715	261 342	80 128	156 069	132 668	(37 062)	(191 571)	–		
VEER	308 926	232 360	NA	NA	(180 797)	NA	–			
SPGR	NA	(33 081)	(155 527)	(49 632)	NA	–				
RSHA	187 098	171 474	NA	NA	–					
RECR	NA	143 716	110 579	–						
OSFL	NA	78 824	–							
NOGO	253 775	–								
LEFL	–									
Total	2 425 749	1 881 216	261 734	388 902	850 095	155 527	1 739 160	2 394 748	2 638 032	1 721 958
Minimum	55 498	1 944 750	8 552	Unk	114 911	Unk	311 928	Unk	301 270	5 462

[1] These species have potential habitat models that do not overlap.

[2] The total amount of potential habitat in the study area for that species.

[3] Minimum habitat required to meet population objectives for that species (Beaudry *et al.* 2010).

regional perspective. Our results are important because they highlight two main points. First, efficiency can be gained by using a multispecies optimization approach, which minimizes the area to be managed by capitalizing on habitat overlap. Secondly, this analysis provides a guide for ranking conservation opportunities by their importance for forest bird populations of conservation concern, while accommodating species with incompatible habitat needs.

Potential habitat models and potential distribution maps identify locations where habitat elements needed by a species may be present, but potential distribution maps do not imply occupancy which can be limited, for example, by population fluctuations (e.g. Braunisch & Suchant 2007; McComb *et al.* 2009). Potential habitat models also leave open the possibility of overlapping habitat models between incompatible species whose un-mapped habitat requirements conflict (e.g. species occurring in the same forest type but requiring different understorey density). Incompatibilities can also be attributed to interspecific relationships such as predation, competition, nest parasitism and pathogen transmission between two species. Detailed habitat models can circumvent the incompatibility problems if they sufficiently differentiate the habitats of conflicting species but generally habitat models used at broad scales do not address this important issue, and lack of data for important variables makes habitat conflicts likely. Even for models implicitly representing 'realized' habitat (as opposed to potential habitat), incompatible species can unrealistically be modelled as co-occurring when the habitat characteristics represented are coarse. Currently, regional-scale modelling approaches (e.g. Gap analysis, HSI) and species richness maps generally ignore whether some of the species modelled can actually coexist, and our study rep-

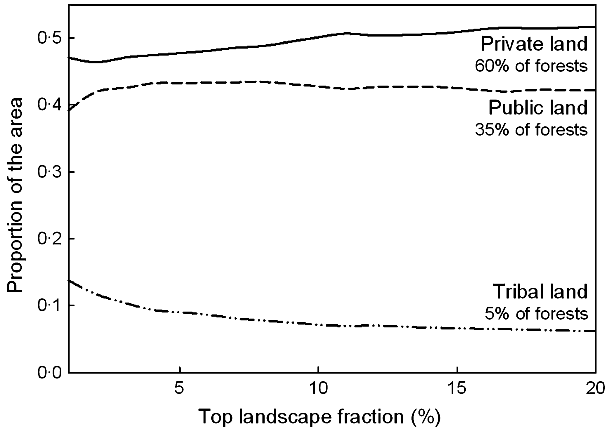

Fig. 5. Land ownership types with increasing hierarchical prioritization of the landscape. The landscape fractions are nested areas with the highest conservation value owing to connectivity and multispecies potential habitat overlap. Public land includes county, state and federal land, and private land includes all the land not identified as public or tribal.

resents, to our knowledge, one of the first to explicitly address this issue.

When confronted with pairs of bird species with overlapping potential habitat, but conflicting habitat needs, we allocated different habitat to each member of the pair following a stepwise approach. This stepwise process could solve most of the incompatibility issues, but not all of them. However, a solution using this *post hoc* approach quickly becomes intractable with an increasing number of species. Furthermore, while the solution obtained is nested within the Zonation-derived optimized landscape, it is not itself optimized, and to our knowledge, there exists currently no method to do this. Negative interactions between species need to be explicitly integrated in the objectives and methods of multispecies conservation planning efforts, preferably integrated in an optimization strategy.

It should be noted that we assume incompatible species show no overlap in their territories and that compatible species can occupy the same space with complete territory overlap. In reality, variations in vegetation and in the bird species' habitat selection process probably result in bird distributing themselves in patterns that are short of these two extremes. For example, while the Canada warbler requires a dense understorey in a mixed deciduous/coniferous forest (Conway 1999), the wood thrush, which requires an open understorey (Roth, Johnson & Underwood 1996), may incorporate some interwoven denser understorey pockets, resulting in some territory overlap. As a result, methods developed to avoid issues with incompatible species may result in conservative habitat management prescriptions when some conflicting species' occurrence is deemed completely irreconcilable.

