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SOPHIE CALMÉ

LES PATRONS DE DISTRIBUTION DES OISEAUX DES TOURBIÈRES DU QUÉBEC MÉRIDIONAL

Thèse
présentée
à la Faculté des études supérieures
de l'Université Laval
pour l'obtention
du grade de Philosophiae Doctor (Ph.D.)

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Faculté des études supérieures

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Ce 11e jour du mois de novembre 1998, les personnes soussignées, en leur qualité de membres du jury de la thèse de Sophie Calmé, ont assisté à la soutenance de cette thèse.

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Marc-André Villard	Moncton	
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André Desrochers	Laval	

SIGNATURE DU PRÉSIDENT DE LA SOUTENANCE

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Autorisation de co-auteur(s) pour un article inclu dans le mémoire ou la thèse

NOM DE L'ÉTUDIANT-E Sophie Calmé

NOM DU PROGRAMME Doctorat en Sciences Forestières

TITRE DU MÉMOIRE OU DE LA THÈSE Les patrons de distribution des oiseaux des tourbières du Québec méridional.

Par la présente, le(s) soussigné(s), co-auteur(s) d'un article intitulé :

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TITRE DU MÉMOIRE OU DE LA THÈSE	Les patrons de distribution des oiseaux des tourbières du Québec méridional.

Par la présente, le(s) soussigné(s), co-auteur(s) d'un article intitulé :

Peatlands : A new habitat for the Upland Sandpiper, Bartramia longicauda, in Eastern Canada.

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RÉSUMÉ COURT

Cette étude avait pour but de déterminer la contribution de l'avifaune des tourbières à la biodiversité régionale du Québec méridional, ainsi que déterminer les facteurs influençant la distribution des espèces, dans une perspective de conservation. Les tourbières supportaient une avifaune diversifiée, étroitement associée à la structure de la végétation. La richesse aviaire était d'ailleurs principalement déterminée par la richesse en microhabitats, mais aussi par la superficie des tourbières puisque ces deux variables étaient corrélées. Par ailleurs, la distribution non-aléatoire des microhabitats dans les tourbières pouvait expliquer la hiérarchisation des assemblages d'espèces d'oiseaux. Les grandes tourbières supportaient donc les assemblages d'espèces les plus riches et les espèces les moins communes, et présentent par conséquent plus d'intérêt pour la conservation. Deux espèces communes des tourbières étaient limitées presque exclusivement à cet habitat dans les régions étudiées, soit le bruant de Lincoln et la paruline à couronne rousse. La présence de cette dernière dépendait aussi de l'abondance régionale des tourbières, ce qui suggère que sa dynamique de population pourrait être affectée par l'isolement grandissant des tourbières naturelles résultant d'activités humaines.

Sophie Calmé

Sophie Calmé, candidate

André Desrochers, directeur

RÉSUMÉ LONG

Cette étude avait pour but de déterminer l'importance de l'avifaune des tourbières du Québec méridional, ainsi que rechercher les facteurs y déterminant la distribution des espèces, dans une perspective de conservation. J'ai donc inventorié les oiseaux dans 112 tourbières le long d'un gradient de 1050 km allant des Basses-Terres du Saint-Laurent aux Cuestas de Havre-Saint-Pierre en 1994 et 67 tourbières dans les Basses-Terres des Appalaches en 1995. J'ai utilisé plusieurs méthodes d'inventaires: points d'écoute de 10 min à rayon illimité (1994) ou de 100 m (1995), appels (1994) et transects de 200 m de largeur (1995). À chaque point d'écoute, j'ai stratifié la végétation et estimé visuellement les pourcentages de recouvrement dans un rayon de 100 m. En 1995, j'ai interprété les photographies aériennes au 1:15 000 des tourbières en utilisant 10 classes de microhabitats reflétant la structure de la végétation arbustive et arborescente. L'avifaune des tourbières variait selon la structure de la végétation et la présence de mares. Localement, elle se distinguait de l'avifaune environnante, surtout dans les régions les plus méridionales. Certaines espèces communes dans les tourbières, comme la paruline à couronne rousse et le bruant de Lincoln, étaient limitées presque exclusivement à cet habitat. La présence de la paruline à couronne rousse dépendait aussi de la superficie des tourbières et de leur abondance relative, à au moins deux échelles spatiales (78,5 et 314,2 km^2; rayons de 5 et 10 km, respectivement). J'ai déterminé l'existence d'un patron de distribution hiérarchique des assemblages d'espèces d'oiseaux dans les tourbières et montré qu'il pouvait être causé par la distribution non-aléatoire des microhabitats dans les tourbières. La richesse aviaire des tourbières était d'ailleurs principalement déterminée par la richesse en microhabitats. La superficie des tourbières était cependant un facteur significatif, surtout parce qu'elle était corrélée à la richesse en microhabitats. À cause de cette corrélation, les grandes tourbières semblent avoir plus d'intérêt pour la conservation que celles de superficies modestes.

Sophie Calmé, candidate

André Desrochers, directeur

ABSTRACT

This study aimed at documenting the importance of peatland birds in southern Québec, as well as determining factors accounting for their distribution, with an emphasis on conservation. I surveyed birds in 112 peatlands along a 1050 km gradient from the Lowlands of the St. Lawrence to the Cuestas of Havre-Saint-Pierre in 1994, and 67 peatlands in the Appalachian Lowlands in 1995. I used various songbird methods: 10-min point counts with unlimited radius (1994) or 100-m radius (1995), playbacks recordings (1994), and 200-m wide transects (1995). In each point count I sampled vegetation by stratum, visually estimating their respective percent cover in a 100-m radius. In 1995, I interpreted the 1:15 000 aerial photographs of sampled peatlands, using 10 classes of microhabitats that mostly reflected the structure of treelike vegetation. Peatland avifauna changed according to vegetation structure and the presence of pools, both of which varied geographically. Locally, peatland avifauna differed from that of surrounding areas, especially in southernmost regions. Two species commonly occurring in peatlands, Lincoln's Sparrow and Palm Warbler, were almost exclusively limited to this habitat in these regions. The occurrence of Palm Warbler depended essentially on peatland size and relative abundance, at least at two spatial scales (78.5 and 314.2 km^2; 5 and 10 km radiuses, respectively), stressing the need for peatland conservation. Peatland bird species assemblages were strongly nested within peatlands, and this could be caused by the nested distribution of microhabitats within peatlands. Bird species richness in peatlands was also mainly determined by microhabitat richness. However, peatland size remained an significant factor, because it was correlated to microhabitat richness. Therefore, large peatlands appear of greater importance than small ones from a conservation point of view.

Sophie Calmé

Sophie Calmé, candidate

André Desrochers, advisor

AVANT-PROPOS

Il va sans dire qu'un doctorat est le résultat de nombreux efforts et sacrifices, mais c'est aussi les supports moral et financier des proches et des organismes de financement, la confiance du directeur de recherche, les nombreuses discussions avec des collègues et l'appui logistique indispensable de plusieurs. Je suis reconnaissante à toutes ces personnes.

Les quatre articles scientifiques qui composent le corps de la thèse et l'annexe sont les fruits de ma collaboration avec les différents co-auteurs. Ils ont aussi été l'objet de discussions et ont bénéficié de commentaires par les membres du jury de thèse et des collègues, qui ont ainsi contribué à leur amélioration. Ces dernières personnes sont remerciées à la fin de chacun des chapitres correspondants.

Le premier article scientifique a été écrit en collaboration avec un des membres de mon comité de thèse *ad hoc*, le Dr Jean-Pierre Savard, chercheur au Service canadien de la faune à Québec et mon superviseur de thèse, le Dr André Desrochers. Cet article sera soumis à une revue générale traitant de biologie de la conservation. Les deux articles scientifiques suivants ont été écrits en collaboration avec André Desrochers. Le chapitre II a été accepté pour publication à la revue Oecologia, alors que le chapitre III sera soumis au Journal of Biogeography. L'article scientifique constituant l'annexe de cette thèse a été écrit en collaboration avec Stéphanie Haddad, M.Sc. Il a été publié dans le numéro 2 du volume 110 de la revue du Canadian Field-Naturalist, aux pages 326 à 330.

Les organismes qui ont financés cette recherche ont été: le CRSNG par l'attribution d'une bourse doctorale à moi-même et d'une subvention à André Desrochers, le Service canadien de la faune, la Société Québécoise pour la Protection des Oiseaux, ainsi que le Centre de Recherche en Biologie Forestière.

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INTRODUCTION GÉNÉRALE

Au Québec, les tourbières constituent les milieux humides les plus abondants, recouvrant près de 10% du territoire. La vaste majorité de ces tourbières est de type ombrotrophe (Buteau 1989), ou bogs. Leur régime hydrologique est régulé par les précipitations. Malgré leur apparente abondance au Québec, les tourbières ombrotrophes sont cependant principalement distribuées dans le Nord du Québec, dans la vaste dépression de la Baie d'Hudson. Dans le Sud, les tourbières ombrotrophes sont beaucoup plus rares et font face à une pression industrielle croissante en raison des nouvelles techniques de transformation de la tourbe et de la mise en marché de nouveaux produits. Si on connaît aujourd'hui assez bien la composition floristique de ce milieu unique (ex.: Couillard et Grondin 1986), les tourbières sont relativement méconnues comme habitat faunique (Desrochers 1994). Pourtant, leurs caractéristiques physiques et leur végétation pourraient bien en faire un milieu tout aussi unique pour la faune. De plus, l'intérêt grandissant pour la conservation de la diversité biologique exige qu'une connaissance et une compréhension de cet écosystème soient acquises rapidement, au moins dans les régions habitées.

Peu d'études ont porté sur l'avifaune des tourbières dans l'est du Canada (voir Erskine 1977, DesGranges 1989) ou du nord-est des États-Unis (Stockwell 1994). Par exemple, on ignore si les espèces d'oiseaux rencontrées dans les tourbières varient selon les régions, ou si les assemblages demeurent relativement stables. On ne sait pas non plus à quel point les assemblages d'espèces nichant dans les tourbières diffèrent des assemblages présents dans la même région. En effet, il est possible que l'avifaune des tourbières ne représente qu'un amalgame d'espèces des milieux agricoles environnants et d'espèces des milieux en régénération ou forestiers. Cette question est importante, puisque l'unicité des assemblages d'espèces est un facteur de choix dans la désignation des zones protégées.

Si les tourbières dominent certains paysages nordiques. elles forment plus au sud un vaste "archipel" d'habitats naturellement isolés les uns des autres. Ceci fait donc des tourbières

---

[1] Dans tout le texte, je référerai au terme "assemblage" et non au terme "communauté", car je n'ai pas cherché à reconnaître les liens fonctionnels entre les espèces (coexistence, compétition, etc). Comme j'ai ignoré cet aspect de la communauté, le terme assemblage, qui fait uniquement référence à l'existence simultanée d'espèces (Beard 1944) dans une fenêtre temporelle quelconque, apparait plus approprié.

un milieu de choix pour appliquer en milieu terrestre la théorie biogéographique insulaire (MacArthur et Wilson 1967, Diamond 1984). L'utilisation de cette théorie en biologie de la conservation des milieux terrestres a été l'objet de critiques, notamment parce que la matrice séparant les îlots d'habitat, contrairement au milieu océanique, ne constitue pas nécessairement une entrave majeure à la dispersion des individus ou à la colonisation des îlots (cf Wiens 1994). Ainsi, en milieu terrestre, les îlots d'habitats se comportent rarement comme des îles au sens strict du terme, puisque les espèces qui les occupent peuvent aussi être présentes dans la matrice.

