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## Nested bird and micro-habitat assemblages in a peatland archipelago

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**Abstract** Biotic assemblages of insular habitats are nested when poor assemblages are subsets of richer ones. Nestedness of species assemblages is frequent and may result from selective extinction or frequent colonization in insular habitats. It may also be created by a nested distribution of habitats among islands or by sampling bias. We sampled 67 isolated peatlands (7–843 ha) in southern Quebec, Canada, to measure nestedness of bird species assemblages among peatlands and assess the habitat nestedness hypothesis. Species and microhabitat assemblages were both strongly nested among peatlands. Whether sites were ranked by species richness, microhabitat richness or peatland area had no effect on nestedness. However, microhabitat nestedness was significantly reduced when sites were sorted by area rather than by microhabitat richness. As expected, if bird-microhabitat associations are responsible for the nested pattern of distribution, we found a positive correlation between the contributions of bird species and microhabitats to individual site nestedness. Nevertheless, microhabitat assemblages were significantly less nested than bird species assemblages, possibly because of frequent recolonization by birds or uneven sampling among sites.

**Key words** Nestedness · Peatland · Bird · Pattern of distribution · Conservation

### Introduction

Subsets of species inhabiting islands or patchily distributed habitats are nested when species assemblages of

species-poor sites are subsets of all species assemblages of richer sites. Nested patterns of species occurrence are common among a wide variety of isolated habitats, and for various taxa, e.g. terrestrial and flying mammals, birds, reptiles, arthropods and plants (Cook 1995; Boecklen 1997; Wright et al. 1998).

Four hypotheses can account for nested patterns of species distribution (Worthen 1996; Cook and Quinn 1998; Wright et al. 1998): (1) passive sampling, (2) selective extinction, (3) selective colonization and (4) habitat nestedness. Passive sampling simply reflects the fact that abundant species have a higher probability of being sampled than rare ones. If one draws species (with replacement) from a population characterized by strong differences in abundance to form a number of samples varying in size, then nestedness is likely to appear (Cutler 1994). Common/abundant species will occur in most samples, whereas rare species will be drawn mainly in the largest samples. Several authors have stressed that data should be tested for passive sampling prior to other hypotheses (Andrén 1994; Worthen 1996; Worthen et al. 1998; Wright et al. 1998). The selective-extinction hypothesis is based on the assumption that in systems experiencing species loss or ‘relaxation’ sensu Patterson and Atmar (1986), species disappear from sites in a predictable sequence (Patterson 1987, 1990), without replacement by nearby colonists. Indeed, species with large minimum-area requirements or species found in small populations have higher extinction risks (Connor and McCoy 1979; Simberloff and Levin 1985). The selective-extinction hypothesis predicts that area is the main factor explaining species occurrence (Lomolino et al. 1989). According to the selective-colonization hypothesis, a differential in dispersal ability will lead strong dispersers to occupy most sites because local extinction will be quickly reversed for these species, whereas poor dispersers will be encountered only in sites where extinction rates are low, i.e. the largest ones (Cook and Quinn 1995). If selective colonization occurs, “island” area should be an important determinant of bird species occurrence, as with the previous hypothesis. In contrast with the pre-

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vious hypothesis however, species common in the vicinity of habitat islands should be well represented within those islands. Finally, the habitat nestedness hypothesis (Cook and Quinn 1995) considers the nestedness of species assemblages as a consequence of their close association to habitats which have a nested distribution. If the latter hypothesis is true, then habitat nestedness should be of the same magnitude as bird species nestedness. Species nestedness, as measured by Patterson and Atmar's (1986)  $N$ , should also not be different when sites are ranked by habitat richness or species richness. Figure 1 illustrates a hypothetical case where habitats among sites are perfectly nested. Each habitat supports a set of species, among which some are shared with other habitats, while others are specialists of the habitat. Subsets of species in this case exhibit a nested pattern of occurrence among sites as shown in the matrix on the right. Recently, some authors (Cutler 1994; Cook and Quinn 1995; Worthen 1996; Wright et al. 1998) stressed that few studies (Cody 1983; Simberloff and Martin 1991) have considered the role of habitat on nestedness of species subsets despite its theoretical and practical interest.

Peatlands of southern Canada are patchily distributed, thus forming a natural "archipelago" in a matrix of forests, built areas and fields. Peatlands isolated from the surrounding drainage basin, for peat accumulation causes the water table to rise locally, are called ombrotrophic peatlands or bogs (Zoltai and Vitt 1995). Nutrient input is reduced to rainfall, severely limiting the growth of vascular plants. Finally, the vegetation structure of peatlands is generally stable over many decades (Damman 1986). Therefore, bird species assemblages in peatlands are presumably not affected by plant succession over short time scales, which facilitates the study of nestedness of animal species assemblages.

In this paper, we document nestedness of bird species and microhabitats among peatlands, and we evaluate bird-microhabitat associations within peatlands, and

relationships between species richness, microhabitat richness and peatland area. We assess the selective-extinction, selective-colonization, passive-sampling and habitat nestedness hypotheses.

