

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

## Within-site habitat configuration in reserve design: A case study with a peatland bird

Monique Poulin<sup>a,b,\*</sup>, Marc Bélisle<sup>c,d</sup>, Mar Cabeza<sup>c</sup>

<sup>a</sup>Groupe de recherche en écologie des tourbières, Département de phytologie, Pavillon Paul-Comtois, Université Laval, Qué., Canada G1K 7P4

<sup>b</sup>Department of Forest Ecology, University of Helsinki, P.O. Box 27, Helsinki FIN-00014, Finland

<sup>c</sup>Metapopulation Research Group, Department of Ecology and Systematics, University of Helsinki, Helsinki FIN-00014, Finland

<sup>d</sup>Département de biologie, Université de Sherbrooke, 2500 boul. de l'Université, Sherbrooke, Qué., Canada J1K 2R1

### ARTICLE INFO

#### Article history:

Received 18 October 2004

Received in revised form

5 August 2005

Accepted 20 September 2005

Available online 17 November 2005

#### Keywords:

Reserve design

Site selection algorithms

Within-site habitat configuration

Remote sensing

Population persistence

Habitat loss

### ABSTRACT

This study assesses the effects of considering within-site habitat configuration when designing reserve networks. This attribute takes all its importance in situations where the long-term integrity of (within-site) habitat patches cannot be preserved without protecting their surrounding environment. We addressed this issue through the concrete problem of selecting a reserve network of natural peatlands in southern Québec, Canada. We used a reserve-selection algorithm that minimized the total number of peatlands to include within networks. The algorithm was constrained to include peatlands containing habitat patches that met specific size thresholds. Five habitat-clustering thresholds were used to set the eligibility of each site to the selection process. The resulting reserve networks were evaluated according to their representation efficiency and to the expected consequences for the Palm Warbler (*Dendroica palmarum*), an area and isolation-sensitive bird restricted to peatlands in southern Québec.

Constraining the algorithm to include peatlands showing increasingly larger patches of habitats led to larger networks, both in terms of area and number of sites, and to networks composed of smaller sites. These effects increased with the representation target (i.e., the % of each habitat preserved). With respect to the Palm Warbler, selecting peatlands with larger patches of habitats had only an indirect effect on its site-occupancy pattern. Indeed, despite the fact that the probability of occurrence of the warbler was negatively correlated with the size of habitat patches, the habitat-clustering threshold influenced the incidence of the warbler mainly via its effect on the physical attributes of the selected networks – including the area, isolation level, and the number of selected sites. Because increasing the habitat-clustering threshold led indirectly to a greater regional availability of prime breeding habitats for the Palm Warbler, it mitigated the severe negative impact of an hypothetical alteration or destruction of non-selected peatlands. Our study thus emphasizes the importance of determining how the different factors describing within-site configuration are correlated with other intrinsic characteristics of the sites available to the selection process before opting for a site-selection strategy.

© 2005 Elsevier Ltd. All rights reserved.

\* Corresponding author. Tel.: +1 418 656 2131x13035; fax: +1 418 656 7856.

E-mail address: [monique.poulin@plg.ulaval.ca](mailto:monique.poulin@plg.ulaval.ca) (M. Poulin).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.09.016

## 1. Introduction

Reserve-selection algorithms have been developed to propose optimized solutions for a set of management objectives given limited nature conservation funds (Margules et al., 1988; Pressey and Nicholls, 1989a; Margules and Pressey, 2000). However, optimizing conservation cost by minimizing the area or number of sites needed to represent all species of interest is no guarantee that the latter will persist in the network (Virolainen et al., 1999; Rodrigues et al., 2000b,c; Cabeza and Moilanen, 2001). In that respect, reserve-selection algorithms have seldom been used to meet species ecological requirements, but were mainly designed to satisfy arbitrary representation targets (e.g., % of each habitat to preserve or  $x$  occurrences for each species). Yet, site-specific species abundance is likely to be correlated to local population viability, and has been suggested as a good indicator on which to set reserve design goals (Rodrigues et al., 2000b; Turpie et al., 2000; Araújo and Williams, 2001; Lopez and Pfister, 2001). Because this information is seldom available, land classifications are often used as surrogates for species abundance (based on the coarse-filter approach; Lombard et al., 2003; Noss, 1996; Rodrigues et al., 2000a). In this paper, we explore further the use of habitat types for selecting a reserve network and its influence on the expected occurrences of a bird species of interest.

Most of the reserve-selection studies based on habitat surrogates have considered coarse habitat classes based on small-scale maps (e.g., 1:250,000; Pressey and Nicholls, 1989a). The resulting habitat patches thus remained large, often approaching the size of the planning units considered (e.g., grid cells, land properties or circumscribed ecosystems). Even when habitats were defined finely enough to produce as much as 11–31 classes (Nicholls and Margules, 1993; Lombard et al., 1997), planning units usually remained homogeneous. This has resulted in the elaboration of reserve-selection algorithms neglecting the spatial configuration of habitats within planning units. For example, whether 10 ha of a certain land class is subdivided into numerous small patches or is grouped into a single large patch can have significant impacts on the persistence of the species associated with this habitat type, especially for territorial and central-place foraging animals (Dunning et al., 1992; Hinsley, 2000). Likewise, within-site habitat mosaics imply natural edges that reduce patch area for core-habitat species and should be considered when selecting reserves (Murcia, 1995; Matlack and Litvaitis, 1999; Harrison et al., 2001). It follows that aside from the isolation of sites (Bedward et al., 1992; Nicholls and Margules, 1993; Freitag et al., 1996, 1997; Lombard et al., 1997; Heijnis et al., 1999; Wessels et al., 1999; McDonnell et al., 2002; Cabeza et al., 2004a,b), the scale of habitat units (Rouget, 2003), or the discrepancy between the spatial mapping resolution of reserves and species data (Araújo, 2004), spatial constraints have rarely been incorporated into reserve-selection processes. This is surprising given the accumulating evidence that both landscape composition and configuration can influence the spatial distribution and abundance of plants and animals. As remote sensing tools are becoming increasingly efficient at representing landscape patterns (Roughgarden et al., 1991; Goward and Williams, 1997), the mapping of more

detailed or refined land classifications will unravel within-site spatial heterogeneity and allow the possibility to take it into account (Palmeirim, 1988; Kerr et al., 2001).

Different habitats present different aggregation levels in nature. Hence, the average habitat patch size may vary greatly among planning units. If within-site configuration has to be taken into account, an intuitive way would be to respect the relative frequency distribution of patch sizes in which the various habitats occur in the region of interest. However, a higher representation of large patches could favor area-sensitive species, which are often of special conservation interest and/or considered as potential umbrella species (Berger, 1997; Carroll et al., 2001; Suter et al., 2002). Since species persistence remains the long-term goal when establishing a reserve network (Cabeza and Moilanen, 2001), occurrence or abundance data of area-sensitive species could be used to set the optimal size of habitat patches.

Here, we evaluate the effect of considering within-site habitat configuration when selecting reserve networks representing a variety of habitat types. We address this issue through the concrete problem of selecting a reserve network of natural peatlands in southern Québec, Canada. The problem of within-site configuration as addressed here is not only a matter of scale, but also one of nestedness. Indeed, peatlands must be integrally protected to remain functional. Otherwise, the hydrology of these ecosystems can be impaired and the long-term integrity of the vegetation compromised due to drainage effects (Poulin et al., 1999; Pellerin and Lavoie, 2000; Lachance and Lavoie, 2004). Hence, it is not only the habitat patches of interest that need to be protected, but the peatlands containing those patches. In this context, it was preferable to use a reserve-selection algorithm that minimize the number of sites needed to represent all habitat types rather than an algorithm that minimize the total network area.