Selon la théorie de la biogéographie insulaire, la probabilité de trouver une espèce i sur une île j (notée J_{ij}) dépend des taux d'immigration (I_{ij}) et d'extinction (E_{ij}), eux-mêmes des fonctions de certaines caractéristiques de l'espèce i et de île j (MacArthur et Wilson 1967, Diamond 1984). Pour la population i, sa densité, la propension à disperser, la distance qu'ils peuvent parcourir (excluant la distance parcourue lors de la migration annuelle) ainsi qu'une constante spécifique dépendant de la longueur des générations et de la variation interannuelle de la population sont les variables dont I_{ij} et E_{ij} dépendent (Diamond 1984). Pour l'île j, sa superficie, son isolement ainsi que la superficie de la source d'où proviennent les éventuels immigrants sont les variables explicatives de I_{ij} et E_{ij}. Ainsi, les espèces rares ou les populations isolées des milieux insulaires (ou fragmentés) risquent plus facilement l'extinction locale que les espèces communes ou les populations en milieu continu.

La croissance des industries de la tourbe (Bergeron 1995) et de la canneberge contribuent à la raréfaction et à l'isolement croissants des tourbières ombrotrophes. En effet, ces industries utilisent de grandes superficies de tourbières naturelles qui sont alors perturbées à long terme. Ces tendances à la réduction et à l'isolement, en plus d'entraîner une perte de diversité biologique à l'échelle locale, pourraient, selon la théorie biogéographique de l'insularité, conduire à la réduction de la diversité des tourbières restantes. En milieu terrestre, puisque le paysage environnant n'est pas forcément hostile, cette réduction est incertaine. En effet, les espèces présentes dans le paysage environnant peuvent éviter l'extinction par l'effet-rescousse (*"rescue effect"*; Brown et Kodric-Brown 1977). De plus, des espèces généralistes peuvent occuper la niche laissée vacante par une espèce éteinte localement. Cependant, simultanément à une augmentation de la similarité entre les assemblages d'espèces de tourbières et celles de la matrice environnante, on devrait observer une réduction de la diversité originale des tourbières.

La notion d'isolement des "îles" joue un rôle central dans la théorie de la biogéographie insulaire. Cependant, il existe peu de données supportant directement cette théorie en milieu terrestre. En conséquence, l'usage de la théorie en conservation des habitats fauniques est rarement justifié biologiquement. Le manque de données est explicable par la difficulté d'estimer les taux d'immigration et d'extinction locale. Toutefois, la théorie de la biogéographie insulaire est accompagnée d'autres prédictions plus aisément mesurables, comme la relation aire-espèces (cf Connor et McCoy 1979) ou l'effet des sous-ensembles hiérarchisés d'espèces (*"nested subsets"*; Patterson 1984).

La relation aire-espèce

La théorie biogéographique prédit entre autres qu'il existe une relation entre la superficie de l'habitat et le nombre d'espèces qu'il supporte. Cependant, cette prédiction est encore l'objet d'une controverse car on soupçonne que cette relation ne soit généralement qu'un épiphénomène (Boecklen 1986), pour deux raisons. La première est l'hypothèse de la diversité de l'habitat (Williams 1964), qui assume une relation positive entre la diversité et la superficie de l'habitat, compte tenu des besoins diversifiés des espèces. La deuxième est l'hypothèse de l'artéfact d'échantillonnage (Connor et McCoy 1979). On peut en effet montrer que la diversité d'objets augmente avec la superficie échantillonnée indépendamment des processus écologiques.

Plusieurs études réalisées en milieu forestier fragmenté montrent que la diminution de la superficie des fragments rémanents (Howe 1984, Freemark et Merriam 1986, Askins et al. 1987), ainsi que leur isolement relatif (Howe 1984, Askins et al. 1987) influencent négativement la richesse spécifique. Dans des marais de l'Iowa, 69% de la variation de la richesse en espèces est ainsi expliquée par la superficie des marais (Brown et Dinsmore 1991). En milieu agricole, les espèces sensibles à la superficie de leur habitat forestier, parfois considérées typiques des forêts profondes, peuvent être absentes des plus petits fragments forestiers (Ambuel et Temple 1983, Brown et Dinsmore 1986, Freemark et Merriam 1986, Askins et al. 1987). Cependant, l'effet spécifique de la superficie des fragments d'habitats est difficile à isoler et parfois moins important que celui d'autres variables de l'habitat (Ambuel et Temple 1983, Blake et Karr 1987). Il n'existe à ma connaissance aucune étude portant sur l'effet de la superficie et de l'isolement des tourbières quant à la distribution des espèces d'oiseaux qu'elles supportent. En Finlande, Hakala (1971) avait pourtant ouvert la voie en remarquant que les grandes tourbières de son étude étaient plus riches en espèces que les plus petites.

Les sous-ensembles hiérarchisés d'espèces

En plus de la relation aire-espèces, la théorie biogéographique prédit aussi que les espèces des assemblages pauvres constituent des sous-ensembles des assemblages plus riches (Patterson 1984). Un assemblage à n espèces est ainsi représenté dans un autre à n+1 espèces et ainsi de suite. Ce phénomène est très répandu en nature dans de nombreux types d'habitats et pour plusieurs groupes animaux ou végétaux (Cook 1995, Boecklen 1997, Wright et al. 1998). Plusieurs hypothèses sont proposées pour expliquer de tels patrons de distribution d'espèces. La plus ancienne est l'hypothèse des extinctions sélectives (Brown 1971). Cette hypothèse suppose que l'archipel considéré est toujours en phase de “relâchement”, donc que les processus d'extinction locale ont toujours lieu. Les sommets de montagne du Grand Bassin de l'Ouest états-unien, qui formaient un ensemble continu lors des périodes froides du Pléistocène, ont servi de modèle aux patrons hiérarchisés de distribution des espèces (Patterson 1984). Cet auteur a montré que les extinctions subséquentes à cette insularisation des sommets de montagne se sont déroulées en séquences prévisibles. Un autre exemple est fourni par Bolger et al. (1991) dans des canyons isolés par l'urbanisation en Californie. Les espèces d'oiseaux rencontrées dans ces canyons ne représentent qu'une version appauvrie du milieu continu correspondant, formant des hiérarchies d'assemblages telles que toutes les espèces des assemblages pauvres se retrouvent dans celles plus riches, c'est à dire emboîtées (hiérarchisées) un peu à la manière des poupées russes. L'existence d'une telle disposition des assemblages d'espèces suppose que les espèces disparaissant les premières, donc les plus vulnérables, sont aussi celles dont la capacité de dispersion ou l'abondance sont les plus faibles (Patterson 1987).

Cependant, Cook et Quinn (1995) ont montré que dans de nombreux cas des colonisations sélectives répétées pouvaient produire ce type de distribution. En effet, les espèces plus vagiles peuvent coloniser les ilôts les plus éloignés et sont donc rencontrées dans presque tous les ilôts, alors que les espèces moins vagiles atteignent seulement les ilôts les plus proches de la source de colonisateurs. Les oiseaux seraient donc probablement plus sujets à des colonisations répétées (ou effet-rescousse par dispersion) que les autres vertébrés terrestres non volants (Cook et Quinn 1995, Cutler 1991, 1994, Wright et al. 1998).

Comme pour la relation aire-espèce, certains auteurs ont commencé à soupçonner que "l'échantillonnage passif" ou artéfact d'échantillonnage, pourrait produire des sous-ensembles hiérarchisés d'espèces (Andrén 1994, Cutler 1994, Worthen 1996). En effet, Cutler (1994) a démontré pour une association hypothétique d'espèces distribuées sur des îles hypothétiques de superficie variant par un facteur d'ordre 500, qu'il était possible d'obtenir des sous-ensembles fortement hiérarchisés. La distribution des espèces suivait une courbe d'abondance log-normale, c'est-à-dire que les espèces fréquentes présentaient les abondances les plus élevées. On devrait tester l'existence d'un tel phénomène avant d'émettre d'autres hypothèses sur les mécanismes produisant des patrons hiérarchisés (Andrén 1994, Cutler 1994, Worthen 1996, Worthen et al. 1998, Wright et al. 1998).

Enfin, dans une étude sur les îles de la mer de Cortez, Cody (1983) a suggéré qu'une hiérarchisation des types d'habitats pouvait être à l'origine de ce type de distribution, chaque type d'habitat supportant un ensemble propre d'espèces. Plusieurs auteurs (Cook et Quinn 1995, Worthen 1996, Wright et al. 1998) ont mentionné la possibilité que des sous-ensembles hiérarchisés d'espèces soient créés par ce processus. Cependant, aucune étude n'a démontré cette possibilité.

Importance des facteurs locaux

En plus des relations inter-tourbières, les caractéristiques individuelles des tourbières peuvent aussi avoir un impact sur la répartition des oiseaux. Ainsi, la composition d'une avifaune peut refléter fidèlement les caractéristiques de son habitat, particulièrement la structure de la végétation lors de la nidification (Rotenberry et Wiens 1980, Rice et al. 1983, Wiens 1989). Dans des tourbières finlandaises, les caractéristiques des microhabitats de 14 espèces de passereaux ont pu être déterminées (Kouki et al. 1992). Cependant, les espèces ou les associations d'espèces associées à un type de végétation donné n'incluent que des espèces communes, les espèces rares ne pouvant être correctement modélisées (Recher et al. 1991).

En milieux ouverts naturels comme les prairies, les steppes et les tourbières, la hauteur et la densité des arbres ou arbustes apparaissent comme les principaux critères déterminant la répartition des espèces d'oiseaux (Cody 1968, Rotenberry et Wiens 1980, Wiens et Rotenberry 1981, Kouki et al. 1992, Desrochers 1994, Stockwell 1994). Une explication possible de l'importance de cette strate est que lorsqu'ils chantent, les mâles recherchent les branches d'arbres ou d'arbustes dominant la végétation environnante (Kouki et al. 1992). Les arbres et arbustes doivent jouer un rôle important dans l'augmentation de la diversité de tels habitats. Or, l'hétérogénéité de l'habitat s'avère l'élément clé de la relation entre la superficie de l'habitat et la diversité spécifique selon l'hypothèse de la diversité de l'habitat (Williams 1964). Cette relation a été démontrée pour la diversité des oiseaux de stations forestières assemblées de façon à produire divers degrés d'hétérogénéité (Boecklen 1986).

Objectifs de l'étude et organisation de la thèse

Il s'agit de déterminer l'influence (1) de la distribution des tourbières du Québec méridional, (2) de leur superficie et (3) de la structure de leur végétation sur la distribution des espèces d'oiseaux associées à ces tourbières et (4) d'appliquer les résultats à un contexte de conservation de la diversité faunique. La thèse est divisée en trois chapitres, rédigés sous forme d'articles scientifiques. Dans le premier chapitre, je montre comment les oiseaux des tourbières contribuent à enrichir l'avifaune locale et régionale. Je montre aussi que les assemblages d'espèces varient régionalement et que ces variations peuvent être associées à des changements dans les caractéristiques des tourbières ou de leurs environs. Le chapitre deux s'intéresse à l'existence de patrons hiérarchisés de distribution des sous-ensembles d'espèces et aux mécanismes qui peuvent être à leur origine. Dans le dernier chapitre, je montre que les assemblages d'oiseaux n'ont pas un “comportement insulaire” et j'examine les exigences des espèces d'oiseaux en regard à la superficie d'habitat, sa richesse, son hétérogénéité et son isolement relatif.