## Materials and methods

### Study area

The study area was located in southern Quebec, within a region homogeneous in terms of its geologic and climatic history. In this region, most peatlands are located in the Saint Lawrence River valley, and belong to the continental semiforested bog type (Glaser and Janssens 1986). We sampled 67 ombrotrophic peatlands, i.e. half the total number of peatlands present in the region. The most distant peatlands were separated by 160 km, the closest by 30 m, and peatland areas ranged from 7.4 to 843 ha. We also sampled open habitats surrounding 1 km of each peatland, to assess the extent to which species were confined to peatlands. These habitats included hayfields, pastures, abandoned farmlands, recent clear-cuts, grain crops, fields of clover, food crops, a cranberry farm and a young plantation.

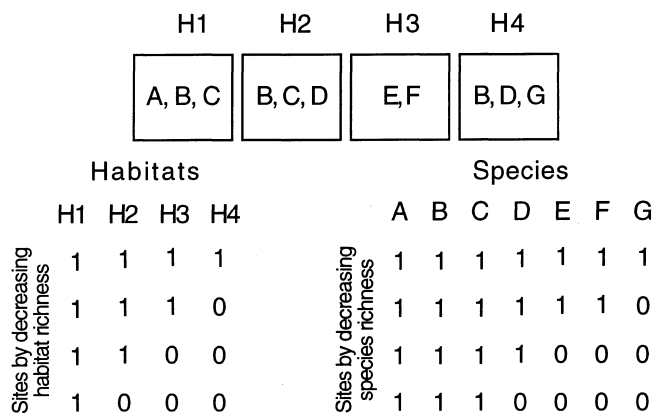
### Bird sampling

Two methods were used to sample birds within peatlands: transect lines for exhaustive species lists and fixed-radius point counts for microhabitat-specific abundance estimates (Ralph et al. 1993). Point counts had a 100-m radius and lasted 10 min, during which all birds seen or heard were recorded. We placed one point count station in each type of microhabitat we defined. Thus, the number of point counts in one peatland depended on both number and size of microhabitats (minimum 3 ha) found in a given peatland. We also made one or two point counts in open habitats surrounding each peatland ( $n = 56$ ). Along transect lines, all birds seen or heard were recorded up to 100 m from the line. The total length of transect lines in each peatland was proportional to peatland area, but the ratio of area sampled to peatland area was negatively related to area (unpublished data) and thus was accounted for in analyses dealing with peatland area. Transect lines and point counts were located at least 150 m from peatland edges. Thus, a 50-m-wide buffer zone was not sampled, to avoid observations of birds in or near the edge of adjacent habitats (mostly forest).

We recorded birds flying over peatlands only if they were less than 10 m aboveground. We considered only species breeding during the sampling period, i.e. 4 June–14 July. Thus, we excluded cedar waxwings (*Bombycilla cedrorum*), evening grosbeaks (*Coccothraustes vespertinus*), and American goldfinches (*Carduelis tristis*). Also, species whose territories may encompass the peatland and the surroundings were excluded. This was the case of Icteridae (except red-winged blackbird, *Agelaius phoeniceus*), and raptors (except for northern harrier, *Circus cyaneus*). We retained ubiquitous species but excluded species not reported to breed in peatlands (Gauthier and Aubry 1995). Twenty-two species were kept for analyses. For each peatland, we estimated species richness from both transect and point count data. While transects documented species not found in point counts, the converse was not true. Species abundances were calculated from transect data. For most species, especially abundant ones, individuals of pairs were often seen together, so abundances were estimated for pairs. We assume that in each peatland, few nesting species from the set used for analyses were undetected.

### Vegetation mapping

We established ten classes of microhabitats found in peatlands in the study area (Table 1). Classes were based mainly on height and



**Fig. 1** Hypothetical case of nestedness of species subsets caused by nestedness of microhabitats. The four microhabitats  $H1$ ,  $H2$ ,  $H3$  and  $H4$  share common species ( $B$ ,  $C$ ,  $D$ ), but also support specialists ( $A$ ,  $E$ ,  $F$ ,  $G$ ).  $H1$  is found in sites  $S1$ ,  $S2$ ,  $S3$  and  $S4$ ;  $H2$  in sites  $S1$ ,  $S2$  and  $S3$ ;  $H3$  in sites  $S1$  and  $S2$ ; and  $H4$  is found only in  $S1$

**Table 1** Classes of microhabitats found in peatlands in southern Quebec [BS black spruce (*Picea mariana*), L larch (*Larix laricina*), B old-field birch (*Betula populifolia*)