Specifically, we assessed the influence of constraining a reserve-selection algorithm to select peatlands containing habitat patches of different size on the probability of occurrence of the Palm Warbler (*Dendroica palmarum*) in the resulting reserve networks. The evidence suggests that this species may act as a good umbrella (sensu Roberge and Angelstam, 2004). Indeed, this bird is strictly associated to peatlands in southern Québec (Calmé et al., 2002) and is sensitive to habitat disturbance (Desrochers et al., 1998) as well as to peatland size and isolation (Calmé and Desrochers, 2000; Delage et al., 2000). Moreover, because bird species assemblages were found to be nested within peatlands as the latter increased in size, and that both the incidence of the Palm Warbler and the habitat richness are positively correlated to the size of peatlands (Calmé and Desrochers, 1999), the Palm Warbler should be present only in sites that show a high diversity of biotic and abiotic conditions.

In our study area, peatlands suffer from a diversity of threats, such as agriculture, forestry, hydro-electricity production, cranberry farming, and peat moss extraction (Poulin and Pellerin, 2001). We thus measured the potential effects of habitat loss on the probability of occurrence of the Palm Warbler by disregarding non-selected peatlands when computing the bird's expected incidence in the reserves, thereby mimicking the situation where non-selected sites would have been strongly altered or destroyed. We stress that the method

developed here does not aim at designing the best possible reserve network for the long-term persistence of the Palm Warbler, but rather seeks to select reserve networks representative of all peatland habitats, while exploring the influence of within-site habitat configuration on the physical characteristics of the selected networks, as well as on the probability of occurrence of the Palm Warbler within these networks.

## 2. Methods

### 2.1. Study region

The peatland network is located within ca. 10,000 km<sup>2</sup> of lowlands bordering the South shore of the St. Lawrence River in southern Québec, Canada. Peatlands cover about 4% of the region and are mainly ombrotrophic or weakly minerotrophic. The whole peatland network is therefore *Sphagnum* dominated. The remaining landscape is mainly covered by forests (45%) and agricultural lands (40%; Robitaille and Saucier, 1998). Forests neighboring peatlands consist of mixed-tolerant hardwood dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and balsam fir (*Abies balsamea*). Such forests are improper breeding habitats for the Palm Warbler which strictly occurs in peatlands in that region (Ibarzabal and Morrier, 1995; Calmé et al., 2002).

### 2.2. Peatland habitat map

The peatland habitat map was obtained from a satellite image classification performed on a Landsat 7/ETM+ scene taken on 14 July 1999 (see Poulin et al., 2002 for details). The image was classified in two major steps. First, a mask procedure was used to isolate peatlands from the surrounding matrix. The mask identified 629 peatlands covering 18,103 ha (Fig. 1). Second, the pixels within each of the delineated peatland polygons were classified using a weighted maximum likelihood classifier based on a supervised approach (Richards and Jia, 1999). This resulted in a map of 13 habitat types (H1–H13), defined a priori according to the structural properties of the vegetation (Table 1). The size of patches varies considerably among habitats, as well as within and among peatlands, emphasizing the potential importance of taking within-site spatial configuration into account when selecting reserves. A validation based on 626 locations revealed a low rate of omission errors (see Poulin et al., 2002). Moreover, ordinations indicated that the 13 a priori-defined habitat types explained as much or more variation in the plant species distribution and vegetation structure than 15 commonly measured environmental variables describing shading, hydrological conditions and water chemistry (Poulin et al., 2002).

### 2.3. Selecting reserve networks

#### 2.3.1. Data pre-processing

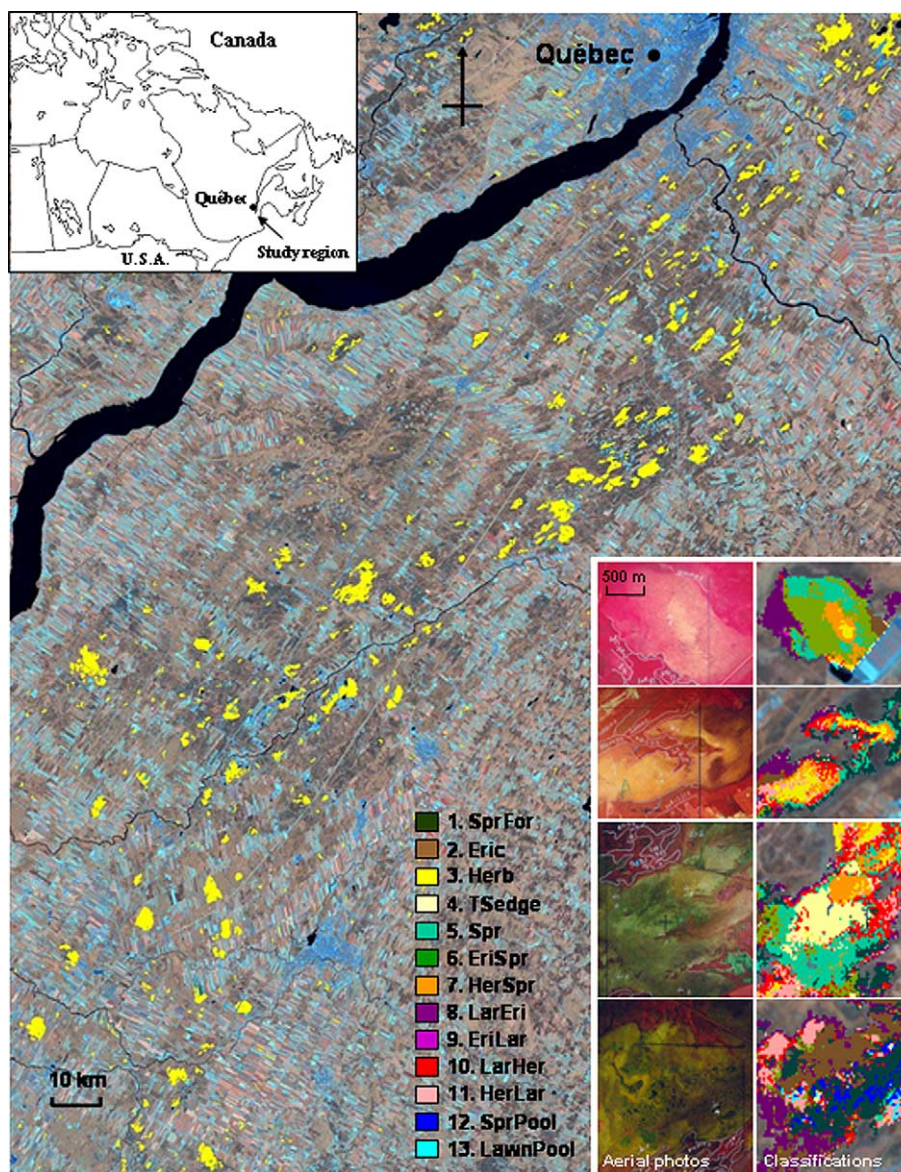
Small river wetlands are likely to be mistakenly classified as peatlands when analyzing remote sensing data. We therefore eliminated peatlands <10 ha from the original peatland system. When selecting reserve networks, we considered the peatlands as the planning units and the 13 different habitats

(Table 1) as the target features to be represented in the reserve networks. We use the term *site* as an equivalent to peatland and the term *patch* when referring to a continuous extent of the same habitat type within a peatland (Fig. 2). In order to assess the effects of within-site habitat configuration, we applied the selection methods to different versions of the original dataset. We used five *habitat-clustering thresholds* that filtered the habitats patches that were present within sites. The thresholds set the smallest patch size for each of the 13 habitats in order for them to be contributing to the site-selection process. Therefore, at different thresholds, the eligible peatlands were different and so was their contribution to the total amount of preserved habitat, for each habitat type, in the reserve networks (Fig. 2). Because some habitats are more interspersed than others in nature we opted for keeping the current natural distribution among all habitat types when setting clustering thresholds. The five habitat-clustering thresholds were set according to different percentiles (from 25th to 95th) of the patch size distribution in the original peatland system (Table 2). For instance, when considering the 75th percentile threshold, the minimum patch size varied from 6 to 26 pixels, depending on the habitat (Table 2). Note that the 25th percentile threshold corresponds to the situation of no clustering (single pixels) for all habitats. By using clustering-thresholds, our intention was to quantify the effects of considering only significant (i.e., large) patches of habitats. These significant patches could correspond to what area-dependent species would actually consider as habitat to breed or forage. Other patches would be too small to be used by these species. We did not consider that landscape supplementation or complementation (sensu Dunning et al., 1992) could occur within peatlands as there is very few empirical data on these phenomenon. Otherwise, we would have been obligated to rely on purely speculative relationships of habitat equivalence.