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Chapitre I

Regional significance of peatlands for avifaunal diversity in southern Québec

Regional importance of peatlands for birds in southern Québec. Sophie Calmé[1], Jean-Pierre Savard[2], and André Desrochers[1]. [1]Centre de recherche en biologie forestière, Faculté de Foresterie et de Géomatique, Université Laval, Sainte-Foy, Québec, Canada G1K 7P4, [2] Canadian Wildlife Service, Québec region, Sainte-Foy, Québec, Canada G1V 4H5

Résumé Les tourbières du Québec méridional font face à une pression importante de la part de plusieurs industries comme celles de la mousse de tourbe, de la canneberge ou de la forêt. Cependant, aucune mesure de protection spécifique et substantielle n'existe pour cet habitat. Nous avons déterminé la contribution des tourbières à la diversité régionale pour les oiseaux, qui constituent le groupe de vertébrés le plus diversifié dans les tourbières. Pour ce faire, 112 tourbières distribuées le long du fleuve Saint-Laurent ont été échantillonnées pendant une saison de reproduction. Nous avons ensuite utilisé l'*Atlas des oiseaux nicheurs du Québec* pour comparer les assemblages d'espèces d'oiseaux des tourbières visitées à la liste des espèces nicheuses dénombrées lors des travaux de l'atlas. Les sites échantillonnés étaient localisés sur la grille de base de l'atlas, constituée de quadrats de 10 × 10 km. La comparaison des espèces s'effectuait avec les quadrats adjacents (≤ 8) aux tourbières étudiées. De plus, pour un sous-échantillon de 23 tourbières, nous avons déterminé à partir d'une spatiocarte[1] la composition du paysage dans des rayons de 2 et 5 km autour des stations d'écoute. Nous avons alors comparé les occurrences des oiseaux des tourbières selon les types et les superficies d'habitats entourant ces tourbières pour les deux rayons sus-mentionnés. Certaines espèces d'oiseaux préféraient les tourbières dans toute l'aire d'étude, alors que pour d'autres espèces cette préférence était limitée à certaines régions. Nous concluons que les tourbières contribuent à l'enrichissement de la diversité aviaire locale et régionale, particulièrement dans la vallée du Saint-Laurent. La présence de la Paruline à couronne rousse (*Dendroica palmarum*), une espèce spécialiste des tourbières, était liée à la disponibilité régionale de cet habitat, soulignant ainsi l'importance de conserver les tourbières pour le maintien régional de l'espèce.

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[1] Spatiocarte: carte thématique provenant de l'analyse d'une image satellitaire.

Introduction

Peatlands occur throughout southeastern Canada among a wide variety of ecosystems, ranging from hardwood forests to boreal spruce forests, and within landscapes often heavily transformed by human activity. Urban sprawl and agriculture have led to the loss or reduction of more than 25 000 km^2 of peatlands in southernmost regions (Keys 1992; Bergeron 1995). Furthermore, forestry and peat mining have changed the structure and dynamics of 400 km^2 more of peatlands. With an increasing demand for peat moss (Bergeron 1995) and cranberry derived products, threats to peatlands will continue as long as protection measures are not taken. The Brisbane Conference (Ramsar Convention 1996) recognized that peatlands were under-representated wetlands in the global network of wetlands of international importance.

Peatlands support a wide variety of plants specialized for the extreme conditions of acidity that characterize this ecosystem. Many animal species also breed or forage in peatlands, among which birds are the most diverse vertebrate group. However, the significance of this ecosystem for the regional avifauna is not well documented. We sought to evaluate the regional sgnificance of peatlands for birds by answering the following questions: (1) How much do peatland bird assemblages differ from those of surrounding habitats ? (2) To what extent does the contribution of peatland birds to local bird diversity vary among regions ? (3) To what extent does the composition of peatland birds assemblages reflect the composition of the surrounding landscape ?

In this paper, we analyze the composition of peatland bird assemblages along a 1050 km geographical gradient, and compare these assemblages to those found in surrounding landscapes. For each region, we evaluate the similarity of bird species assemblages among peatlands. We also relate the occurrence of peatland birds to the types and amounts of habitats surrounding the peatlands at 12.6 km^2 (2 km radius) and 78.5 km^2 (5 km radius) spatial scales. We then determine whether the difference between bird assemblages in peatlands and surrounding landscapes varies regionally.

Material and Methods

Study area

Peatlands of southern Québec (south of 52°N) are concentrated in the lowlands of the gulf and estuary of the St Lawrence River, the lowlands of Lac Saint-Jean, and, in the western part of the province, in the Abitibi plain (former Ojibway glacial lake). We included in our sample all these regions except Abitibi. Eight natural regions based on geomorphology, climate and vegetation cover were comprised in our study area (Government of Québec 1984; Fig. 1).

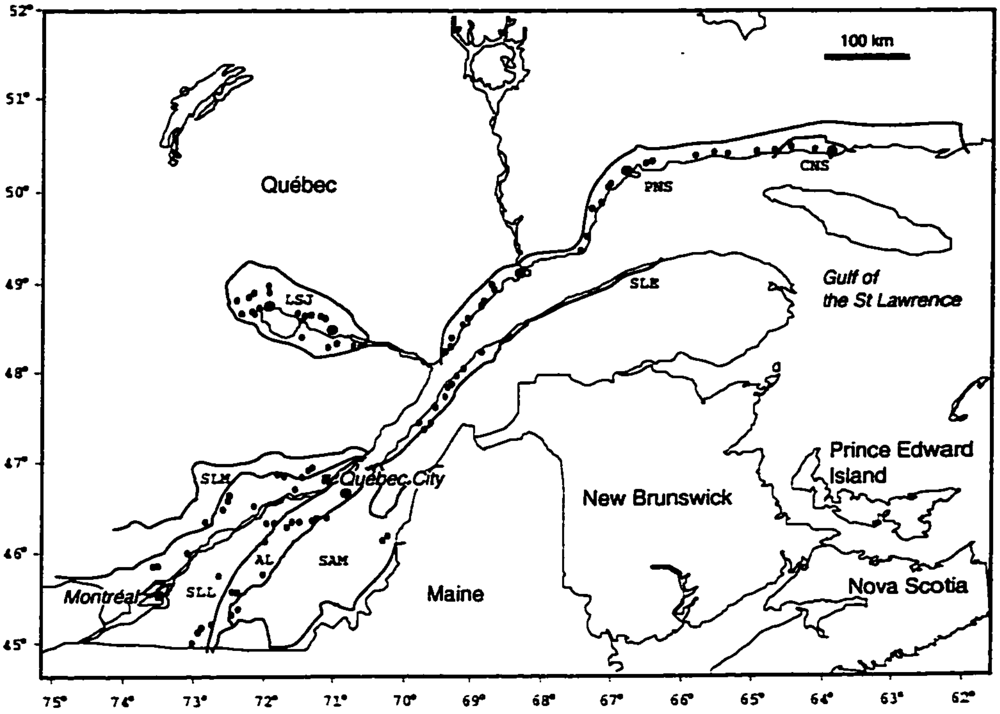

Figure 1. Location of the 112 peatlands studied. Each dot represents one (small dots) or three to five (large dots) studied peatlands. Natural regions are indicated according to the following codes: LSJ, Lac Saint-Jean Lowlands; SLE, Southern Littoral of the Estuary; SLM, Southern Laurentian Montains; AL, Appalachian Lowlands; SLL, St Lawrence Lowlands; PNS, Coastal Plain of the North Shore; CNS, Cuestas of the North Shore; SAM, Secondary Range of Appalachian Mountains. Limits of natural regions are approximative.

One hundred and twelve bogs (ombrotrophic peatlands) were selected from the Atlas of peatlands of southern Québec (Buteau 1989), so that their number in each natural region was proportional to their abundance (Fig. 1). We measured peatland area on 1:15 000 aerial photographs, using a digital planimeter. Sampled peatlands ranged in size from 0.09 to 48.40 km^2 (median = 0.68 km^2).

Peatland birds and vegetation

We censused birds from 27 May to 2 July 1994, under conditions with no rain or strong winds. Each visit consisted in one point count followed by one playback recording (Johnson et al. 1981) in 63 peatlands and one playback recording only in the other peatlands. In larger peatlands, we placed two sampling points separated by at least 1 km. Point counts were located at least 200 m from the peatland edge (% trees > 5 m exceeding 50%), except in smaller peatlands, where we placed sampling points at their approximate centroids. In each peatland, we paid attention to locate point counts in a section representative of its physiognomy. Point counts had unlimited recording distance, and lasted 10 min during which all birds seen or heard within the peatland were recorded, and the position of birds was noted. Playback recordings included vocalizations of 35 bird species previously observed in the bogs under study, and associated with wetlands (Godfrey 1986). Playback broadcasts of a given species stimulates responses by territorial conspecific individuals, which increases their probability of detection. The sequence of species on the tape reflected their increasing frequency of observation during a pilot study conducted the previous year, except for Short-eared Owl (*Asio flammeus*) which was added at the end of the tape. Each song was repeated three times with intervening periods of 5 seconds, and the complete tape lasted 32 min. Responses to playbacks were noted when a bird sang, called, or came to the speaker within three minutes after its conspecific vocalization started. Meanwhile, we recorded other birds seen or heard, following the unlimited radius point count method. Birds in flight were recorded only if they were less than 10 m above ground. We made a single-visit per site during the breeding season of 1994 (late May to early July). progressing towards the north. We are confident in the value of the data, because the composition of peatland bird assemblages remained stable in undisturbed sites from 1993 to

1996 (Desrochers et al. 1998; unpublished data).

We described vegetation according to the following strata: mosses, lichens, herbs, ericaceous shrubs, and trees (< 2 m, 2-5 m, > 5 m). The latter group was identified to the species level. We visually estimated the percent cover of each of the strata and of open water (pools) in a 100-m radius from bird sampling points, allowing total percent cover to exceed 100 %.

Regional species assemblages

The Atlas of breeding birds of southern Québec (Gauthier & Aubry 1996) was used to determine which bird species nest, at least probably, around peatlands. Atlas data were collected during six consecutive breeding seasons from 1984 to 1989. We assumed that species breeding ranges did not change between this period and 1994. The territory was divided according to a 10 × 10 km grid that followed the Universal Transverse Mercator (UTM) system. The 112 sampled peatlands were contained in 85 of these 10 × 10 km squares, which we refer to as reference squares. We selected all squares adjoining those comprising at least one sampled peatland. Thus, for a given reference square, eight squares served for comparisons of birds present in peatlands (our data) with those present in surrounding landscapes. Due to the presence of water, however, fewer than eight squares were available by reference square in the regions LSJ, SLE, PNS and CNS. Also, adjoining squares with less than 20 % of land surface because of water or UTM zone limits were pooled with their closest neighbor. Poorly covered squares, i.e., with a lower count of species than expected in the region, were also discarded.

Similarities of bird assemblages between peatlands and surrounding landscapes

We first evaluated whether bird species frequencies of occurrence in peatlands and their surrounding landscape were similar with the Kolmogorov-Smirnov statistic for two samples ($n = 102$ sites for each of the two samples).