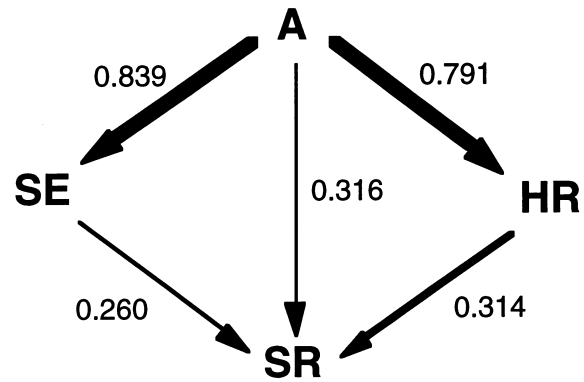
Class	Tree cover (%)	Dominant-tree height (m)	Percent of peatlands	Remarks
1	< 5	Variable	38.8	BS, L, B, separately or together
2	< 20	< 5	77.6	BS, L, B, separately or together
3	< 15	> 5	47.8	BS, L, B, separately or together
4	< 50	< 5	91.0	BS, L, B, separately or together
5	< 40	> 5	83.6	BS, L, B, separately or together
6	20–60	< 5	49.3	Clumps of layers of BS, sometimes with scattered L
7	> 60	> 2	98.5	BS sometimes with L
8	Variable	Variable	31.3	Fen-lag: open water, vegetation dense and diverse
9	Variable	Variable	34.3	Fen: open water, shrubs usually present and diverse
10	> 80	> 10	35.8	Forest soil

density of trees (classes 1–5, 7 and 10), but also on spatial arrangement of trees in the case of clumps of black spruce layers (class 6). Classes 8 and 9 (fens) both reflected the presence of open water and more diverse vegetation. As the peatlands we sampled were ombrotrophic, the latter two classes occurred rarely. No effort was made to classify according to floristic communities. Microhabitats are much easier to detect than are particular species of plants, and thus recorded absences of microhabitats were considered reliable.

We photointerpreted recent 1:15,000 aerial photographs using the classes previously described. The minimum size of a microhabitat was about 0.1 ha, and was similar across all microhabitat types. Interpretation was validated in the field by both verifying if classification and limits between microhabitats were correct. This was done for all doubtful cases and along transects for each peatland. Validation was important since interpretation is sometimes difficult due to the low height of the vegetation. Finally, maps obtained were captured in a Geographic Information System in which each microhabitat patch was labelled. Optical distortion on aerial photographs was considered negligible since we used as many photographs as possible, and also because peatlands in the study region have little relief.

#### Bird-microhabitat associations

We evaluated the associations between birds and microhabitats with two-way contingency tables. Cell counts that exhibited large adjusted residuals ( $< -2$  or  $> 2$ ) indicated strong responses to



**Fig. 2** Path diagram of the relationships between species richness (*SR*), microhabitat richness (*HR*), sampling effort (*SE*) and peatland area (*A*). Values of path coefficients are placed along the arrows. Arrows indicate the direction of causality, and their thickness, the strength of the relationships (thick  $P < 0.001$ , medium  $P < 0.01$ , thin  $P < 0.05$ ). Based on  $n = 67$  peatlands

microhabitats (Agresti 1996). The level of rejection of the null hypothesis of no general linear association for each species was corrected by dividing it by the number of species analysed.

#### Relationship between species richness, microhabitat richness, and peatland area

We used confirmatory path analysis to evaluate the relationships between species richness (*SR*), microhabitat richness (*HR*), sampling effort (*SE*) and peatland area (*A*). This analysis has the advantage over correlations in that causal links between variables can be clearly specified. The model specified used structural equations (Bentler 1985) that described the relationships between the variables involved in the theoretical model. Path coefficients were calculated between *A*, *SE*, *HR*, and *SR* linked together according to the path diagram (Fig. 2). These coefficients indicate the strengths of associations as well as their direction. We normalized distributions of *HR* and *A* by transforming *HR* to its squared-root and *A* to its natural logarithm. For each variable, we subtracted its mean from each observation to control for multicollinearity (Kleinbaum et al. 1988). The highest condition index after this procedure was applied was 4.2, indicating that multicollinearity was low.

#### Passive sampling

We used the random placement model (Coleman 1981; Coleman et al. 1982) to test whether the distribution of individuals of bird species across peatlands was random. The expected species-area curve generated under the hypothesis of random individual distribution was obtained using abundance data. Species richness was plotted against this curve and deviation from the expectation was tested using chi-square. The hypothesis of random distribution should be rejected if more than one-third of the points lie outside one standard deviation of the expected curve, and if the points are not evenly distributed about it (Coleman et al. 1982).

#### Nestedness

We calculated nestedness of bird and microhabitat assemblages with the *N* index initially developed by Patterson and Atmar (1986). The *N* index counts the number of “unexpected” absences of species/microhabitats in all sites with more species/microhabitats than the poorest one in which they are found (Patterson and Atmar 1986). Thus, an *N* value of zero describes perfect nestedness.

Moreover,  $N$  allows the decomposition of individual species scores. Patterson and Atmar's  $N$  also allows testing nestedness with respect to any site measure (e.g. area, species richness) using a routine that ranks sites according to the measure. We calculated bird species nestedness by ranking sites by decreasing bird species richness ( $N_{sr}$ ), as does the 'RANDOM0' procedure of Patterson and Atmar (1986). We also ranked sites by microhabitat richness ( $N_{hr}$ ), and peatland area ( $N_a$ ). Besides Patterson and Atmar's  $N$  index, we used a standardized form of  $N$ , PNO (Wright et al. 1998), which allows comparisons between matrices of different sizes. It is calculated according to the formula:

$$PNO = 100 \times (EN0 - N)/EN0$$

where EN0 is the expected  $N$  under an equiprobable species null hypothesis (Wright and Reeves 1992).