We define the *Clustered\_Area<sub>ij</sub>* of a particular habitat *j* within a given peatland *i* as the number of pixels in patches of the same size or larger than the clustering threshold for that habitat (i.e., *Threshold<sub>j</sub>*; see Fig. 2 for an example). Table 3 presents the total area of each habitat as well as their effective area after considering each of the five habitat-clustering thresholds (i.e., the sum of *Clustered\_Area* across all peatlands for each habitat).

We chose nine representation targets varying between 1% and 50% of the regional extent of each of the 13 habitats. We use the expression *representation target* to refer to the conservation goal, in our case to the proportion of each habitat that should be included in the selected reserve networks. By using the same proportional representation target for all habitats, we could assess the independent effect of using different thresholds on reserve network design (Table 3). Hence, we calculated the target area of each habitat to include in selected networks before filtering below-threshold patches. When the total availability of the summed *Clustered\_Area<sub>ij</sub>* across sites for a given habitat was smaller than its required representation target, all the sites containing patches equal or larger than *Threshold<sub>j</sub>* were selected. This happened for the two habitats characterized by pools. Indeed, 45% was the maximal representation target that could be reached for H13 under the 90th clustering threshold





**Fig. 1** – Study area with peatland polygons (in yellow) resulting from the mask procedure applied to a Landsat 7/ETM+ scene from 1999 (see Poulin et al., 2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

constraint, whereas 40% and 33% were the maximal targets for H12 and H13 under the 95th clustering threshold constraint, respectively.

### 2.3.2. Reserve-selection algorithm

The selection of a network of peatlands was approached as a minimum-set problem with proportional representation targets (Camm et al., 1996; Pressey et al., 1997). All peatlands were treated as being of equal cost and so the optimization problem was applied to the number of peatlands. Therefore, the site-selection algorithm determined: what is the minimum number of peatlands required to represent x% of the area of each habitat type.

We used a common stepwise algorithm (Araújo and Williams, 2000; Williams and Araújo, 2000). First, the algo-

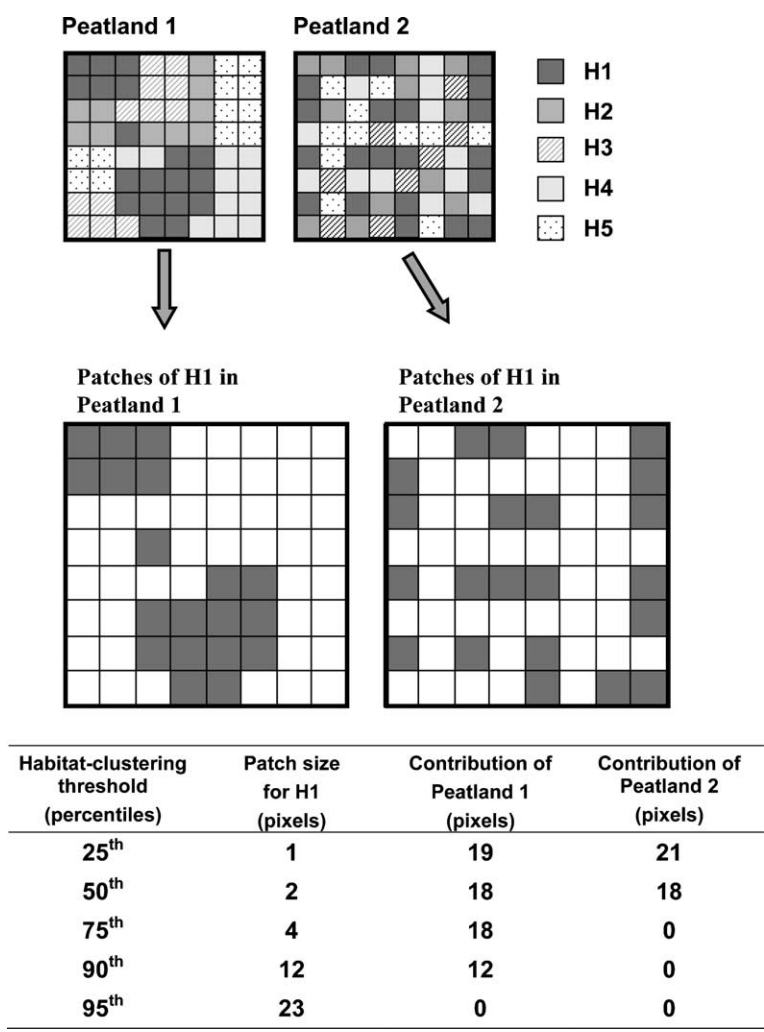
rith identifies the habitats for which the effective area ( $Clustered\_Area_i$ ; summed across sites) is smaller than the targeted area. All peatlands with patches equal or larger than indicated by the threshold are then selected. For the remaining habitats, the algorithm evaluates how much each peatland contributes in filling the gap between the current representation of all habitats and their target. The peatland that contributes the most across all habitats is then selected. This process is repeated until all habitats had reached their representation target.

When ties occurred among peatlands, the algorithm chose one at random. We added checks that excluded redundant sites in order to improve the efficiency of the algorithm (Pressey et al., 1997). Twenty replicates were run for each combination of habitat-clustering threshold and

**Table 1 – The 13 habitat classes defined a priori and classified from a 1999 Landsat 7/ETM+ scene**

Habitat number	Habitat code	Description
H1	SprFor	Spruce forest with open canopy
H2	Eric	Ericaceous shrubs
H3	Herb	Herbs (including both forbs and sedges other than tall <i>Carex</i> )
H4	TSedge	Tall sedges
H5	Spr	Spruce thickets
H6	EriSpr	Ericaceous shrubs with spruce thickets
H7	HerSpr	Herbs with spruce thickets
H8	LarEri	Larch with ericaceous shrubs
H9	EriLar	Ericaceous shrubs with larch
H10	LarHer	Larch with herbs
H11	HerLar	Herbs with larch
H12	SprPool	Spruce thickets with pools
H13	LawnPool	Lawn with pools

The rank of a specific vegetation *stratum* within a habitat type determines its dominance. For example, larches are dominant in habitat 8 but are more scattered in habitat 9; the density of the tree cover represents the main difference between the two habitat types. A more detailed description is given in Poulin et al. (2002).