For each natural region, we calculated the percent species occurrence in peatlands to create a dichotomic occurrence index. Species were classified as either common (occurrence ≥ 50%) or uncommon (occurrence < 50%). For birds outside peatlands, the procedure was similar, except that we calculated percent occurrences for each set of eight (or fewer) adjoining atlas squares, and not for entire natural regions. Similarity on bird species occurrence between peatlands and surrounding atlas squares were calculated with the Jaccard similarity index. We chose the Jaccard similarity index because it is not sensitive to sample size, and gives an equal weight to all species without regard for abundance, which was not reliable with the census method we used. We ran multiple comparisons using the Tukey-Kramer method for all possible pairs of similarities to determine whether similarities in bird composition between peatlands and surrounding landscapes varied among regions. The Tukey-Kramer procedure is conservative, but is well suited for samples of unequal sizes (Sokal & Rohlf 1995).

Similarities of peatland bird assemblages within natural regions

To provide insight on the similarity of bird assemblages of peatlands from the same region, we calculated similarities between sites (within-region) for six of the eight natural regions encompassed in the study area, the two remaining regions having too few sites. As for the comparisons involving birds of peatlands and surrounding habitats, we ran multiple comparisons for all possible pairs of inter-region similarities using the Tukey-Kramer method.

Similarities do not allow to identify species which contribute to regional variations, so we also performed a correspondence analysis (CA). In this analysis, bird occurrences (presence/absence), reference squares (those with sample peatlands) and associated natural regions were projected in the same factorial space, allowing to visualize regional bird species associations.

Changes in peatland vegetation structure along the geographic gradient

We performed a principal coordinate analysis (PCO) to evaluate whether peatland vegetation structure varied along a geographic gradient. PCO allows the use of similarity cofficients other than Euclidian distance (van Tongeren 1995), and performs well even for similarity matrices with many double zeros (Legendre & Legendre 1984). Environmental variables were latitude, longitude, peatland size, and the set of vegetation data (ground cover of each stratum, including open water). To perform the analysis, data were standardized and then distributed among eight classes for each variable. We then calculated similarities between sites with the Gower index (Gower 1971), because variables of different types can be used with this general index. We used a Shepard diagram (Shepard 1962) to evaluate whether original distances were correctly represented by the first dimensions, i.e., whether the ordination fitted well.

Landscape composition data

We used classified satellite imagery (Bélanger et al. 1998) to determine habitat composition within landscapes surrounding peatlands within 2 000 m and 5 000 m around sampling points. These values fall within the range of natal and breeding dispersal distances of many bird species (Paradis et al. 1998). The satellite imagery covered 23 of the peatlands sampled. Relationships between species occurrences within peatlands and surrounding landscape composition were analyzed with logistic regression using type III sums of squares, to estimate the contribution of each variable to the model after factoring out the effects of all other variables (Littell, Freund & Spector 1991).

The original classification included 28 cover types, of which 24 were terrestrial. We grouped types on the basis of the structure of the habitats they described to reduce their number to 11 (Table 1). For instance, the 'agriculture' class was obtained by grouping the following five original classes: corn, cereals, truck farms, hay and alfalfa, pastures and golf courses.

Table 1. Habitat classification of the southermost regions of southern Québec.

Class	Code	Description
Urban	URBA	Urban zone, roads, gravel mines, some bare soils
Agriculture	AGRI	Corn, cereals, truck farms, hay, alfalfa, pastures, golf courses, parks
Fallow land	FALL	Abandoned agricultural lands
Peat mined	PLOW	Mined peatlands, ploughed fields
Broad-leaf forest	DECI	Deciduous broad-leaf stands of shade-tolerant or -intolerant trees
Mixed forest	MIXT	Mixed forest stands
Dense coniferous forest	COND	Coniferous stands with a ground cover of 60 to 80%
Coniferous forest	CONO	Coniferous stands with a ground cover of 25 to 60%
Regeneration	REGE	Clearcuts, regeneration of deciduous, coniferous or mixed stands (<3 m)
Water	AQUA	Open water; flooded vegetation and marshes of the St Lawrence River
Peatlands	PEAT	Peatlands, swamps, alder thickets

Results

Similarity of bird assemblages between peatlands and surrounding landscapes

Peatland and surrounding bird species assemblages were very different not only because the former was a small subset of the latter, but also because of different species rankings by occurrence (KS = 0.647, $p = 0.0001$). For all blocks of nine (or fewer) atlas grid squares, similarities were low, varying between 0.06 and 0.22. These low values resulted in part from the discrepancy between the number of bird species recorded in peatlands and their surroundings, the latter covering many habitat types, which increased the species richness. There were few inter-regional differences (Fig. 2), as only the southernmost region (SLL) differed from almost all the others. Peatland bird species contrasted increasingly with regional avifauna from North to South or from undisturbed to managed landscapes ($r_s = 1.0$, $n = 6$, $p < 0.01$).

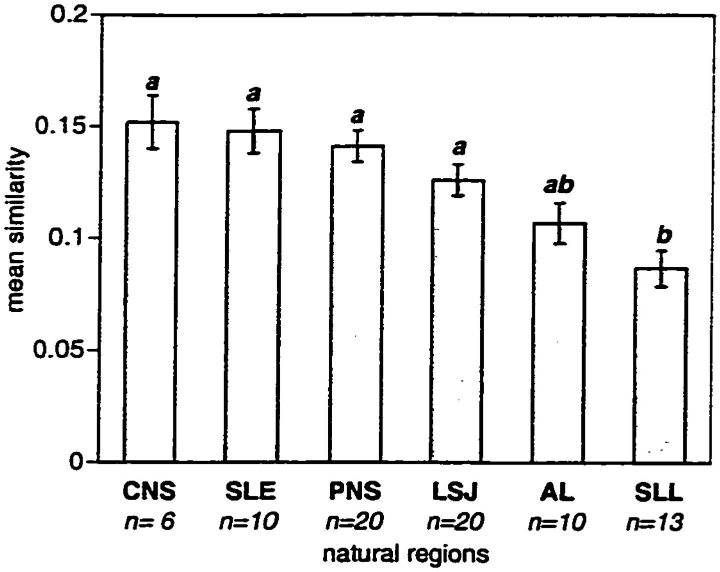

Figure 2. Mean similarity of bird species between peatlands and surrounding landscapes within regions. The same letter above bars indicates that regions did not differ at p = 0.05 (Tukey-Kramer's test). See caption in Fig. 1 for natural region codes. Note that, from left to right, regions are ordered from North to South.

A total of 17 bird species were regionally common in peatlands and uncommon in surrounding habitat types for at least one 100 km^2 reference square. However, this occurred in more than 10 % of the 85 references squares for only four species: White-winged Crossbill (8 times), Nashville Warbler (12 times), Lincoln's Sparrow (20 times) and Palm Warbler (28 times). White-winged Crossbills were more common in peatlands than regionally in more than half the sites of the North Shore; Nashville Warblers in one-third of the sites of the North Shore and Southern Littoral of the Estuary. Lincoln's Sparrows were far more common in peatlands than in the St Lawrence Lowlands region (85 % of the sites), in half of the sites of the Appalachian Lowlands, and one-quarter of the sites of the Secondary Range of Appalachian Mountains. Finally, Palm Warblers were typically found in peatlands in the Lowlands of Lac-Saint-Jean, the Secondary Range of Appalachian Mountains (common in peatlands vs. uncommon regionally in 100 % of the sites in both regions), and also in 80 % of the sites of the Appalachian Lowlands.

Similarities of peatland bird assemblages within natural regions

Similarities between peatland bird assemblages within each region varied between 0.223 for the Cuestas of the North Shore and 0.385 for the Lowlands of the Lac Saint Jean (Fig. 3). These values were about twice as high as those calculated to compare bird assemblages in peatlands and surrounding habitats. Therefore, peatland avifaunas within regions were more similar to each other than to their regional avifauna.

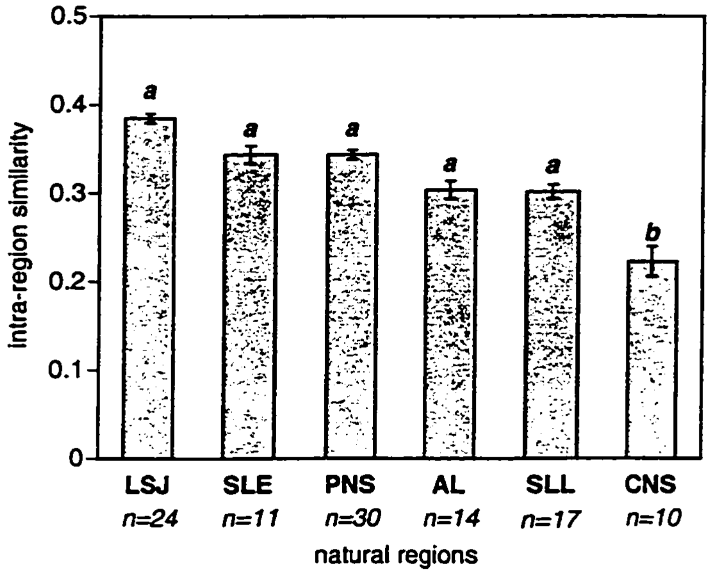

Figure 3. Variation in intra-regional similarity in bird composition. The same letter above bars indicates that regions did not differ at p = 0.05. See caption in Fig. 1 for natural region codes.

Peatlands of the Cuestas of the North Shore were significantly less similar to one another than peatlands in other regions, because they supported many uncommon shorebirds or aquatic species with patchy distributions, such as Common Terns, Common and Red-throated Loons, Ospreys, or Greater Yellowlegs. While for clarity most of these species are not represented on Fig. 4, this plot shows that the Cuestas of the North Shore (CNS) clearly stood out from the other regions. The St Lawrence Lowlands (SLL) had typically fewer forest species, and were well represented by species such as Song Sparrow, Northern Harrier or

American Goldfinch. By contrast, the peatlands of the Coastal Plain of the North Shore (PNS) were characterized by the presence of boreal forest species such as Tennessee Warbler, White-winged Crossbill and Winter Wren, and the presence of Common Loons and Herring Gulls.