It is difficult to assess analytically the standard error of  $N$  and PNO indices; we therefore used a bootstrap procedure (Efron and Tibshirani 1993) to estimate standard errors of these indices. The bootstrap procedure sampled 67 peatlands (and their associated species and microhabitat lists) with replacement from the 67 peatlands visited, calculated the  $N$  and PNO indices, and repeated these steps 1000 times to obtain a sampling distribution from which estimates and their standard error were calculated. The program for the bootstrap procedure was written in Excel Visual Basic and is available from A. Desrochers upon request.

## Results

Bird species assemblages of peatlands were strikingly different from assemblages found in nearby habitats. Based on 1009 occurrences of 20 species across all stations, 11 species were found more frequently in peatlands than in nearby habitats, 3 were found only in peatlands, while 4 species were more strongly associated with nearby habitats (Table 2). Five other species were statistically equally present in peatlands and open nearby habitats of which only the savannah sparrow occurred frequently (> 50%) in both habitats. All other common species in peatlands, i.e., Lincoln's sparrow, palm warbler, Nashville warbler, white-throated sparrow, common yellowthroat and hermit thrush, occurred far more frequently in peatlands than in nearby open habitats.

### Bird-microhabitat associations

Associations of bird species with microhabitats were stronger for frequent bird species (occurrence > 50%) than for other species, with the notable exception of swamp sparrows (Table 3). Six of the seven most common species in peatlands were closely associated with the most common microhabitats characterized by short trees (< 5 m) and a tree cover of at least 20%. These species avoided open habitats or semi-open habitats with tall trees (> 5 m). By contrast, commonly occurring savannah sparrows were strongly associated with microhabitats 1 and 2 (open), while they avoided microhabitats 4, 5 and 7 (more trees). Less common species (relative frequency between 15% and 45%), were associated with one microhabitat type, but did not avoid any particular microhabitat (Table 3). American robins, eastern kingbirds and red-winged blackbirds had no preferences for any microhabitat.

Species richness, microhabitat richness, and peatland area

Bird species richness, microhabitat richness, peatland area and sampling effort were strongly and significantly correlated (Table 4). The linear relationship between bird species richness and the three other variables combined was highly significant (adjusted  $R^2 = 0.66$ ,  $n = 67$ ,  $P \leq 0.0001$ ). The fit of the theoretical path model described in Fig. 2 was satisfactory (chi-square = 0.95,  $df = 1$ ,  $P > 0.33$ ). For all endogenous variables, i.e. variables whose variability is assumed to be causally affected by other variables in the model, the amount of variance explained was high ( $R^2 > 0.62$ ). All path coefficients were significant according to  $t$ -values, and standardized coefficients were non-trivial in magnitude (i.e. > 0.05; Billings and Wroten 1978) (Fig. 2). Peatland area strongly influenced microhabitat richness, and the area sampled by peatland was highly area dependent (for both  $P < 0.001$ ). Meanwhile, species richness depended on HR ( $P < 0.01$ ),  $A$  ( $P < 0.05$ ), but also on SE ( $P < 0.05$ ), suggesting that passive sampling influenced observed species richness.

### Passive sampling

Half of the points lay within  $\pm 1$  SD from the expected species-area (Fig. 3). Only 18 of the 67 experimental points lay above the curve, and several of those below the curve departed strongly from it. However, distribution of bird species according to peatland area did not strongly differ from random expectations (chi-square = 3.5,  $df = 1$ ,  $P = 0.06$ ). This result is rather inconclusive, largely due to the nature of our abundance estimates, which were based on single-visit censuses. Kouki and Järvinen (1980) found that in Finnish peatlands, 60% of the bird breeding population is recorded on a single-visit. Because their censuses included forested areas where detection rates are lower than in open areas, we believe that the bias was lower in our study which did not include such forested areas. Nonetheless, our underestimation of bird abundance lowered the expected species richness curve, thus making it closer to observed species richnesses. Although we cannot reject it, we conclude that there was only weak evidence for a passive-sampling effect.

### Nestedness

Species and microhabitat assemblages were strongly nested among peatlands. Both matrices of species and microhabitats present in the 67 sites can be viewed at the Peatland Ecology Research Group's Web site (<http://www.fsa.ulaval.ca/gret-perg/index.html>). The bird species  $\times$  sites matrix was significantly nested regardless of site ranking method (Table 5). Five species were found only in the 20 species-richest peatlands: common

**Table 2** Bird species found in peatlands and sites of open vegetation in the vicinity (< 1000 m) of each peatland. Only species recorded in at least ten sites are shown. Species were sorted according to their preference for bogs or surrounding open sites