**Fig. 2 – Example showing the contribution of two hypothetical peatlands to the representation target of habitat H1 under the five habitat-clustering thresholds (i.e., 25th, 50th, 75th, 90th, 95th; see Table 2). Pixels occurring in patches smaller than the threshold do not contribute to the area preserved for that particular habitat. The column entitled “Patch size for H1” indicates the minimal number of pixels for a patch of H1 to be considered in the peatland selection process. The two right columns indicate the contribution of each hypothetical peatland to the representation target of H1. At high clustering thresholds, Peatland 1 contributes more to the representation target due to the occurrence of larger patches of H1.**

**Table 2 – Habitat-clustering thresholds for each of the 13 habitat types used in the site-selection process**

Percentile	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13
25th	1	1	1	1	1	1	1	1	1	1	1	1	1
50th	2	2	2	1	1	1	1	2	1	1	1	2	1
75th	4	5	6	3	3	3	3	7	4	2	3	4	3
90th	12	26	25	11	11	10	13	26	15	6	8	12	7
95th	23	80	63	28	26	26	31	75	35	11	19	28	9

Peatlands having patches smaller than these thresholds for a particular habitat do not contribute to its representation target. The percentiles were derived from the patch size distribution among all peatlands >10 ha of the study area. For example, 90% of patches of habitat 8 (H8) were  $\leq 26$  pixels. For all habitat types, 50% of all patches, were  $\leq 2$  pixels (pixel size = 0.09 ha).

representation target. The best replicates (networks with the smallest number of sites) were selected.

Although reserve networks resulting from this type of algorithm are not optimal (Underhill, 1994; Pressey et al., 1996; Csuti et al., 1997; Önal, 2003), we opted for such an algorithm since the aim of the paper was not to discuss the efficiency of the algorithm but to assess the role of taking within-site habitat configuration into account. Constraints such as the time required to process large spatially explicit datasets and the problem of dealing with quantitative representation targets also dictated our choice.

#### 2.4. Evaluating reserve networks

We evaluated the reserve networks based on their representation efficiency (sensu Pressey and Nicholls, 1989b) and the predicted occupancy of the Palm Warbler. The representation efficiency of a network was assessed in terms of its requirements in total area and number of sites to reach a given representation target for a certain habitat-clustering threshold. The incidence of the Palm Warbler was summarized using (1) the mean probability of occurrence across the selected peatlands, and (2) the expected number of sites in which

the warbler should occur (i.e., mean probability of occurrence  $\times$  number of sites in the network; see below).

#### 2.5. Predicting Palm Warbler occurrence

We built a logistic regression model to predict the probability of occurrence of the Palm Warbler within the peatlands selected to be part of the reserve networks. The presence/absence data used for the regression originated from Calmé and Desrochers (2000), whereas the explanatory variables were derived from the classified satellite image. The presence of the warbler was determined in 61 peatlands between 4 June and 14 July 1995, during the breeding season, using both line transects and fixed-radius point counts (see Calmé and Desrochers, 2000 for details). We considered as main explanatory variables: (1) the area of the peatland, (2) the area of prime breeding habitats for the Palm Warbler within 5 km of the focal peatland centroid minus the area of prime breeding habitats found within the focal peatland, (3) the area of prime breeding habitats for the Palm Warbler within 10 km of the focal peatland centroid minus the area of prime breeding habitats found within 5 km of the focal peatland centroid, and (4) the mean patch size of prime breeding habitats within

**Table 3 – Amount of peatland habitats available to the site-selection process under the five habitat-clustering thresholds**

Habitat	Total area (ha)	Sum of Clustered Area (ha) across all peatlands for each habitat <sup>a</sup>					Area under 10% representation target (ha)
		25th	50th	75th	90th	95th	
H1	1307	1307	1215	1107	892	723	131
H2	3050	3050	2978	2872	2607	2241	305
H3	647	647	626	594	509	432	65
H4	1096	1096	1096	988	874	767	110
H5	899	899	899	825	745	673	90
H6	1679	1679	1679	1526	1357	1220	168
H7	736	736	736	689	624	571	74
H8	3723	3723	3629	3329	2842	2295	372
H9	793	793	793	690	585	477	79
H10	793	793	793	667	494	413	79
H11	1318	1318	1318	1130	976	849	132
H12	74	74	69	58	43	30	7
H13	23	23	23	16	11	8	2

Total area represent the area covered by each habitat type among all peatlands >10 ha in the region under study. Clustered Area is the area covered by each habitat type found in patches that met the habitat-clustering thresholds (see Table 2). The area to preserve for each habitat type under an hypothetical target of 10% is shown in the last column. Note that the latter is calculated based on the total area. a Effective area after considering the clustering threshold.



the focal peatland. To determine prime breeding habitats for the Palm Warbler, we showed a random series of 175 pictures of all 13 habitat types used in the classification procedure to an expert (i.e., A. Desrochers) and asked the latter whether the warbler would occur or not in the habitat depicted. Habitats were designated as prime breeding habitat when  $\geq 80\%$  of the pictures of each habitat type were classified as warbler habitat by the expert. Prime breeding habitats included H5, H9, H10, and H12; see Table 1. We consider that variables (2) and (3) indicate the level of isolation of a focal peatland.

The logistic regression model used to predict the probability of occurrence of the Palm Warbler was chosen based on an information-theoretic approach (Burnham and Anderson, 2002). First, we selected a set of eight candidate models for which we had a biological rationale (Table 4). We then calculated the second-order Akaike criterion index ( $AIC_c$ ) for each of the candidate models. The model with the lowest  $AIC_c$  is considered to be the model that approximates best the information contained in the data, relative to the other candidate models and given a trade off between bias and variance (Burnham and Anderson, 2002). Using the  $AIC_c$  values, we calculated the Akaike weight ( $w_i$ ) of each candidate model (Table 4). These weights indicate the likelihood of the models given the data (Burnham and Anderson, 2002). The best model identified based on these measures was model 3 in Table 4. According to this model, the Palm Warbler occurrence was best predicted by the area of the peatland and the amount of prime breeding habitats within 5 and 10 km from that peatland (see Table 4 for more details). As recommended when the objective is prediction, we calculated model-averaged parameters and their unconditional standard errors based on the Akaike weights for each of the variables appearing in the initial set of candidate models (Burnham and Anderson, 2002, pp. 150–164). The predictions based on such model-averaged estimates are typically more robust than when based on a single, best model (Burnham and Anderson, 2002). The regres-

sions were fitted using the GENMOD procedure of SAS 8.01, with a logit link function and binomial errors (SAS Institute, 1993). The proportion of the peatland covered while searching for the warbler (log-transformed) was used as an offset variable in the model to control for its effect on the likelihood of detecting the warbler. We performed the model selection after checking that the global model (i.e., #8 in Table 4, Nagelkerke  $R^2 = 0.35$ ) fitted the data properly using the Hosmer-Lemeshow goodness-of-fit test.

### 3. Results

#### 3.1. Representation efficiency of the reserve networks

The total area of the selected reserve networks increased relatively linearly with the representation target (Fig. 3(a)). On the other hand, the number of sites in the selected networks increased at an increasing rate with the representation target (Fig. 3(b)). This was due to the availability of peatlands that could be selected. Indeed, 52% of the 629 peatlands were  $< 10$  ha, while 21% ranged 10–20 ha, and 20% ranged 20–100 ha. Only 27 (4%) peatlands covered 100–200 ha, and a mere 15 (2%) were  $> 200$  ha; the largest peatland being 756 ha. Since large peatlands tended to be selected first to minimize the number of sites to preserve, increasing the representation target required the inclusion of numerous smaller sites in the networks. This is also reflected in the mean area of sites within selected networks, which first increased from 331 to 418 ha (averaged across habitat-clustering thresholds) as the representation target went from 1% to 2%, but decreased from 368 to 126 ha as the representation target increased to 50% (Fig. 3(c)).