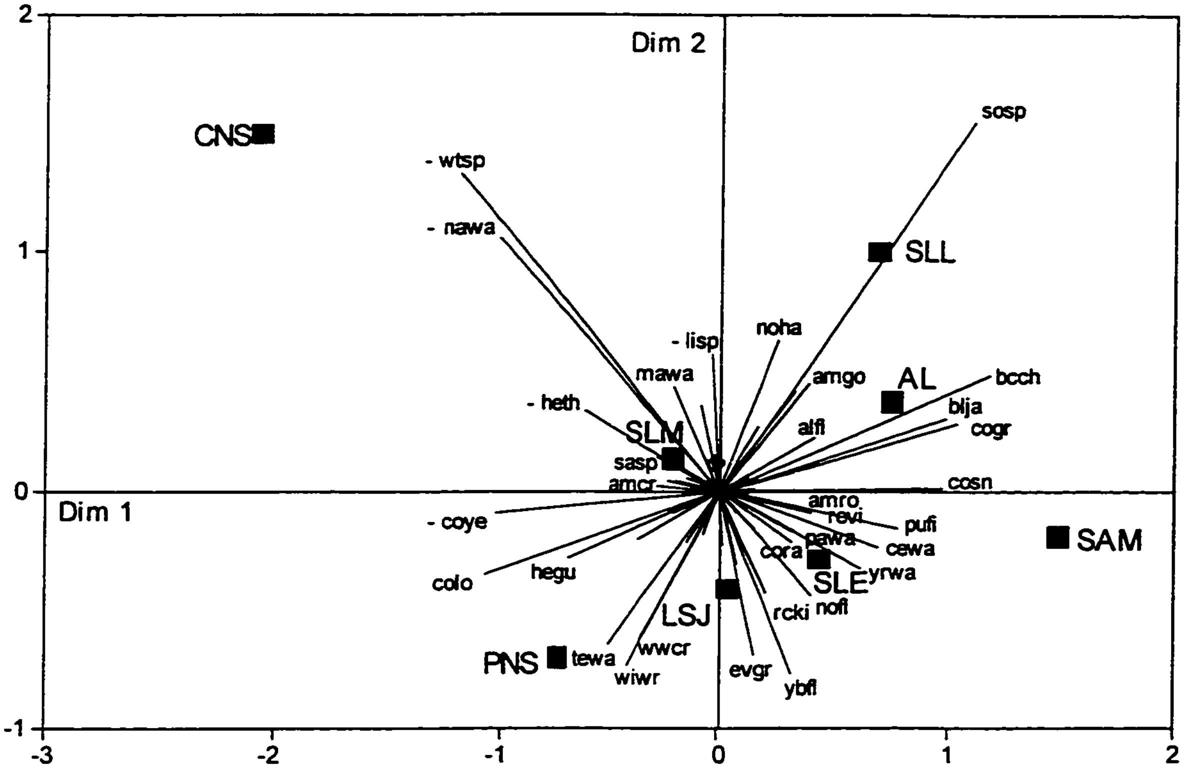

Figure 4. Graphical representation of the results of correspondence analysis between regions and bird species. The first two axes explained 10.5% of total inertia. See appendix for the meaning of species code. Codes for natural regions are in Fig. 1 caption.

Changes in peatland vegetation structure along the geographic gradient

The first three eigenvalues of the PCO explained 15 % of the model's variance. The ordination fitted well according to the Shepard diagram. The correlation analysis indicated that there was a striking contrast between southern and northern peatlands. Northern peatlands were larger, and were characterized by numerous, and often very large, pools. By contrast, peatlands in other parts of the study area lacked such large pools. Peatlands on the North Shore and the Cuestas also had fewer and, typically, smaller (< 2 m high) trees. Otherwise, tree species remained identical over all the study area. Northern peatlands also were more subject to lichen colonization. Thus, we observed a parallel change in bird species assemblages and peatland physiognomy as latitude increased.

Peatland bird occurrences and landscape composition

The response to landscape composition of 18 species was modeled using logistic regression. These species were present in 22-82 % of the study sites. Although other species were recorded, their occurrence was either too low or too high to be correctly modeled, as indicated by likelihood-ratio tests. Results differed according to the scale considered (Table 2). However, the occurrence of correctly modeled species (i.e., low residual deviance) was negatively related to the presence of agricultural activities in the landscape at all scales (except Black-capped Chickadee within a 5000 m-radius). Moreover, occurrence of most bird species in peatlands was also negatively correlated with the amount of forest habitat, which could indicate that forested peatlands may act as reserves for forest birds when forest cover is rare, as was the case in the southernmost part of the region covered by the satellite imagery.

The occurrence of five species was negatively correlated with the amount of peatland habitat. Common Ravens became rarer in peatlands when this habitat increased in the landscape at the 5 km scale, which may reflect the absence of potential nest sites (cliffs or large trees; Roy & Bombardier 1996) in lowlands where peatlands are numerous and/or large. The occurrences of the four other species, Ruby-crowned Kinglet, American Robin, Magnolia Warbler, and Purple Finch, were negatively related to the area of peatland habitat at the 2 km scale. This result is consistent with the preference of these species for wooded areas in peatlands. In effect, at this scale, a large amount of peatland habitat is often due to the large size of the focal peatland, which means more open areas and fewer tall trees. The occurrence of only one species, Palm Warbler, was positively correlated with the amount of peatland habitat in the landscape.

Table 2. Cover types present within radius of 2000 m and 5000 m of sampling points that were significantly ($p < 0.10$) associated with species occurrence in peatlands, as calculated by logistic regression. The sign of the relationship (+/-) and the significance of the chi-square associated with type III estimates are given according to: +/-, $p < 0.10$; ++/--, $p < 0.05$; +++/---, $p < 0.01$. F is the frequency of peatland bird occurrences from a set of N = 23 peatlands. Codes for cover types are listed in Table 1.

Species	F	Radius	Explanatory variables							
			AGRI	FALL	DECI	MIXT	COND	CONO	REGE	PEAT
Yellow-bellied Flycatcher	6	2000 m	-						--	
Blue Jay	9	2000 m				-				
		5000 m						--		
Common Raven	7	5000 m			+	+++		---	++	--
Black-capped Chickadee	1	2000 m			+++				+++	
	1	5000 m	+		++		-			
Ruby-crowned Kinglet	1	2000 m				--				--
	0	5000 m			-					
Hermit Thrush	1 9	5000 m	--	--	-				---	
American Robin	1 1	2000 m	---		---	---	---	--		---
Red-eyed Vireo	1	2000 m							++	
	1	5000 m						--	+	
Magnolia Warbler	1 1	5000 m	---	--	---			--		-
Yellow-rumped Warbler	1	2000 m	-	---			+++	--	---	
	2	5000 m		---			+++	-	-	
Palm Warbler	9	2000 m				-				
		5000 m							--	+++
Lincoln Sparrow	1 7	5000 m							--	
Common Grackle	8	5000 m				++				
Purple Finch	8	2000 m	---	---				---		---
American Goldfinch	9	2000 m	--	---	---	--	---		---	

Discussion

Contribution of peatlands to local and regional avian diversity

Peatland bird assemblages were not mere subsets of those found in surrounding landscapes, but comprised species uncommon outside peatlands. Here, we want here to stress that the method we used was very conservative, as we compared bird data from a single season and small areas (sampled peatlands) to bird data from several years and much larger areas (200-800 km^2; atlas squares), which also included peatlands. Therefore, the power of detecting a species more common in peatlands than in the surrounding landscape was actually small. Nevertheless, 17 of the 102 bird species recorded in peatlands were more common in this habitat than elsewhere in the surrounding landscape.

Two conditions were necessary in order species be more common in peatlands than in surrounding landscapes. First, peatlands must be relatively rare in the landscape. According to the habitat diversity hypothesis (Williams 1964), increasing habitat diversity leads to an increase in species diversity by adding new resources. Böhning-Gaese (1997), for instance, showed that for spatial scales ranging from 4 to 36 km^2, habitat diversity was the main factor influencing avian diversity. In our study, Palm Warblers, which are peatland specialists (Wilson 1996), were not only more commonly found in peatland than in other habitats, but their presence was also strongly influenced by the amount of peatland habitat present at the 78.5 km^2 scale. In Chapter III, we found a similar result at a larger scale (314.2 km^2), though data were from another breeding season, and a different geographic range. Both results point that when peatlands were too rare at broader scales, peatland bird assemblages could ultimately be depauperate.

Second, peatlands must represent the most suitable habitat for the species more frequent in them than elsewhere in the landscape. Lincoln's Sparrows in the Lowlands of the St Lawrence river illustrate well this situation. In this region, we found that they occurred almost exclusively in peatlands (Chapter II), although the species is relatively common in the brushy and humid habitats of the boreal forest (Langevin 1996). Thus, the contribution of Lincoln's

Sparrows found in peatlands to avian diversity was far more important in the southern regions than in the boreal zone.

Our study area encompassed eight natural regions, which comprised a wide array of ecosystems, ranging from deciduous broad-leaf forests in the south to black spruce forests in the north, and including shore habitats and agroecosystems. It is no surprise that along this gradient, bird species varied greatly. Meanwhile, peatland physiognomy varied along this gradient, but it was essentially due to the peatlands of the North Shore, and especially those of the Cuestas. As indicated by similarity analyses, structural variation in peatlands was closely related to the variation in bird species composition, which is consistent with Stockwell's (1994) finding that peatland vegetation structure is a good predictor of bird species occurrence.

The peatland avifauna in the Cuestas could not differ much from that of the surroundings, because peatlands dominated the landscape at the spatial scale we selected. In this region, the low similarity between avifaunas in peatlands and surroundings probably resulted from markedly low similarity among peatland avifaunas themselves. On the other hand, peatlands in the St Lawrence Lowlands contrasted with the surrounding habitats (farmlands and deciduous forests). As a result, it was also the region where similarity between bird assemblages of peatlands and surrounding habitats was lowest.

Finally, the presence of various peatland birds in the southern portion of the study area "spilled over" from the surrounding landscape, though very common species for which we could not obtain information might not have responded to the composition of the surrounding landscape. First, species such as Hermit Thrush or Yellow-rumped Warbler appeared to "invade" peatlands from surrounding habitats. Other species such as Common Raven might use peatlands as hunting territories. Second, many species could be detected more often in peatlands when their favorite habitat was reduced in the region. It was probably the case for Yellow-bellied Flycatcher and Purple Finch. For these species, the presence of peatlands could help maintain populations regionally, though this habitat might be suboptimal for them.

Conservation of peatlands

Peatlands are not well represented in the worldwide system of protected areas (Ramsar Convention 1996). In Canada, three sites have been recently recognized as Wetlands of International Importance, but cover less than 10 000 ha. Only one National Park, Kouchibougac, in New Brunswick, supports a large area (3 000 ha) consisting of peatlands. Therefore, bird species that are mainly confined to peatlands, like Palm Warbler, lack the protection ensured by nature reserves. As a matter of fact, we found that Palm Warblers were absent from regions where peatlands occurred as small and isolated remnants.

Virkkala et al. (1994) stated that the conservation status of a given location should be justified by its significance for certain species, either because an important proportion of their regional population is found at this location or because they are rare and vulnerable. In the present, however, no peatland would support enough individuals of a given species to justify its protection. We argue that peatlands should rather been considered as clusters, just as they usually developed, and should be managed and protected as such.

We showed that both peatlands and their associated avifauna changed along the geographical gradient we sampled. Nevertheless, peatland bird assemblages in the southermost regions of Québec differed even more from their surroundings than in boreal regions. Thus, not only peatlands should be preserved along all the geographical gradient, but a special effort should be put on southern peatlands, both because they are very distinctive in the "avianscape", but also because they suffer from stronger human pressures in these regions.

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Appendix. List of the species found in the peatlands in the study area.