Common name	Scientific name	Code	Percent of peatlands plots (n = 67)	Percent of nearby plots (n = 56)	Chi-square	P <sup>a</sup>
Lincoln's sparrow	<i>Melospiza lincolni</i>	LISP	92.5	1.8	100.5	**
Palm warbler	<i>Dendroica palmarum</i>	PAWA	88.1	0.0	94.8	**
Nashville warbler	<i>Vermivora ruficapilla</i>	NAWA	86.6	7.1	77.0	**
White-throated sparrow	<i>Zonotrichia albicollis</i>	WTSP	91.0	14.3	73.0	**
Common yellowthroat	<i>Geothlypis trichas</i>	COYE	100.0	30.4	68.3	**
Hermit thrush	<i>Catharus guttatus</i>	HETH	70.1	1.8	59.9	**
Alder flycatcher	<i>Empidonax alnorum</i>	ALFL	43.3	3.6	25.5	**
Yellow-rumped warbler	<i>Dendroica coronata</i>	YRWA	19.4	0.0	12.1	**
Northern harrier	<i>Circus cyaneus</i>	NOHA	34.3	8.9	11.2	**
Magnolia warbler	<i>Dendroica magnolia</i>	MAWA	20.9	1.8	10.4	**
Swamp sparrow	<i>Melospiza georgiana</i>	SWSP	16.4	0.0	10.1	**
Eastern kingbird	<i>Tyrannus tyrannus</i>	EAKI	28.3	10.7	5.9	n.s.
American robin	<i>Turdus migratorius</i>	AMRO	35.8	23.2	2.3	n.s.
Tree swallow	<i>Tachycineta bicolor</i>	TRSW	22.4	14.3	1.3	n.s.
Savannah sparrow	<i>Passerculus sandwichensis</i>	SASP	67.2	69.6	0.09	n.s.
Barn swallow	<i>Hirundo rustica</i>	BASW	4.5	19.6	6.9	n.s.
Song sparrow	<i>Melospiza melodia</i>	SOSP	38.8	66.1	9.1	*
Red-winged blackbird	<i>Agelaius phoeniceus</i>	RWBL	17.9	42.9	9.2	**
Killdeer	<i>Charadrius vociferus</i>	KILL	0.0	17.9	13.0	** <sup>b</sup>
Bobolink	<i>Dolichonyx oryzivorus</i>	BOBO	1.5	28.6	18.8	**

<sup>a</sup> The level of significance is corrected for the dependence between the 20 chi-square tests using  $\alpha/n$ ; \*\* tests significant at the 5% level (corrected  $P \leq 0.0025$ ); \* significant at the 10% level (corrected  $P \leq 0.005$ ); n.s. non-significant ( $P > 0.005$ )

<sup>b</sup> Fisher's exact test, because there were less than five observations in half of the cells

snipe, upland sandpiper, American bittern, clay-coloured sparrow, and field sparrow. The microhabitats  $\times$  sites matrix was also strongly and significantly nested except when ranked by area. In fact, no microhabitat class was restricted to the 33 largest (upper half) peatlands.

Standard and normalized indices both showed strong nestedness for a given matrix (Table 5). Ranking method had no effect on the nestedness of bird species  $\times$  sites matrix ( $t$ -tests on PN0 indices, all  $P > 0.09$ ). On the other hand, the microhabitats  $\times$  sites matrix was significantly less nested when sites were sorted by area rather than by microhabitat richness ( $t = 2.9$ ,  $P < 0.005$ ), indicating that though peatland area and microhabitat richness were strongly correlated, there were no predictable area-de-

pendent subsets of microhabitats among peatlands. More importantly, bird species assemblages (with sites sorted by species richness) were significantly more nested than microhabitat assemblages (with sites sorted by microhabitat richness) using PN0 (50.8 vs 29.1,  $t = 3.7$ ,  $P < 0.001$ ). The nestedness of bird and microhabitat matrices were markedly different when based on peatland ranking by area ( $t = 5.1$ ,  $P < 0.0001$ ).

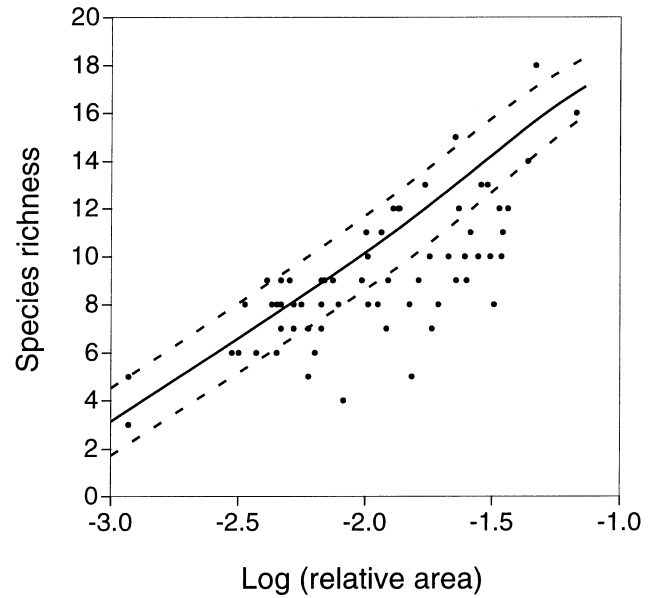
All bird species did not apparently contribute equally to nestedness of species assemblages. One way to assess species differences is to use a partial nestedness index, Ni, which simply denotes the number of unexpected absences of a given species/microhabitat (Patterson and Atmar 1986). Thus, the smaller its Ni value, the more a species conforms to nestedness. However, with common