When forcing the algorithm to include peatlands showing increasingly larger patches of habitats, larger reserve networks (both in terms of area and number of sites) were needed to achieve the same representation target (Fig. 3(a) and (b)). This effect was stronger at large representation targets, especially

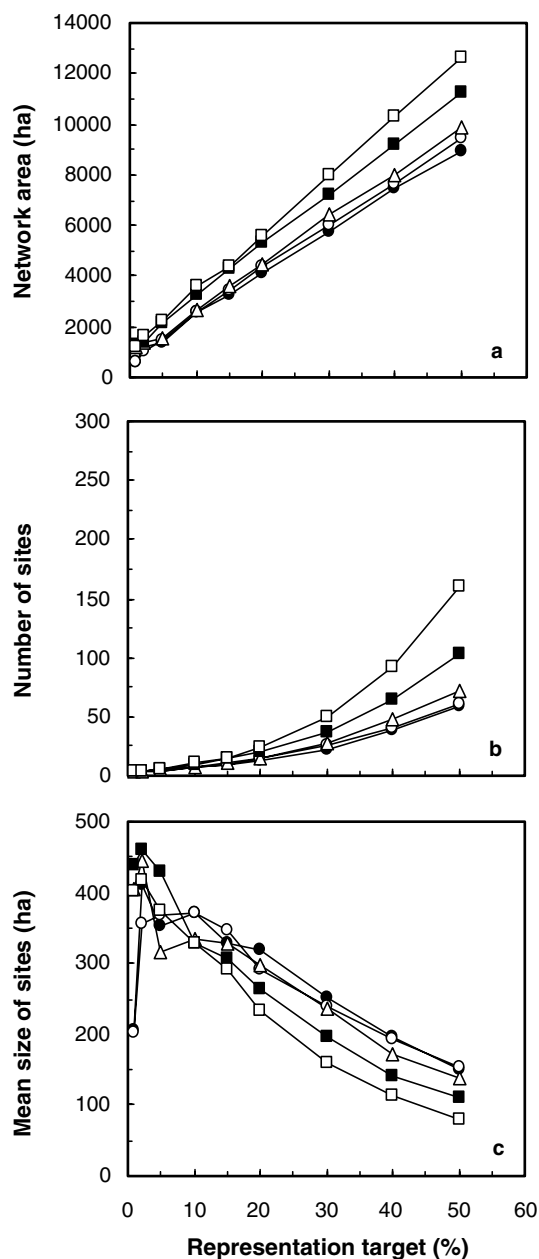
**Table 4 – Logistic regression models ( $n = 61$ ) used to predict the probability of occurrence of the Palm Warbler within peatlands of the reserve networks**

Model <sup>a</sup>	Deviance	df	$AIC_c^b$	$\Delta_i$	$w_i$
1. AREA ISOL5KM ISOL10KM	25.6	57	34.3	6.2	0.02
2. AREA ISOL5KM ISOL10KM ISOL5KM*ISOL10KM	23.7	56	34.8	6.7	0.02
3. AREA ISOL5KM ISOL10KM AREA*ISOL5KM ISOL5KM*ISOL10KM	14.6	55	28.1	0.0	0.51
4. AREA MPS ISOL5KM ISOL10KM	25.2	56	36.2	8.1	0.01
5. AREA MPS ISOL5KM ISOL10KM ISOL5KM*ISOL10KM	23.7	55	37.2	9.1	0.01
6. AREA MPS ISOL5KM ISOL10KM AREA*ISOL5KM ISOL5KM*ISOL10KM	13.0	54	29.1	1.0	0.32
7. AREA MPS ISOL5KM ISOL10KM AREA*MPS ISOL5KM*ISOL10KM	23.6	54	39.8	11.6	0.00
8. AREA MPS ISOL5KM ISOL10KM AREA*MPS AREA* ISOL5KM ISOL5KM*ISOL10KM	12.4	53	31.2	3.0	0.11

The model with the lowest  $AIC_c$  is considered to be the model that approximates best the information contained in the data, relative to the other candidate models and given a trade off between bias and variance (Burnham and Anderson, 2002). The Akaike weight ( $w_i$ ) indicates the likelihood of the models given the data (Burnham and Anderson, 2002).

a Main explanatory variables include: (1) the area of the peatland (AREA), (2) the area of prime breeding habitats for the Palm Warbler within 5 km of the focal peatland centroid minus the area of prime breeding habitats found within the focal peatland (ISOL5KM), (3) the area of prime breeding habitats for the Palm Warbler within 10 km of the focal peatland centroid minus the area of prime breeding habitats found within 5 km of the focal peatland centroid (ISOL10KM), and (4) the mean patch size of prime breeding habitats within the focal peatland (MPS). All variables are in hectares. The proportion of the peatland covered while searching for the warbler (log-transformed) was used as an offset variable in the model.

b Multimodel inference was based on the second-order Akaike criterion index ( $AIC_c$ ).  $\Delta_i$  is equal to the  $AIC_c$  of model  $i$  minus the lowest  $AIC_c$  of the set of candidate models. This quantity is then used to derive the Akaike weights ( $w_i$ ).



**Fig. 3 – Representation efficiency of reserve networks. The different lines represent the five habitat-clustering thresholds used for constraining the site-selection algorithm (percentiles: 25th = ○; 50th = ●; 75th = △; 90th = ■; 95th = □). These thresholds refer to the minimal patch size for a habitat type to be eligible to the selection process (see Table 2).**

when the latter were  $\geq 30\%$ . Surprisingly, increasing the habitat-clustering threshold led on average to the inclusion of smaller sites within networks, especially when the representation target was  $>10\%$  (Fig. 3(c)). This trend resulted from the fact that large patches of habitat H8 occurred mainly within small peatlands. Indeed, when present in large peatlands, this habitat (H8) was mostly found in small patches located at the fringe of the sites. With larger clustering thresholds, these small, marginal patches of H8 were filtered out and thereby

prevented the peatlands containing them to contribute to the representation target.

### 3.2. Palm Warbler occurrence

According to the model-averaged parameter estimates, the probability of occurrence of the Palm Warbler increases rapidly with the area of peatlands, especially when the amount of prime breeding habitats found regionally is high, and vice versa. This leads to the situation where the Palm Warbler is very unlikely to be found in small ( $<20$  ha), isolated peatlands (see Table 5 for the parameter estimates). Interestingly, the probability of occurrence of the Palm Warbler is expected to increase more rapidly with the area of peatlands in sites with small patches of prime habitats than in sites with large patches of prime habitats. Under average conditions, the probability of occurrence of the Palm Warbler decreases with the mean patch size of prime habitats until the area of the peatland reaches  $>50$  ha, when the probability of occurrence tends towards one independently of the size of the patches of prime habitats.

Based on the results above, the mean probability of occurrence per site of the Palm Warbler was higher in scenarios where the reserve networks were assumed to remain surrounded by non-selected peatlands (Fig. 4(a)). Indeed, when simulating that non-selected peatlands were strongly altered or destroyed, the mean probability of occurrence per site was severely reduced, especially at small representation targets because of isolation effects (Fig. 4(b)). Yet, the mean probability of occurrence per site decreased slightly at large representation targets when non-selected peatlands were kept unaltered (Fig. 4(a)). This was caused by the necessity of including small sites that are unlikely to be colonized by the Palm Warbler in the networks (Fig. 3(c)). On the contrary, the mean probability of occurrence per site increased with the representation target when non-selected sites were considered strongly altered or destroyed (Fig. 4(b)). In this case, the increase in regional availability of prime breeding habitats overcompensated the negative effects of including smaller sites in the networks.