English name	*Scientific name*	Code
Red-throated Loon	*Gavia stellata*	RTLO
Common Loon	*Gavia immer*	COLO
American Bittern	*Botaurus lengitinosus*	AMBI
Blak-crested Night-Heron	*Nycticorax nycticorax*	BCNH
Canada Goose	*Branta canadensis*	CAGO
American Black Duck	*Anas rubripes*	ABDU
Mallard	*Anas platyrhynchos*	MALL
Ring-necked Duck	*Aythya collaris*	RNDU
Turkey Vulture	*Cathartes aura*	TUVU
Osprey	*Pandion haliaetus*	OSPR
Northern Harrier	*Circus cyaneus*	NOHA
Sharp-shinned Hawk	*Accipiter striatus*	SSHA
Broad-winged Hawk	*Buteo platypterus*	BWHA
Red-tailed Hawk	*Buteo jamaicensis*	RTHA
American Kestrel	*Falco spalverius*	AMKE
Merlin	*Falco columbarius*	MERL
Greater Yellowlegs	*Tringa melanoleuca*	GRYE
Spotted Sanpiper	*Actitis macularia*	SPSA
Upland Sandpiper	*Bartramia longicauda*	UPSA
Least Sandpiper	*Calidris minutilla*	LESA
Short-billed Dowitcher	*Limnodromus griseus*	SBDO
Common Snipe	*Gallinago gallinago*	COSN
Ring-billed Gull	*Larus delawarensis*	RBGU
Herring Gull	*Larus argentatus*	HEGU
Iceland Gull	*Larus glaucoides*	ICGU
Great Black-backed Gull	*Larus marinus*	BBGU
Common Tern	*Sterna hirundo*	COTE
Mourning Dove	*Zenaida macroura*	MODO
Black-billed Cuckoo	*Coccyzus erythropthalmus*	BBCU
Short-eared Owl	*Asio flammeus*	SEOW
Common Nighthawk	*Chordeiles minor*	CONI
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA
Northern Flicker	*Colaptes auratus*	NOFL
Olive-sided Flycatcher	*Contopus borealis*	OSFL
Yellow-bellied Flycatcher	*Empidonax flaviventris*	YBFL
Alder flycatcher	*Empidonax alnorum*	ALFL
Eastern Phoebe	*Sayornis phoebe*	EAPH
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
Tree Swallow	*Tachycineta bicolor*	TRSW
Bank Swallow	*Riparia riparia*	BKSW
Barn Swallow	*Hirundo rustica*	BNSW
Gray Jay	*Perisoreus canadensis*	GRJA
Blue Jay	*Cyanocitta cristata*	BLJA
American Crow	*Corvus brachyrhynchos*	AMCR
Common Raven	*Corvus corax*	CORA
Black-capped Chickadee	*Parus atricapillus*	BCCH
Boreal Chickadee	*Parus hudsonicus*	BOCH
Red-breasted Nuthatch	*Sitta canadensis*	RBNU

House Wren	*Troglodytes aedon*	HOWR
Winter Wren	*Troglodytes troglodytes*	WIWR
Golden-crowned Kinglet	*Regulus satrapa*	GCKI
Ruby-crowned Kinglet	*Regulus calendula*	RCKI
Eastern Bluebird	*Sialia sialis*	EABL
Veery	*Catharus fuscescens*	VEER
Swainson's Thrush	*Catharus ustulatus*	SWTH
Hermit Thrush	*Catharus guttatus*	HETH
American Robin	*Turdus migratorius*	AMRO
Cedar Waxwing	*Bombycilla cedrorum*	CEWA
Solitary Vireo	*Vireo solitarius*	SOVI
Philadelphia Vireo	*Vireo philadelphicus*	PHVI
Red-eyed Vireo	*Vireo olivaceus*	REVI
Tennessee Warbler	*Vermivora peregrina*	TEWA
Nashville Warbler	*Vermivora ruficapilla*	NAWA
Yellow Warbler	*Dendroica petechia*	YEWA
Chestnut-sided Warbler	*Dendroica pensylvanica*	CSWA
Magnolia Warbler	*Dendroica magnolia*	MAWA
Yellow-rumped Warbler	*Dendroica coronata*	YRWA
Black-throated Green Warbler	*Dendroica virens*	BGWA
Blackburnian Warbler	*Dendroica fusca*	BNWA
Palm Warbler	*Dendroica palmarum*	PAWA
Bay-breasted Warbler	*Dendroica castanea*	BBWA
Blackpoll Warbler	*Dendroica striata*	BLWA
Black-white Warbler	*Mniotilta varia*	BWWA
American Redstart	*Setophaga ruticilla*	AMRE
Ovenbird	*Seiurus aurocapillus*	OVEN
Northern Waterthrush	*Seiurus noveboracensis*	NOWA
Mourning Warbler	*Oporornis philadelphia*	MOWA
Common Yellowthroat	*Geothlypis trichas*	COYO
Canada Warbler	*Wilsonia canadensis*	CAWA
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR
Chipping Sparrow	*Spizella passerina*	CHSP
Clay-colored Sparrow	*Spizella pallida*	CCSP
Savannah Sparrow	*Passerculus sandwichensis*	SASP
Fox Sparrow	*Passerella iliaca*	FOSP
Song Sparrow	*Melospiza melodia*	SOSP
Lincoln's Sparrow	*Melospiza lincolnii*	LISP
Swamp Sparrow	*Melospiza georgiana*	SWSP
White-throated Sparrow	*Zonotrichia albicollis*	WTSP
Dark-eyed Junco	*Junco hyemalis*	DEJU
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL
Common Grackle	*Quiscalus quiscula*	COGR
Brown-headed Cowbird	*Molothrus ater*	BHCO
Purple Finch	*Carpodacus purpureus*	PUFI
House Finch	*Carpodacus mexicanus*	HOFI
White-winged Crossbill	*Loxia leucoptera*	WWCR
Pine Siskin	*Carduelis pinus*	PISI
American Goldfinch	*Carduelis tristis*	AMGO
Evening Grosbeak	*Coccothraustes vespertinus*	EVGR

Chapitre II

Nested bird and micro-habitat assemblages in a peatland archipelago

Nested bird and micro-habitat assemblages in a peatland archipelago. Sophie Calmé and André Desrochers. Centre de recherche en biologie forestière, Faculté de foresterie et de géomatique. Université Laval, Québec, Canada G1K 7P4

Résumé Les assemblages biotiques des habitats insulaires sont hiérarchisés quand les assemblages comportant peu d'espèces sont des sous-ensembles des assemblages plus riches en espèces. Cette hiérarchisation des assemblages d'espèces est fréquente et peut résulter en milieu insulaire de processus d'extinction sélective ou de colonisation fréquente. Elle peut aussi être créée par une distribution hiérarchisée des habitats parmi les îles ou encore par un artéfact d'échantillonnage passif. Nous avons échantillonné 67 tourbières (7-843 ha) du Québec méridional afin de mesurer le degré de hiérarchisation des assemblages d'espèces d'oiseaux parmi ces tourbières et évaluer l'hypothèse de la distribution non aléatoire des habitats. Les assemblages d'espèces et de microhabitats étaient fortement hiérarchisés entre les tourbières. Le tri des sites selon la richesse en espèces, la richesse en microhabitats ou la superficie des tourbières n'avait aucun effet sur le degré de hiérarchisation des assemblages d'oiseaux. Cependant, les microhabitats étaient significativement moins hiérarchisés lorsque les sites étaient ordonnés selon les superficies des tourbières que lorsqu'ils étaient ordonnés selon la richesse en microhabitats. Tel qu'attendu si les associations entre les oiseaux et les microhabitats sont responsables du patron de distribution hiérarchisé, nous avons trouvé une corrélation positive entre la contribution des espèces d'oiseaux et celle des microhabitats au degré de hiérarchisation des sites individuels. Malgré cela, le degré de hiérarchisation des assemblages de microhabitats était significativement moindre que celui des assemblages d'espèces d'oiseaux, possiblement à cause des colonisations fréquentes des sites par les oiseaux, ou par un effet d'échantillonnage passif.

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 occurrences 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; Wright et al. 1998).

Four hypotheses can account for nested patterns of species distribution (Worthen 1996; Cook and Quinn 1998; Wright et al. 1998). They are: (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, then "island" area should be an important determinant of bird species occurrence, as with the previous hypothesis. In contrast with the previous 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 Atmar and Patterson's N (1986), should also not be different when sites are ranked by habitat richness or species richness. Fig. 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.

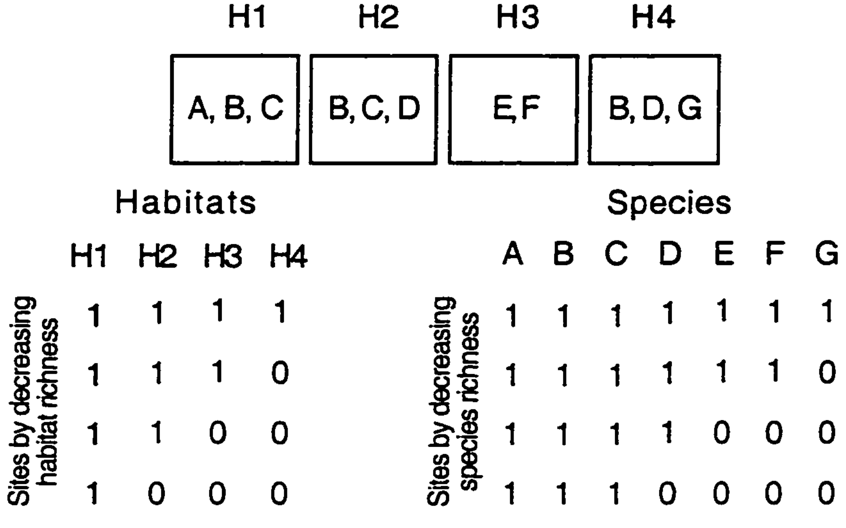

Fig. 1 Hypothetical case of nestedness of species subsets caused by nestedness of microhabitats. The four microhabitats H1, H2, H3, and H4 share common species (B, C, D), but also support specialists (A, E, F, G).

Peatlands of southern Canada are patchily distributed, thus forming a natural "archipelago" in a matrix of forests, built areas, and fields. Peatlands are isolated from the surrounding drainage basin, for peat accumulation causes the water table to raise 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, 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, relationships between species richness, microhabitat richness, and peatland area. We assess the selective extinction, selective colonization, passive sampling and habitat nestedness hypotheses.

Methods

Study area

The study area was located in southern Québec, 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 to what extent species were confined to peatlands. These habitats included hayfields, pastures, abandoned farmlands, recent clearcuts, 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 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. The number of surrounding habitat counts (n = 56) was smaller than the number of sampled peatlands, because some of the former were in proximity to more than one peatland. 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 above ground. 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 phoenicus*), and raptors (except for northern harrier, *Circus cyaneus*). We kept 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, pair members 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 10 classes of microhabitats found in peatlands in the study area (Table 1). Classes were based mainly on height and density of trees (classes 1 to 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 of 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 assemblages. Microhabitats are much easier to detect than are particular species of plants, and thus recorded absences of microhabitats were considered reliable.

Table 1 Classes of microhabitats found in peatlands in Southern Québec

Class	Tree cover (%)	Dominant tree height (m)	% of peatlands	Remarks
1	< 5	variable	38.8	BS[a], L[b], B[c], 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

[a] BS, Black Spruce *(Picea mariana)*
[b] L, Larch *(Larix laricina)*
[c] B, Old-field Birch *(Betula populifolia)*

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 labeled. 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 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 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 a path diagram. These coefficients indicate the strengths of associations as well as their direction. For instance, the structural equation that described SR was:

$$\mathrm{SR} = p_1 \cdot \mathrm{HR} + p_2 \cdot \mathrm{A} + p_3 \cdot \mathrm{SE} + \mathrm{var}\ e$$

where p_1, p_2, and p_3, are the path coefficients between SR and HR, A, and SE, respectively, and var e is the variance associated with the error term of SR.

To meet assumptions of normality of the variables, we transformed HR to its squared-root, and A to its natural logarithm. For each variable, we substracted 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. According to Coleman et al. (1982), the hypothesis of random distribution should be rejected if more than one-third of the points lay outside one standard deviation of the expected curve, and/or if the points are not evenly distributed about it.