**Table 3** Adjusted standardized residuals of the microhabitat × species contingency tables, based on point counts. Only those species clearly associated with at least one microhabitat type (residuals with absolute values higher than 2.0; *italicized*) are shown. *P*-values of the test of general linear association are given after the species code [<sup>\*</sup>chi-square values significant at the 5% level (corrected  $P \leq 0.0033$ ); *n.s.*: non-significant (corrected  $P > 0.0067$ ); the level of significance is corrected for the dependence between the 15 chi-square tests using  $\alpha/n$ ; Fisher's exact test is used when at least 25% of the cells have an expected count smaller than 5). Species are in decreasing order of relative frequency of occurrence in peatlands. None of the 15 species was found in either microhabitats 8 and 10 during point counts. Codes for microhabitat classes and species are given in Tables 1 and 2, respectively

Micro-habitat	COYE	LISP	WTSP	PAWA	NAWA	HETH	SASP	ALFL	SOSP	NOHA	TRSW	MAWA	YRWA	SWSP	UPSA
1	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.05 <sup>n.s.</sup>	0.07 <sup>n.s.</sup>	0.09 <sup>n.s.</sup>	0.14 <sup>n.s.</sup>	0.11 <sup>n.s.</sup>	0.31 <sup>n.s.</sup>	<0.001*	0.11 <sup>n.s.</sup>
2	<i>-4.1</i>	<i>-2.6</i>	<i>-4.0</i>	<i>-3.7</i>	<i>-2.7</i>	<i>-2.0</i>	<i>7.0</i>	<i>-1.9</i>	0.0	2.1	-0.1	-1.2	-1.1	0.0	-0.6
3	<i>-1.5</i>	0.2	-1.0	-1.6	-2.4	-2.2	4.1	-0.6	0.3	-1.4	-0.6	-0.6	-1.4	-0.5	0.8
4	-1.0	-1.4	-2.7	-2.1	-2.3	-0.8	0.9	-1.6	-1.4	0.2	-1.0	-1.0	0.2	-1.0	3.5
5	2.3	2.9	0.6	0.5	0.1	-0.9	-2.3	1.2	2.7	-0.9	3.5	-1.0	-0.1	0.7	-1.0
6	0.4	-1.6	-0.4	0.7	0.1	1.3	-3.1	2.1	-0.9	1.0	-0.2	-0.2	-0.1	-1.1	-0.6
7	2.1	3.0	3.8	3.6	4.8	5.1	-1.7	-1.0	-0.6	1.3	-1.1	2.2	0.2	-1.0	-0.6
9	0.5	-1.5	3.9	2.1	3.1	0.8	-4.1	1.5	-1.9	-1.3	-1.4	2.3	2.5	-1.3	-0.7
	1.6	0.6	-1.3	0.7	-1.3	-1.4	-0.5	-0.8	-0.7	-0.5	-0.5	-0.5	-0.5	8.8	-0.3

**Table 4** Correlations (Pearson's product-moment) between species richness (*SR*), sampling effort (*SE*), peatland area (*A*), and microhabitat richness (*HR*). All correlations are statistically significant ( $P \leq 0.0001$ ). Based on  $n = 67$  peatlands

	<i>SR</i>	<i>SE</i>	<i>A</i>
<i>SR</i>	-		
<i>SE</i>	0.74	-	
<i>A</i>	0.78	0.84	-
<i>HR</i>	0.74	0.70	0.79



**Fig. 3** Expected species-area curve generated under the hypothesis of random species distribution among peatlands. Expected values (*solid line*) and associated confidence limits ( $\pm 1$  SD; *dashed lines*) are shown. *Filled circles* represent observed species richness

species,  $N_i$  values cannot be high, since those species are seldom absent from sites. To account for this bias, we adjusted  $N_i$  values by dividing them by the total number of absences for each species. There was a strong relationship between species occurrences and their adjusted  $N_i$  ( $R^2 = 0.72$ ,  $n = 21$ ,  $P < 0.001$ ), indicating that relative contribution to nestedness increased with species rarity.

Nested species and microhabitat subsets could arise for independent reasons. In this case however, sites departing from microhabitat nestedness should not be the same as those departing from species nestedness. Comparing numbers of unexpected absences of birds and microhabitats in given sites is one way to assess whether microhabitat and species nestedness are dependent. Partial  $N$  scores of sites from the bird × sites matrix were correlated to corresponding site scores in the microhabitats × sites matrix (birds sorted by *SR* and *HR*:  $r_s = 0.23$ ,  $P = 0.03$  and  $r_s = 0.36$ ,  $P = 0.001$ , respectively; one-tailed tests). Thus, habitat and species nestedness not only occurred, but they coincided spatially.