Constraining the site-selection algorithm to select peatlands comprising larger patches of habitats also influenced the mean probability of occurrence per site of the Palm Warbler (Fig. 4). In scenarios where non-selected peatlands were considered unaltered, selecting sites with larger patches of habitats decreased the mean probability of occurrence of the Palm Warbler at representation targets  $>20\%$  (Fig. 4(a)). This resulted from the inclusion of numerous small sites within the networks (Fig. 3(c)). The regional availability of prime breeding habitats around selected peatlands clearly could not compensate for the reduction in peatland area (Fig. 4(a)). Despite the decrease in mean probability of occurrence per site, selecting peatlands with larger patches of prime habitats caused more peatlands to be included in the networks (Fig. 3(b)), and in turn, to a greater expected number of sites where the Palm Warbler should occur (Fig. 4(c)). This positive effect augmented at an increasing rate with the representation target. Finally, when the peatlands located outside selected networks were considered strongly altered or destroyed, selecting peatlands with larger patches of habitats also had a beneficial effect on the number of expected



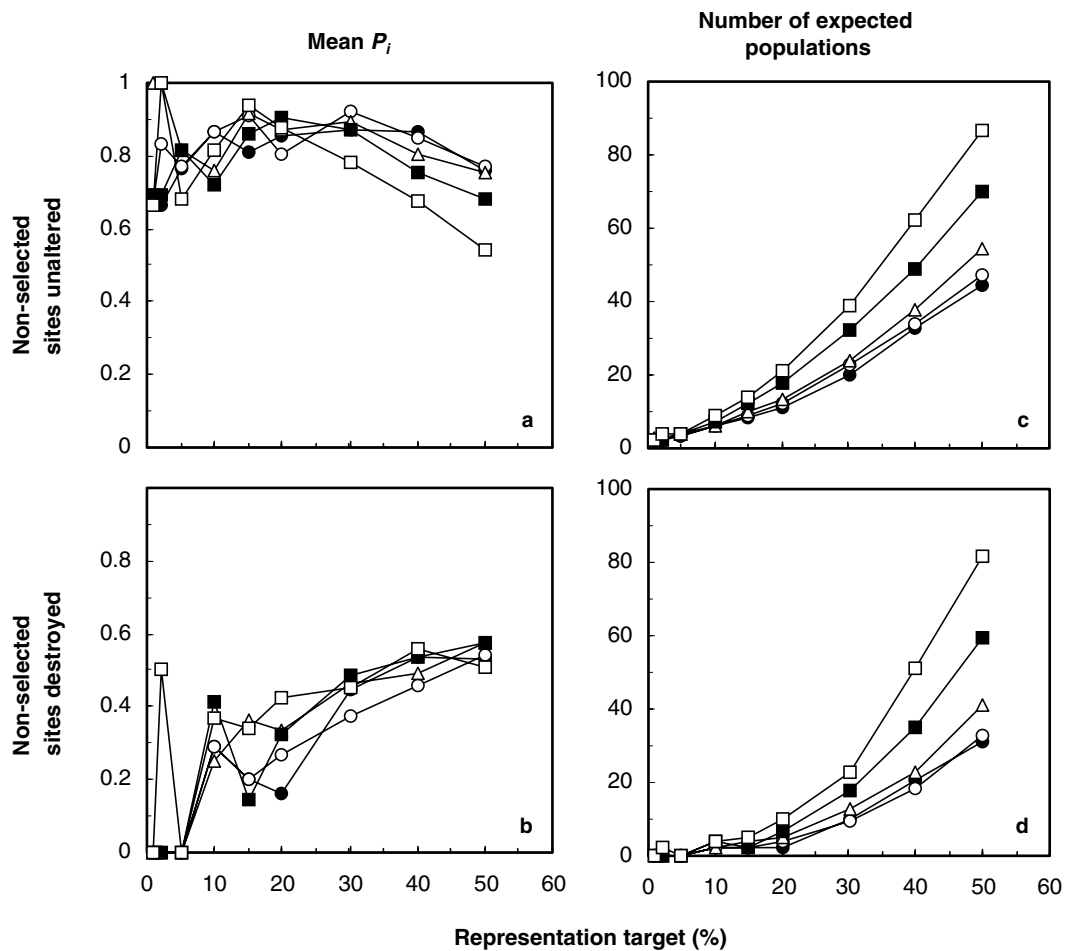
**Table 5 – Range of the main explanatory variables and parameter estimates of the logistic regression model (n = 61) used to predict the probability of occurrence of the Palm Warbler within peatlands of the reserve networks**

Variable <sup>a</sup>	Minimum (ha)	Maximum (ha)	Parameter estimates <sup>b</sup>	SE <sup>c</sup>
Intercept	–	–	–7.5366	2.5522
AREA	5.9	756.0	–0.0085	0.0420
MPS	0.0	4.3	–2.4694	2.3940
ISOL5KM	0.1	269.3	0.0178	0.0652
ISOL10KM	0.8	328.1	0.0657	0.0375
AREA*MPS	–	–	0.0170	0.0266
AREA*ISOL5KM	–	–	0.0072	0.0050
ISOL5KM*ISOL10KM	–	–	–0.0018	0.0011

a Main explanatory variables include: (1) the area of the peatland (AREA), (2) the area of prime breeding habitats for the Palm Warbler within 5 km of the focal peatland centroid minus the area of prime breeding habitats found within the focal peatland (ISOL5KM), (3) the area of prime breeding habitats for the Palm Warbler within 10 km of the focal peatland centroid minus the area of prime breeding habitats found within 5 km of the focal peatland centroid (ISOL10KM), and (4) the mean patch size of prime breeding habitats within the focal peatland (MPS). All variables are in hectares. The proportion of the peatland covered while searching for the warbler (log-transformed) was used as an offset variable in the model.

b Model averaged parameters calculated according to Eq. (4.1) (Burnham and Anderson, 2002, p. 150).

c Unconditional standard errors calculated according to Eq. (4.9) (Burnham and Anderson, 2002, p. 162).



**Fig. 4 – Incidence (mean  $P_i$  = mean probability of occurrence per site) and expected number of populations of the Palm Warbler in reserve networks. These were contrasted under the situations where the non-selected sites were either considered unaltered or destroyed. The different lines represent the five habitat-clustering thresholds used for constraining the site-selection algorithm (percentiles: 25th = ○; 50th = ●; 75th = △; 90th = ■; 95th = □). These thresholds refer to the minimal patch size for a habitat type to be eligible to the selection process (see Table 2).**

populations (Fig. 4(d)). Indeed, a greater number of peatlands ensured a certain regional availability of prime breeding habitats across the networks. This beneficial effect was, however, less important than in unaltered landscapes, especially at representation targets <30% where the number of peatlands with Palm Warblers remained very low (Fig. 4(c) and (d)).

#### 4. Discussion

This study has brought some significant insights on the importance of considering within-site habitat configuration when selecting reserve networks. Forcing a reserve-selection algorithm that minimized the number of sites to preserve to choose peatlands with habitats clumped into larger patches, led to larger networks both in terms of total area and total number of sites. This trend was driven by the larger extent of each habitat type that was not eligible to the reserve selection process. More sites, and thus more area, were then needed to reach a given representation target for each type of habitat. This increase in the number of sites and total area of networks was more severe at high representation targets. One could have expected that habitat patch size would be correlated with peatland area, a relation that would have forced the algorithm to select larger peatlands when larger habitat-clustering thresholds were targeted for each habitat type. This was not the case as the mean area of peatlands was lower for higher thresholds when the representation target was  $\geq 10\%$ ; a result caused by the lack of large peatlands and the fact that large patches of some habitat types mostly occurred in small peatlands. These trends resulted from the site-specific characteristics of the peatland archipelago under study and are thus likely to be different for other systems or regions.

In order to evaluate the benefits of taking within-site habitat configuration into account, we also assessed its potential influence on the incidence of an area and isolation-sensitive, peatland bird species within the selected reserve networks. At high representation targets, increasing the habitat-clustering threshold decreased the mean probability of occurrence per site of the Palm Warbler through the selection of smaller sites. As large patches of certain habitat types only occurred in small peatlands, more sites had to be included in the networks to reach a given representation target. This increase in the number of sites limited isolation effects and also led to a greater number of sites in which the Palm Warbler was likely to occur. Imposing habitat-clustering thresholds can therefore influence the incidence of species via their consequence on the physical attributes of the selected reserve networks – including the area, isolation level, and the number of selected sites composing the network.