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 descriptors (species and microhabitats) in all sites with more items than the poorest one in which they are found (Patterson and Atmar 1986). Thus, a 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, PN0 (Wright et al. 1998), which allows comparisons between matrices of different sizes. It is calculated according to the formula:

$$PN0 = 100 \times (EN0 - N) / EN0$$

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

It is difficult to assess analytically the standard error (SE) of N and PN0 indices. Thus, we used a bootstrap procedure (Efron and Tibshirani 1993) to estimate SEs 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 PN0 indices, and repeated these steps 1000 times to obtain a sampling distribution from which estimates and their SE 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, three were found only in peatlands, while four species were more strongly associated with nearby habitats (Table 2).

The occurrence of five other species was similar in peatlands and open nearby habitats. However, only 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 by 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 (< 5m) and a tree cover of at least 20%. These species avoided open habitats or semi-open habitats with tall trees (> 5m). By contrast, commonly-occurring savannah sparrows were strongly associated with microhabitats 1 and 2 (open), while they avoided microhabitats 4, 5 and 7 (more treed). 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.

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 10 sites are shown. Species were sorted according to their preference for bogs or surrounding open sites.

Common name	Scientific name	Code	% of peatlands plots (n=67)	% of nearby plots (n=56)	Chi-square	P^a
Lincoln's sparrow	*Melospiza lincolnii*	LISP	92.5	1.8	100.5	**
palm warbler	*Dendroica palmarum*	PAWA	88.1	0.0	94.8	**
Nashville warbler	*Vermivora ruficapilla*	NAWA	86.6	7.1	77.0	**
white-throated sparrow	*Zonotrichia albicollis*	WTSP	91.0	14.3	73.0	**
common yellowthroat	*Geothlypis trichas*	COYE	100	30.4	68.3	**
hermit thrush	*Catharus guttatus*	HETH	70.1	1.8	59.9	**
alder flycatcher	*Empidonax alnorum*	ALFL	43.3	3.6	25.5	**
yellow-rumped warbler	*Dendroica coronata*	YRWA	19.4	0.0	12.1	**
northern harrier	*Circus cyaneus*	NOHA	34.3	8.9	11.2	**
magnolia warbler	*Dendroica magnolia*	MAWA	20.9	1.8	10.4	**
swamp sparrow	*Melospiza georgiana*	SWSP	16.4	0.0	10.1	**
eastern kingbird	*Tyrannus tyrannus*	EAKI	28.3	10.7	5.9	ns
american robin	*Turdus migratorius*	AMRO	35.8	23.2	2.3	ns
tree swallow	*Tachycineta bicolor*	TRSW	22.4	14.3	1.3	ns
savannah sparrow	*Passerculus sandwichensis*	SASP	67.2	69.6	0.09	ns
barn swallow	*Hirundo rustica*	BASW	4.5	19.6	6.9	ns
song sparrow	*Melospiza melodia*	SOSP	38.8	66.1	9.1	*
red-winged blackbird	*Agelaius phoeniceus*	RWBL	17.9	42.9	9.2	**
killdeer	*Charadrius vociferus*	KILL	0.0	17.9	13.0	**[b]
bobolink	*Dolichonyx oryzivorus*	BOBO	1.5	28.6	18.8	**

[a] The level of significance is corrected for the dependance between the 20 chi-square tests using α / n; ** tests significant at the 5% level (corrected $P \leq 0.0025$); * significant at the 10% level (corrected $P \leq 0.005$); ns, non significant ($P > 0.005$).

[b] Fisher's exact test in this case, because there were less than five observations in half of the cells.

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; underlined) are shown. *P*-values of the test of general linear association appear on the second line. 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 in Table 1, for species in Table 2.

Microhabitat	COYE	LISP	WTSP	PAWA	NAWA	HETH	SASP	ALFL	SOSP	NOHA	TRSW	MAWA	YRWA	SWSP	UPSA
	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.05^{ns}	0.07^{ns}	0.09^{ns}	0.14^{ns}	0.11^{ns}	0.31^{ns}	<0.001*	0.11^{ns}
1	-4.1	-2.6	-4.0	-3.7	-2.7	-2.0	7.0	-1.9	0.0	2.1	-0.1	-1.2	-1.1	0.0	-0.6
2	-1.5	0.2	-1.0	-1.6	-2.4	-2.2	4.1	-0.6	0.34	-1.4	-0.6	-0.6	-1.4	-0.5	0.8
3	-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
4	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
5	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
6	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
7	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
9	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

* Chi-square values significant at the 5% level (corrected $P \leq 0.0033$); ns, non significant (corrected $P > 0.0067$). The level of significance is corrected for the dependance between the 15 chi-square tests using α / n. Fisher's exact test is used when at least 25% of the cells have expected count smaller than 5.

Species richness, microhabitat richness, and peatland area

Bird species richness, microhabitat richness, peatland area, and sampling effort were highly correlated (Table 4).

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.

	SR	SE	A	HR
SR	1			
SE	0.74	1		
A	0.78	0.84	1	
HR	0.74	0.70	0.79	1

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.

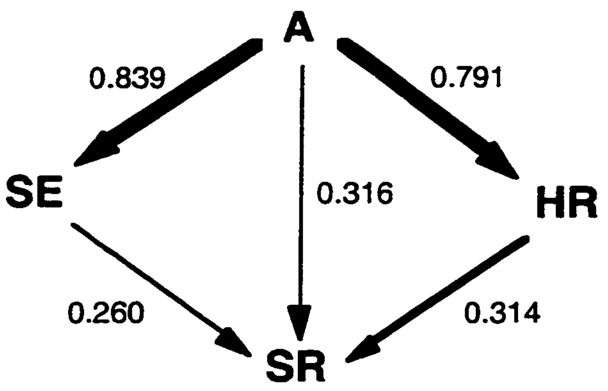

Fig. 2 Path diagram of the relationships between species richness, microhabitat richness, sampling effort and peatland area. Values of path coefficients are placed along the arrows. Arrows indicate the direction of causality, and their thickness, the strength of the relationships (thick for $p<0.001$,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

Passive sampling

Half of the points lay within ± 1 SD from the species-area relationship expected if species were randomly distributed among peatlands (Fig. 3). It is more than the limit fixed by Coleman et al. (1982) at one-third of the points. Only 18 of the 67 experimental points lay above the curve, and several of those below the curve strongly departed. According to Coleman et al. (1982), the hypothesis of random placement does not hold if the distribution of experimental points about the curve is not even. However, distribution of bird species according to peatland area did not strongly differ from random expectations (Chi-square = 3.5, df = 1, $P = 0.06$).

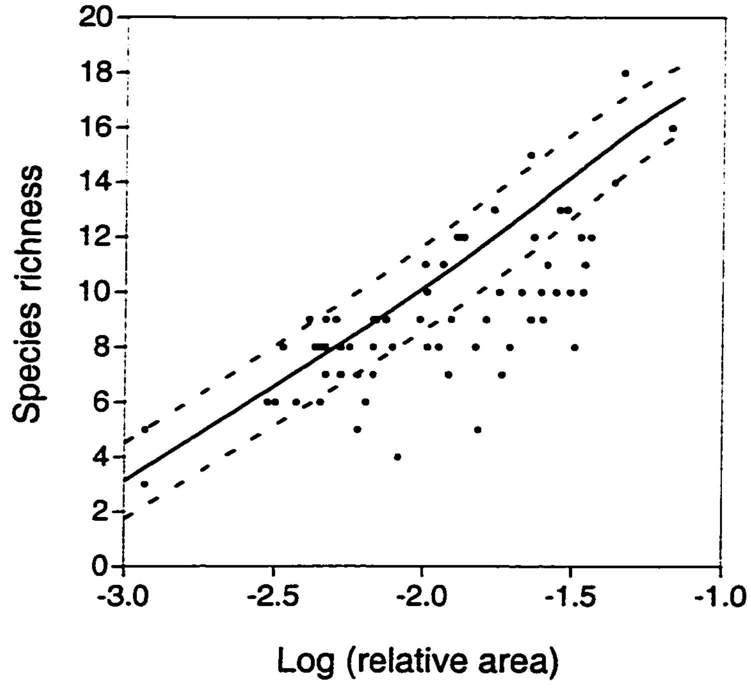

Fig. 3 Expected species-area curve generated under the hypothesis of random species distribution among peatlands. Expected values (solid line) and associated ± 1 SD limits (dashed lines) are shown. Dots represent observed species richness.

Nestedness

Species and microhabitat assemblages were strongly nested among peatlands. Both matrices of species and microbitats present in the 67 sites can be viewed at the Peatland Ecology Research Group's Web site [http://www.fsaa.ulaval.ca/gret-perg/index.html]. The bird species × sites matrix was significantly nested regardless of site ranking method (Table 5). Five species were found only in the 20 species-richest peatlands: common snipe, upland sandpiper, american bittern, clay-colored sparrow, and field sparrow. The microhabitats × 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.

Table 5 Nestedness of bird species and microhabitats types within the 67 studied peatlands as calculated by N and standardized PN0.

Index	Birds					Microhabitats				
	Observed	(S.E.)	Random	z	P	Observed	(S.E.)	Random	z	P
N										
Sites sorted by species richness[a]	386	± 24	784	-17.3	*	---		---		
Sites sorted by microhabitat richness[a]	436	± 27	800	-12.6	*	209	± 14	295	-5.7	*
Sites sorted by area	453	± 25	798	-14.4	*	289	± 21	301	-0.6	
PN0										
Sites sorted by species richness	48.0	± 3.1		14.1	*	---		---		
Sites sorted by microhabitat richness	45.5	± 3.3		12.3	*	29.1	± 4.9	0.694	5.8	*
Sites sorted by area	43.2	± 3.1		14.5	*	4.0	± 7.1	0.690	0.5	

[a] The bird species × sites matrix had 1474 cells, while the matrix of microhabitats × sites had 670 cells

* $P < 0.0001$ for observed vs. random

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 × sites matrix (t-tests on PN0 indices, all $P > 0.3$). On the other hand, the microhabitats × sites matrix was significantly less nested when sites were sorted by area 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-dependent 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 (48.0 vs. 29.1, $t = 3.2$, $P = 0.002$). 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 species, Ni values cannot be high, since those species are seldom absent from sites. To account for this bias, we adjusted Ni values by dividing them by the total number of absences for each species. There was a strong relationship between species occurrences and their adjusted Ni's ($R^2 = 0.72$, $n = 21$, $P < 0.001$), 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 respectively: $r_S = 0.23$, $P = 0.03$ and $r_S = 0.36$, $P = 0.001$, one-tailed tests). Thus, habitat and species nestedness not only occurred, but coincided spatially.

Discussion

In this study, we demonstrated that nestedness of microhabitats occurs 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: 231-235), these claims were little supported by distribution data.

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 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 fen sections of peatlands, and their distribution among ombrotrophic peatlands thus depended on the presence of the two vegetation classes representing this uncommon microhabitat. Besides the clear preference for certain microhabitats in several peatland birds, the positive relationship between the contributions of species and microhabitats to the nestedness of individual peatlands provides direct support for Cutler's (1991) point.

Although vegetation structure and composition have often been considered in studies on 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 center 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. Below, we discuss factors that discriminate between alternative hypotheses based on extinction, colonization, passive sampling and microhabitat distribution.

Sampling effect

The random placement model provided a rather inconclusive result, especially 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 breeding bird 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.