**Table 5** Nestedness of birds species and microhabitat types within the 67 studied peatlands as calculated by *N* and standardized PN0. The bird species  $\times$  sites matrix had 1474 cells, while the matrix of microhabitats  $\times$  sites had 670 cells

Index	Birds					Microhabitats				
	Observed	Standard error	Random	<i>z</i>	<i>P</i>	Observed	Standard error	Random	<i>z</i>	<i>P</i>
<i>N</i>										
Sites sorted by species richness	386	$\pm 24$	784	-16.6	*	–	–	–	–	–
Sites sorted by microhabitat richness	436	$\pm 27$	800	-13.5	*	209	$\pm 14$	295	-6.1	*
Sites sorted by area	453	$\pm 25$	798	-13.8	*	289	$\pm 21$	301	-0.6	
PN0										
Sites sorted by species richness	50.8	$\pm 3.1$	0	-16.4	*	–	–	–	–	–
Sites sorted by microhabitat richness	45.5	$\pm 3.3$	0	-13.8	*	29.1	$\pm 4.9$	0	5.9	*
Sites sorted by area	43.2	$\pm 3.1$	0	-13.9	*	4.0	$\pm 7.1$	0	0.6	

\*  $P < 0.0001$  for observed vs random

## Discussion

In this study, we demonstrated that there is nestedness of microhabitats and that it was the best model to explain nested species assemblages. While microhabitat nestedness was thought to cause nestedness of bird species in two archipelagos off the coast of British Columbia (Simberloff and Martin 1991), and in the Sea of Cortéz (Cody 1983, pp 231–235), these claims were poorly supported by distribution data.

In fact, habitat nestedness is the least questionable process to explain bird species nestedness because, unlike colonization or extinction, it ignores population dynamics or life history of species, but rather points to associations between birds and their habitats. Cutler (1991) stressed that unexpected absences or presences of animal species may reflect an underlying patchiness or unevenness in the distribution of resources among islands (see also Cody 1983; Simberloff and Martin 1991). An obvious first step towards demonstrating the role of resource distribution is to document strong species-resource correlations. A large body of literature, including this study, shows that birds often have marked preferences for certain microhabitats (Cody 1985), which may explain nested patterns of species distribution. Swamp sparrows illustrate well the role of microhabitat distribution. They were found exclusively in fens, and their distribution among ombrotrophic peatlands thus depended on the presence of the two vegetation classes representing this uncommon microhabitat. Besides the clear preference of several peatland birds for certain microhabitats, the positive relationship between the contributions of species and microhabitats to the nestedness of individual peatlands provides direct support for Cutler's (1991) argument.

For a system of "islands" like eastern Canadian peatlands, where most bird species were frequent in the surrounding landscape, colonization and especially extinction are unlikely to be major determinants of nested

species subsets. On the other hand, nested assemblages of microhabitats can create this kind of pattern without any underlying assumption of population dynamics. Although vegetation structure and composition have often been considered in studies of real or habitat islands, the role of microhabitat subdivision has been generally overlooked (e.g. Ambuel and Temple 1983; Diamond 1984; Askins et al. 1987; Brown and Dinsmore 1991; but see Cody 1983; Haila 1983; Freemark and Merriam 1986) even if departures from expectation in the distribution of species have sometimes been explained by the absence or presence of microhabitats (see Brown 1978; Diamond 1984; Blake 1991). The premise of biogeographical studies of habitat islands, if not always explicit, is that habitat is homogeneous with respect to species of interest (Diamond 1975). This assumption is difficult to assess as homogeneity is scale dependent (Dutilleul 1993) and because, ultimately, the spatial structure of biological populations or communities is never uniform, but rather forms clusters or gradients (Legendre and Fortin 1989). We showed that peatlands cannot be considered as homogeneous, because of strong species-microhabitat associations.

In accordance with the habitat diversity hypothesis for species-area relationships (Williams 1964), the relationship between microhabitats and area was positive and highly significant, though a great amount of the variation in microhabitat richness was not explained. More importantly, these microhabitats were not distributed randomly among peatlands, but were rather found in relatively predictable combinations, as indicated by nestedness. Typically, there is a sequence of vegetation from the border to the centre of peatlands resulting from both climatic conditions and hydrologic processes (Glaser and Janssens 1986). It is also typical in islands where habitats are often added in a stepwise fashion as area increases (Cody 1983). Despite its importance, documenting habitat nestedness is only a first step towards demonstrating its role in nested bird species

assemblages, for one may argue that nested microhabitat and bird assemblages were independent patterns. However, our demonstration that peatlands departing from the nested microhabitat model also departed from nested bird species model provides more convincing evidence of the link between microhabitat and bird species nestedness.

However, besides the role of habitat nestedness, the greater nestedness of bird species uncovers the role of other processes in shaping bird distribution patterns among peatlands. Several indices have been proposed to express nestedness of species subsets, of which  $N$  and  $D$  (Lomolino 1996) have the main advantage of being sensitive to the ranking of sites according to variables of interest. These variables are used to test hypotheses about underlying causes of nestedness. Below, we discuss factors that discriminate between hypotheses based on extinction, colonization, passive sampling and microhabitat distribution.

#### Sampling effect

Random distribution of species strongly differing in their abundances may produce spurious nested assemblages among sites. Bolger et al. (1991) first suspected sampling effort (which they termed “passive sampling”) as a possible mechanism for creating subsets of species in habitat islands of various sizes, with evidence from species assemblages from virtual islands in continuous habitat. Andr n (1994) showed that nestedness could arise from random samples of species differing in their relative abundances. Cutler (1994) tested the passive-sampling effect with theoretical species assemblages. He used a log-normal species abundance distribution and filled “islands” of different sizes with individuals drawn with replacement from the pool of species of its theoretical distribution. All Cutler’s simulated archipelagos were highly nested. However, Worthen (1996) found some shortcomings to the approach used which can artificially increase nestedness. Among them, the choice of the simulation model coupled with the orders of magnitude of both species abundances and island sizes may have contributed to increase nestedness. Worthen (1996) proposed that a passive-sampling model such as Coleman’s (1981) random-placement model could be used. In a recent paper, Worthen et al. (1998) first tested and rejected this model prior to hypothesizing the role of environmental stress as a mechanism accounting for nestedness in fly communities living in mushrooms.