Another highlight of our study concerns the role of non-selected sites for the occurrence of species within reserve networks. Non-selected sites contribute to the regional availability of habitats where individuals can take refuge or from where individuals can colonize already protected sites (Hanski, 1999; Cabeza and Moilanen, 2001). Depending on the spatial distribution of sites, non-selected sites are likely to be particularly determinant for isolation-sensitive species such as the Palm Warbler. We found that the mean probability of occurrence per site of this species was higher in scenarios where we assumed that non-selected peatlands remained unaltered.

Accordingly, the impact of considering non-selected peatlands as being altered or destroyed lessened when representation targets were raised. Indeed, even if small sites had to be incorporated into the reserve networks at high representation targets, the selected sites contributed to the regional availability of peatland and promoted Palm Warbler occurrences. Our findings are consistent with the results of a spatially explicit, simulation study by Cabeza and Moilanen (2003). These authors showed that the populations of a large array of fictive species within selected networks survive longer when un-selected sites remained unaltered through time.

We emphasize again that we did not aim at identifying the reserve network most likely to ensure the long-term persistence of the Palm Warbler within our study area. We rather sought to investigate the consequences of considering within-site habitat configuration when selecting reserve networks representative of all peatland habitats and their associated biodiversity. We were hence interested to explore the influence of within-site habitat configuration on the physical characteristics of the networks, as well as on the probability of occurrence of a bird that is strictly associated to peatland habitats within our study area. Finding the ‘best’ network for a given species requires a focus on its preferred habitats and the use of an optimization process leading to the network with the highest likelihood of long-term persistence as established by an habitat or a (meta)population model (see Araújo and Williams, 2000; Moilanen and Cabeza, 2002). Although such an approach should be advocated, especially if applied to established umbrella species (Roberge and Angelstam, 2004), it remains that the data necessary to use it are difficult to obtain and thus rarely available.

Our study stresses the importance of knowing how the site-specific characteristics of potential reserves (e.g., area, isolation, mean patch size of targeted habitats, targeted habitat diversity) are intercorrelated as changing the value of one reserve-selection constraint can lead to unexpected, and potentially negative, outcomes. Indeed, imposing a habitat-clustering threshold can not only affect the persistence of species that depend on a certain type of within-site habitat configuration, but also the species for which within-site configuration may be unimportant. For instance, the statistical model used to predict the occurrence of the Palm Warbler did not contain variables directly linked to within-site configuration. Yet the incidence of this species within the reserve networks was strongly affected by the habitat-clustering thresholds imposed on the reserve-selection process. Our assessment of the impact of within-site habitat configuration on both the physical and the functional attributes of reserve networks was nevertheless limited by the lack of knowledge regarding how and which within-site configuration factors affect the incidence or abundance of peatland plants and animals. We believe that more quantitative work will have to be conducted on processes such as landscape/habitat complementation and supplementation (*sensu* Dunning et al., 1992) before general principles or guidelines be established for designing reserve networks. Once such information will be available, it will also be easier to identify meaningful within-site patches of habitat that contribute to the representation target using geographical site-selection procedures (see Church et al., 2003). Meanwhile, systematic methods that

use algorithms to identify conservation priorities should be complemented with expert knowledge on taxonomic, ecological, evolutionary and socio economic aspects of the conservation problem at hand (Cowling et al., 2003). In our study region for example, ornithologists have recently discovered that peatlands are breeding habitats for the Upland Sandpiper, *Bartramia longicauda* (Calmé and Haddad, 1996), a bird species at risk in North America. This bird seems to be occurring only in large peatlands that contain large open areas. This type of expert knowledge should be incorporated at the beginning of the decision process. Detecting the sensitivity of particular species to habitat-clustering level and incorporating their specific needs into the selection process is an approach that deserves more attention. And this, especially since incorporating both land classes and species data simultaneously in the selection process increases only slightly the size of reserve networks (Lombard et al., 2003).

### Acknowledgements

We are indebted to S. Calmé and A. Desrochers for allowing us to use their data on the patch-occupancy pattern of the Palm Warbler. We are also grateful to A. Moilanen for helping us programming the site-selection algorithm. A. Desrochers, P. Glaser, M.J. Mazerolle, A. Moilanen, and O. Ovaskainen, provided insightful comments on previous drafts of this paper. This work was supported by le ministère de l'Environnement du Québec (programme PARDE) and by the Province of Québec Society for the Protection of Birds via research grants to MP. MP benefited from FCAR (Québec) and NSERC (Canada) scholarships. MC was supported by the Academy of Finland, research project #45125 and MB benefited from an NSERC postdoctoral fellowship.

### REFERENCES

- Araújo, M.B., 2004. Matching species with reserves – uncertainties from using data at different resolutions. *Biological Conservation* 118, 533–538.
- Araújo, M.B., Williams, P.H., 2000. Selecting areas for species persistence using occurrence data. *Biological Conservation* 96, 331–345.
- Araújo, M.B., Williams, P.H., 2001. The bias of complementarily hotspots toward marginal populations. *Conservation Biology* 15, 1710–1720.
- Bedward, M., Pressey, R.L., Keith, D.A., 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biological Conservation* 62, 115–125.
- Berger, J., 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. *Conservation Biology* 11, 69–78.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*, second ed. Springer, New York.
- Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution* 16, 242–248.
- Cabeza, M., Moilanen, A., 2003. Site selection algorithms and habitat loss. *Conservation Biology* 17, 1402–1413.
- Cabeza, M., Araújo, M.B., Wilson, R.J., Thomas, C.D., Cowley, M.J.R., Moilanen, A., 2004a. Combining probabilities of occurrence with spatial reserve design. *Journal of Applied Ecology* 41, 252–262.
- Cabeza, M., Moilanen, A., Possingham, H.P., 2004b. Metapopulation dynamics and reserve network design. In: Hanski, I., Gaggiotti, O. (Eds.), *Metapopulation Ecology, Genetics, and Evolution*. Academic press, London.
- Calmé, S., Desrochers, A., 1999. Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia* 118, 361–370.
- Calmé, S., Desrochers, A., 2000. Biogeographic aspects of the distribution of bird species breeding in Québec's peatlands. *Journal of Biogeography* 27, 725–732.
- Calmé, S., Haddad, S., 1996. Peatlands: a new habitat for the Upland Sandpiper, *Bartramia longicauda*, in Eastern Canada. *Canadian Field Naturalist* 110, 326–330.
- Calmé, S., Desrochers, A., Savard, J.-P.L., 2002. Regional significance of peatlands for avifaunal diversity in southern Québec. *Biological Conservation* 107, 273–281.
- Camm, J.D., Polaski, S., Solow, A., Csuti, B., 1996. A note on optimal algorithms for reserve site selection. *Biological Conservation* 78, 353–355.
- Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. *Ecological Applications* 11, 961–980.
- Church, R.L., Gerrard, R.A., Gilpin, M., Stine, P., 2003. Constructing cell-based habitat patches useful in conservation planning. *Annals of the Association of American Geographers* 93, 814–827.
- Cowling, R.M., Pressey, R.L., Sims-Castley, R., le Roux, A., Baard, E., Burgers, C.J., Palmer, G., 2003. The expert or the algorithm. – comparison of priority conservation areas in the Cape Floristic Region identified by park managers and reserve selection software. *Biological Conservation* 112, 147–167.
- Csuti, B., Polaski, S., Williams, P.H., Pressey, R.L., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R., Huso, M., Sahr, K., 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80, 83–97.
- Delage, V., Fortin, M.-J., Desrochers, A., 2000. Effets de lisière et d'isolement des habitats d'oiseaux chanteurs dans les tourbières exploitées. *Écoscience* 7, 149–156.
- Desrochers, A., Rochefort, L., Savard, J.-P.L., 1998. Avian recolonization of eastern Canadian bogs after peat mining. *Canadian Journal of Zoology* 76, 989–997.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Freitag, S., Nicholls, A.O., van Jaarsveld, A.S., 1996. Nature reserve selection in the Transvaal, South Africa: what data should we be using? *Biodiversity and Conservation* 5, 685–698.
- Freitag, S., van Jaarsveld, A.S., Biggs, H.C., 1997. Ranking priority biodiversity areas: an iterative conservation value-based approach. *Biological Conservation* 82, 263–272.
- Goward, S.N., Williams, D.L., 1997. Landsat and earth systems science: development of terrestrial monitoring. *Photogrammetric Engineering and Remote Sensing* 63, 887–900.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Harrison, S., Rice, K., Maron, J., 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biological Conservation* 100, 45–53.
- Heijnis, C.E., Lombard, A.T., Cowling, R.M., Desmet, P.G., 1999. Picking up the pieces: a biosphere reserve framework for a fragmented landscape – The coastal lowlands of the Western Cape, South Africa. *Biodiversity and Conservation* 8, 491–496.