Within the 20% highest-ranked fraction of the landscape, the percentage of potential habitat on public lands was 42% and varied among species, generally between 30% and 55%. This proportion was greater than the proportion of forest land under public ownership in the study area (35%). Tribal lands were disproportionally represented in the 20% highest fraction as well. While occupying only 5% of northern Wisconsin forests, tribal lands contained almost 14% of the top 1% fraction of the landscape. The involvement of some of these very high conservation value areas could provide a significant step towards meeting conservation objectives for at-risk forest species. In general, public and tribal lands contain managed forest resources, and the conditions of the different forest stands are usually known. Thus, managers in those areas are likely to know whether the intrinsic habitat elements needed by each species are present or if they can be actively managed for to promote occupancy by the species. If so, the conservation objectives could be relatively easily integrated into forest management plans in areas that are particularly important for species conservation.

The remainder of the 20% highest-ranked portion was owned privately. There is currently no concerted planning structure that can be used to coordinate management on these properties but incentives could encourage forest management that contributes to regional conservation objectives. For example, Wisconsin has a voluntary forest management programme for private land [the Managed Forest Law; Wisconsin Department of Natural Resources (http://www.dnr.state.wi.us/forestry/ftax/)] that shifts most of the property tax burden from annual payments to a tax on harvesting revenues. Enrolment in that programme is contingent upon adherence to a forest management plan for each property and management plans are largely developed to meet timber management objectives. Integrating conservation objectives into the forest management plans, especially if those are tailored to the landscape context, could significantly contribute to regional conservation objectives.

Other approaches to promote conservation on private lands include conservation easements, the US Fish and Wildlife Service's Safe Harbor programme and forest certification programmes for private industrial forests requiring sustainable management practices. Our results provide spatially detailed information to target such efforts and a benchmark against which sustainability can be measured. Whether public or privately owned, different types of properties can play different conservation roles depending on their primary management goals. Early-successional birds might best be managed on county and private industrial properties where wood production is prioritized and logging occurs in shorter rotations. On state and federal lands with explicit sustainable forest use and conservation objectives, later successional species may be better managed.

The proportion of potential habitat located on public land was low for brown thrasher, yellow-billed and black-billed cuckoos (Table 1). This can be explained by the association of these species with habitat edges along roads, shrublands along power line right-of-ways and shrub-swamps, habitat types that are scarcer in the forest-dominated public lands of northern Wisconsin. Conversely, most black-throated blue warbler potential habitat, i.e. large stands of northern hardwood forest (Holmes, Rodenhouse & Sillett 2005), was located on public lands.

The northern goshawk presents a particular challenge for conservation planning in Wisconsin. The northern goshawk population estimate for the Boreal Harwood Transition region (Bird Conservation Region 12, Rich *et al.* 2004), which includes portions of Minnesota, Wisconsin, Michigan, Ontario, and Quebec, is 6700 individuals (1500 in northern Wisconsin, Rich *et al.* 2004). Owing to its large territory size (average for males in Minnesota: 2593 ha; Boal, Anderson & Kennedy 2003), almost the entire potential habitat identified has to support northern goshawk to match the current population estimate for northern Wisconsin (Beaudry *et al.* 2010). Furthermore, northern goshawks show broad habitat requirements and may be mainly limited by the prey base (Squires & Reynolds 1997). Habitat objectives for northern goshawk are probably best evaluated at even broader spatial extents such as Bird Conservation Regions.

Hierarchical prioritization of the landscape provided an efficient way to plan for multiple species simultaneously, especially as a 'coarse filter' approach (Hunter, Jacobson & Webb 1988) where a large number of species are likely to benefit from conservation efforts. The use of potential habitat models facilitated mapping priorities at the regional scale but also yielded overlaps between species with incompatible habitat needs. These complications arise when habitat is modelled at broad spatial scales, and while they are usually ignored, they may lead to ineffective conservation reserves, unsuccessful habitat management and ultimately unmet conservation objectives. The issue of incompatible habitat requirements needs to be recognized in the objectives and methods of multispecies conservation planning efforts and preferably integrated in an optimization strategy; it can only be partly addressed with a *post hoc*, stepwise heuristic approach.

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