We cannot rule out the role of passive sampling in contributing to the nested pattern of bird species assemblages in peatlands. However, we argue that passive sampling did not account entirely for the nested pattern observed, because of both habitat specialization and the differences in habitat composition between peatlands. Habitat area was a good predictor of species richness, but the number of habitats available to bird species was at least as important.

#### Selective extinction

Highly nested systems believed to be driven by extinction were once continuous (Cook and Quinn 1995), then isolated by climatic events or anthropogenic processes. Extinctions are expected in such systems because total habitat area is reduced and fragments are unlikely to be recolonized. Though their species assemblages were highly nested, peatlands in our study area were not connected in the past, even if they developed at the same period (about 10,000 years ago in the study area), and they have maintained their approximate size until now. Moreover, peatland birds did not meet the assumption stated by Lomolino et al. (1989) that in relaxing faunas, “island” area should be the main determinant of species occurrence. This assumption was verified only for upland sandpiper, a semi-colonial species with large area requirements in eastern Canadian peatlands (Calm  and Haddad 1996), savannah sparrow, tree swallow and red-winged blackbird (unpublished data). Furthermore, species richness, an aggregate measure of species occurrence, was more influenced by microhabitat richness than by peatland area, even if microhabitat richness itself was strongly influenced by peatland area.

#### Selective colonization

Cook and Quinn (1995) found that assemblages of organisms with strong dispersal abilities like birds usually exhibit the strongest nested patterns of distribution, which is consistent with the selective colonization hypothesis. Our results give further support to the selective-colonization hypothesis. Indeed, even though peatland species assemblages were distinct, a large majority of species found in this ecosystem were actually found in the surrounding landscape. For instance, savannah sparrows were almost as common in peatlands as in nearby open sites, thus creating opportunities to counteract local extinctions (Brown and Kodric-Brown 1977). We only provide indirect evidence for the selective-colonization hypothesis, and we emphasize the need for more critical testing, such as documenting a correlation between frequency in habitat islands and dispersal ability. However, we know little, if anything, about the relative dispersal ability of most birds, which precludes strong inferences about selective colonization.

Our finding that habitat nestedness is the only tangible explanation for species nestedness reveals that nestedness might have little to do with insularity, which would explain why nestedness is so commonly observed in nature. Although microhabitat assemblages were strongly nested, they were however insufficient to explain all nestedness of bird species assemblages, since the latter were markedly more nested than microhabitats. The greater nestedness of species assemblages, compared to microhabitats, and the marginal role of passive sampling point to selective colonization as an additional



nesting mechanism, but behavioural work on dispersal should be done to provide more direct evidence.

### Conservation implications

Because microhabitats support sets of species (birds and other taxa), of which some are specialists, and because microhabitats themselves are found in predictable associations, we consider that nestedness of microhabitats has serious implications for the conservation of this wetland ecosystem, and possibly for others. Nestedness allowed us to document not only point richness, but also system richness. Large peatlands were not only more diverse in microhabitats and bird species, but more importantly, they supported biotic assemblages rarely found in smaller, less diverse, peatlands. At least one of the large-peatland species, the upland sandpiper, is of conservation concern (reviewed by Calmé and Haddad 1996).

Though the single large or several small (SLOSS) debate began in the 1970s (Simberloff and Abele 1982), it has become topical again with the literature on nested subsets of species. In theory, if subsets of species are perfectly nested, sites with highest species numbers, also usually the largest ones, will contain species not found in poorer sites (Cutler 1994). During the 1980s, many empirical studies agreed that several small sites encompassed more species than a large one or a few large sites of the same total area (e.g. Järvinen 1982; Simberloff and Abele 1982; Quinn and Harrison 1988). More recently, Cook (1995) and Boecklen (1997) showed that even relatively highly nested subsets of species of different taxa did not fit the single-large strategy, making nestedness indices poor predictors of the best strategy to follow. However, Cody (1983) demonstrated for the islands of the Sea of Cortéz that accumulation of bird species with area increase fits a “staging” model, with a one-third species increase at each stage, each new stage corresponding to the accumulation of another habitat on the island. Cody also wrote that historical factors may explain the overlap in island sizes between different “staging” levels. With such a model, usual comparisons obtained by simply summing island areas may be quite fallacious. For instance, Quinn and Harrison (1988), showed that collections of small parks contain more species than a single large park, but they recognized that these small parks encompass a greater variety of habitats. Therefore, habitat subdivision and the rate at which new habitats or microhabitats are added as area increases are far more important than area itself. As species requirements are the ultimate factors (Cody 1983) of species distribution, they should remain the most important consideration for designing protected areas (Simberloff and Martin 1991).

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