- Hinsley, S.A., 2000. The costs of multiple patch use by birds. *Landscape Ecology* 15, 765–775.
- Ibarzabal, J., Morrier, A., 1995. Paruline à couronne rousse. In: Gauthier, J., Aubry, Y. (Eds.), *Les oiseaux nicheurs du Québec: Atlas des oiseaux nicheurs du Québec méridional*. Association québécoise des groupes d'ornithologues, Société québécoise de protection des oiseaux, Service canadien de la faune, Environnement Canada, région du Québec, Montréal, Québec, Canada, pp. 900–903.
- Kerr, J.T., Southwood, T.R.E., Cihlar, J., 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences of the United States of America* 98, 11365–11370.
- Lachance, D., Lavoie, C., 2004. Vegetation of *Sphagnum* bogs in highly disturbed landscapes: Relative influence of abiotic and anthropogenic factors. *Applied Vegetation Science* 7, 183–192.
- Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas plain, South Africa. *Conservation Biology* 11, 1101–1115.
- Lombard, A.T., Cowling, R.M., Pressey, R.L., Rebelo, A.G., 2003. Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. *Biological Conservation* 112, 45–62.
- Lopez, J.E., Pfister, C.A., 2001. Local population dynamics in metapopulation models: implications for conservation. *Conservation Biology* 15, 1700–1709.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Margules, C.R., Nicholls, A.O., Pressey, R.L., 1988. Selecting networks of reserves to maximise biological diversity. *Biological Conservation* 43, 63–76.
- Matlack, G.R., Litvaitis, J.A., 1999. Forest edges. In: Hunter, M.L., Jr. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge.
- McDonnell, M.D., Possingham, H.P., Ball, I.R., Cousins, E.A., 2002. Mathematical methods for spatially cohesive reserve design. *Environmental Modeling and Assessment* 7, 107–114.
- Moilanen, A., Cabeza, M., 2002. Single-species dynamic site selection. *Ecological Applications* 12, 913–926.
- Murcia, C., 1995. Edge effects in fragmented forests: implication for conservation. *Trends in Ecology and Evolution* 10, 58–62.
- Nicholls, A.O., Margules, C.R., 1993. An upgraded reserve selection algorithm. *Biological Conservation* 64, 165–169.
- Noss, R.F., 1996. Ecosystems as conservation targets. *Trends in Ecology and Evolution* 11, 351.
- Önal, H., 2003. First-best, second-best, and heuristic solutions in conservation reserve site selection. *Biological Conservation* 115, 55–62.
- Palmeirim, J.M., 1988. Automatic mapping of avian species habitat using satellite imagery. *Oikos* 52, 59–68.
- Pellerin, S., Lavoie, C., 2000. Peatland fragments of southern Québec: recent evolution of their vegetation structure. *Canadian Journal of Botany* 78, 255–265.
- Poulin, M., Pellerin, S., 2001. La conservation. In: Payette, S., Rochefort, L. (Eds.), *Écologie des tourbières du Québec-Labrador*. Les presses de l'Université Laval, Québec, Canada, pp. 505–518.
- Poulin, M., Rochefort, L., Desrochers, A., 1999. Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. *Applied Vegetation Science* 2, 169–180.
- Poulin, M., Careau, D., Rochefort, L., Desrochers, A., 2002. From satellite imagery to peatland vegetation diversity: how reliable are habitat maps? *Conservation Ecology* 6 (2), 16. Available from: <<http://www.consecol.org/vol6/iss2/art16>>.
- Pressey, R.L., Nicholls, A.O., 1989a. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. *Biological Conservation* 50, 263–278.
- Pressey, R.L., Nicholls, A.O., 1989b. Efficiency in conservation evaluation: scoring versus iterative approaches. *Biological Conservation* 50, 199–218.
- Pressey, R.L., Possingham, H.P., Day, J.R., 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation* 80, 207–219.
- Pressey, R.L., Possingham, H.P., Margules, C.R., 1996. Optimality in reserve selection algorithms: when does it matter and how much? *Biological Conservation* 76, 259–267.
- Richards, J.A., Jia, X., 1999. *Remote Sensing Digital Image Analysis. An Introduction*. Springer, Berlin.
- Roberge, J.M., Angelstam, P., 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18, 76–85.
- Robitaille, A., Saucier, J.-P., 1998. *Paysages régionaux du Québec méridional*. Gouvernement du Québec, Québec city, Québec, Canada.
- Rodrigues, A.S., Cerdeira, J.O., Gaston, K.J., 2000a. Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. *Ecography* 23, 565–574.
- Rodrigues, A.S.L., Gaston, K.J., Gregory, R.D., 2000b. Using presence-absence data to establish reserve selection procedures that are robust to temporal species turnover. *Proceedings of the Royal Society of London B* 267, 897–902.
- Rodrigues, A.S.L., Gregory, R.D., Gaston, K.J., 2000c. Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London B* 267, 49–55.
- Roughgarden, J., Running, S.W., Matson, P.A., 1991. What does remote sensing do for ecology? *Ecology* 72, 1918–1922.
- Rouget, M., 2003. Measuring conservation value at fine and broad scales: implications for a diverse and fragmented region, the Agulhas Plain. *Biological Conservation* 112, 217–232.
- SAS Institute, Inc., 1993. *SAS/STAT Software: The GENMOD procedure*. SAS Technical Report P-243. SAS Institute, Cary, North Carolina, USA.
- Suter, W., Graf, R.F., Hess, R., 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology* 16, 778–788.
- Turpie, J.K., Beckley, L.E., Katua, S.M., 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation* 92, 59–72.
- Underhill, L.G., 1994. Optimal and suboptimal reserve selection algorithms. *Biological Conservation* 70, 85–87.
- Virolainen, K.M., Virola, T., Suhonen, J., Kuitunen, J., Lammi, A., Siikamäki, P., 1999. Selecting networks of nature reserves: methods do affect the long-term outcome. *Proceedings of the Royal Society of London B* 266, 1141–1146.
- Wessels, K.J., Freitag, S., van Jaarsveld, A.S., 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biological Conservation* 89, 21–38.
- Williams, P.H., Araújo, M.B., 2000. Using probabilities of persistence to identify important areas for biodiversity conservation. *Proceedings of the Royal Society of London B* 267, 1959–1966.