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. Andrén (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 was 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 indeed. Worthen (1996) proposed that a passive sampling model such as Coleman's (1981) random placement model could be used. In a recent paper, Worthen and collaborators (1998) first tested and rejected this model prior to hypothesize 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 maintained their approximate size until now. Moreover, peatland birds did not generally meet the assumption stated by Lomolino et al. (1989), that in relaxing faunas "island" area should be the main determinant of species occurrence. The only exceptions were upland sandpiper, a semi-colonial species with large area requirements in eastern Canadian peatlands (Calmé and Haddad 1996), swamp sparrow, American robin, palm warbler, and red-winged blackbird (Chapter III). 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 than 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 ability to disperse of most birds, which precludes strong inference 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. However, although microhabitat assemblages were strongly nested, they were 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 additionnal 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 70's (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 which are also usually the largest ones will contain species not found in poorer sites (Cutler 1994). During the 80's, many empirical studies agreed that several small sites encompassed more species than a large one or a few large 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 habitat requirements are the ultimate factors (Cody 1983) of species distribution, it should however remain the most important consideration for designing protected areas (Simberloff and Martin 1991).

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Chapitre III

Biogeographic Aspects of the Distribution of Bird Species breeding in Québec's Peatlands

Biogeographic Aspects of the Distribution of Bird Species breeding in Québec's Peatlands. Sophie Calmé and André Desrochers, Centre de recherche en biologie forestière, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Canada G1K 7P4

Résumé Les tourbières méridionales de l'Est du Canada font face à une situation inquiétante: réduction progressive des superficies et destruction causées par l'étalement urbain, l'agriculture, la foresterie et l'exploitation de la mousse de tourbe. Il en résulte une perte d'habitat et un isolement croissant des tourbières rémanentes. Nous avons vérifié si la distribution des espèces d'oiseaux des tourbières était conforme aux prédictions de la biogéographie insulaire pour un échantillon de 63 tourbières d'une même région. Nous avons aussi déterminé les facteurs affectant la présence de 10 espèces d'oiseaux communes dans les tourbières, dont deux montrent une préférence marquée pour cet habitat. Nous avons caractérisé la superficie, la structure de la végétation et l'isolement relatif de chacune des tourbières sélectionnées. À partir de cartes numérisées obtenues par la photointerprétation des tourbières, nous avons sélectionné 18 variables caractérisant la complexité de la composition et de la configuration des parcelles de microhabitats. Nous avons ensuite établi un indice d'hétérogénéité de l'habitat issu de la combinaison de huit de ces variables. La richesse en espèces d'oiseaux était principalement expliquée par la richesse en microhabitats et, dans une moindre mesure, par le biais d'échantillonnage. Ces résultats supportent l'hypothèse de la diversité des habitats et celle de l'échantillonnage passif. Plus de la moitié de la variation de l'occurence des espèces était cependant expliquée par le degré d'hétérogénéité des tourbières, soulignant ainsi la différence existant entre les facteurs influençant la richesse totale en espèces et les espèces individuelles. La présence de la Paruline à couronne rousse, une espèce nichant presque exclusivement dans les tourbières, dépendait à la fois de la superficie des tourbières et de leur isolement relatif. Ce résultat est cohérent avec la théorie biogéographique. Toutefois, l'influence relative de ces variables était trop faible pour justifier des mesures spéciales de protection, d'autant plus que la plupart des autres espèces des tourbières nichaient aussi dans les habitats environnants.

Introduction

Peatlands cover about 111 million hectares in Canada (Zoltai, 1979). It is estimated that 20 million hectares of this ecosystem have disappeared since 1800 in the country, and that millions of others are degraded (Government of Canada, 1991). While this loss represents a relatively small fraction of all peatlands in Canada, pressure on peatlands is high in inhabited regions, because of drainage for agriculture and forestry, urban sprawl and peat moss exploitation (Desrochers, Rochefort & Savard, 1998). Many peatlands either experienced a reduction of their area or were fragmented or disappeared altogether as a result of human activity, and the process is still ongoing.

Will the increasing isolation and reduction of remaining peatlands affect wildlife in the long term? Peatlands are typically distributed as "islands" in the eastern Canadian landscapes. Like real islands, peatland islands can clearly be distinguished from the landscape in which they are embedded, and they have been isolated for considerable periods of time relative to the lifespan of wildlife species. However, unlike oceanic islands, peatlands are not surrounded by a totally inhospitable environment for terrestrial species. Thus many species occurring in peatlands, especially ubiquitous ones, may also have substantial populations in the surroundings, as suggested Margules, Higgs & Rafe (1982) for forest fragments. Whether animal populations in eastern Canadian peatlands are truly discrete or act as subdivided populations is not only of ecological, but also of conservation interest.

One way to assess the relative importance of 'island' vs 'continental' peatland bird dynamics is to use island biogeography (MacArthur & Wilson, 1967) and associated hypotheses as a theoretical framework. Even though island dynamics hinge on dispersal ability (Diamond, 1984), which is hard to document, some predictions can be made if organisms use habitat patches like true isolated islands (Gilbert, 1980). The most basic expectation is a positive species-area relationship following the relationship $S=cA^z$, where S represents species richness, c is a constant, A is the area, and z is the area effect. Besides MacArthur & Wilson's (1967) theory however, at least two explanations unrelated to isolation have been proposed to explain the relationship between area and species richness. A first explanation is the habitat diversity hypothesis (Williams, 1964), which states that the number of habitat types increases along with area as a result of spatial changes, e.g. edaphic conditions, and because each habitat type supports its own set of species. Another explanation unrelated to isolation is the passive sampling hypothesis (Connor & McCoy, 1979), which states that the chance of encountering a new species increases independently of any ecological process, as sample size increases. Before inferring biogeographical mechanisms, one thus needs to test Williams' (1964) and Connor & McCoy's (1979) hypotheses.

In this paper, we determine how bird species distribution in peatlands conforms with expectations from island dynamics. We quantify the species-area relationship, and assess the effect of habitat area and isolation, as well as passive sampling, habitat diversity and heterogeneity, on species richness. Finally, we present the patterns of abundance and occurrence of 19 of the most common bird species in peatlands including two peatland specialists, and discuss implications for peatland conservation in eastern Canada.

Materials and methods

Study area and sites

The study area was located in southern Québec, Canada, within a landscape characterized by a mosaic of forest stands and farmland. Peatlands in this area range approximately from a few hectares to a thousand hectares in size (Fig. 1). The study area lays within the deciduous zone, and is characterized by the presence of red maple (*Acer rubrum* L.) stands on sandy sites (Thibault, 1985), where most peatlands are found. The presence of Balsam fir (*Abies balsamea* L.) is also characteristic except in the southeast portion of the study area. We sampled sixty-three ombrotrophic peatlands ranging in size from 10.9 to 843 ha (Fig. 2). Large peatlands were overrepresented in our sample, as many smaller peatlands were discarded for they were too small to be sampled by transects and/or they were strongly disturbed by drainage. Most peatlands in the region developed after the icefields of the Wisconsin period melted, around 10,000 yrs ago, but some expanded between 6,000 and 4,000 yrs ago, during a cold and humid climatic event, so larger peatlands usually include more recent minerotrophic areas (also called fens).

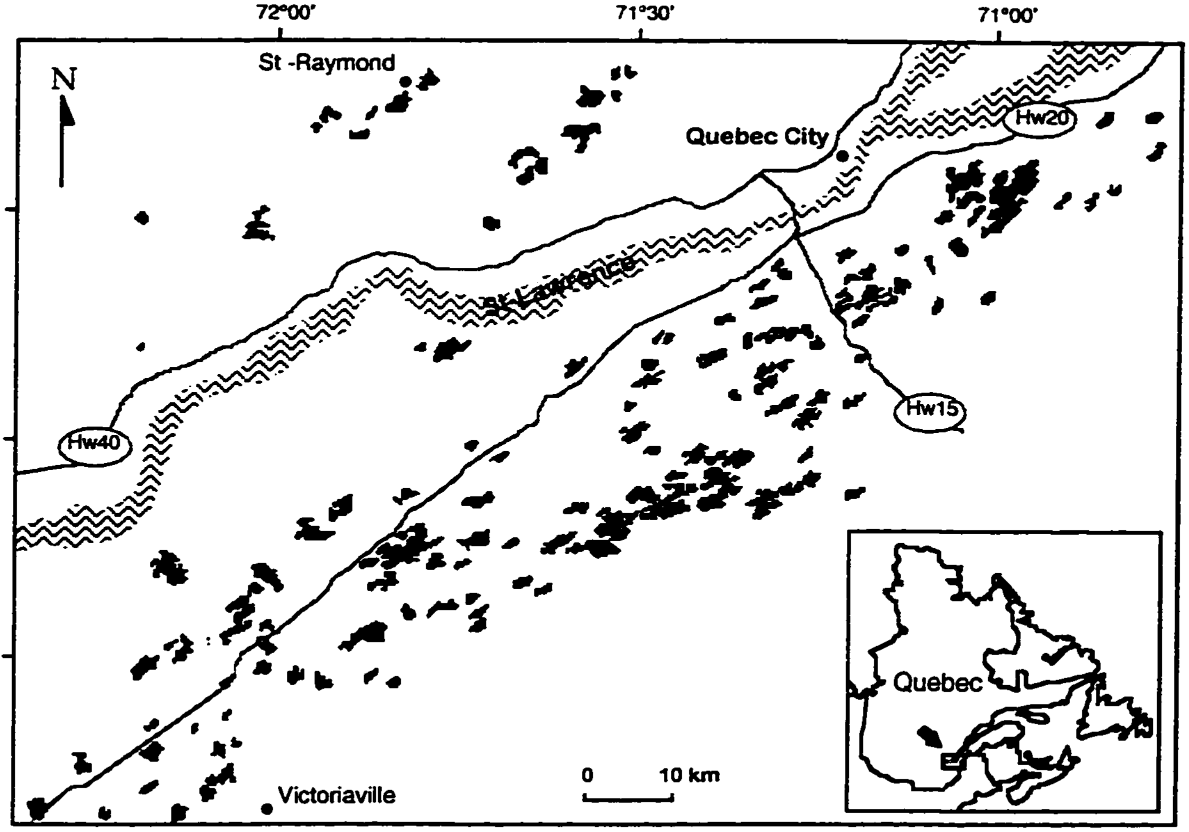

FIG. 1. The "archipelago" of peatlands in the study area. The two most distant peatlands in our sample were separated by 160 km.

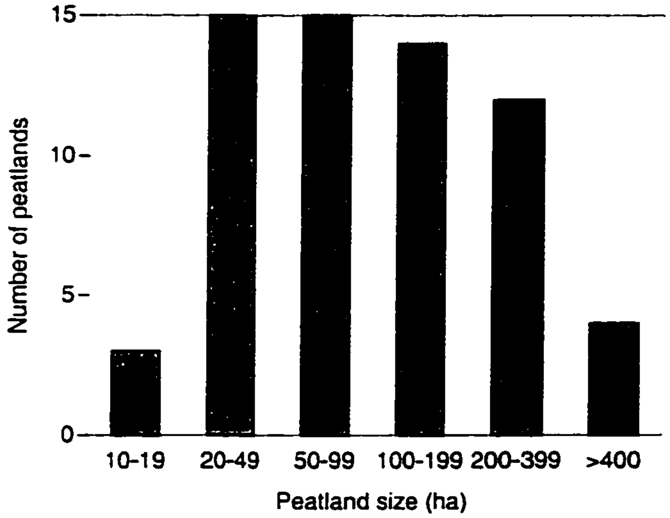

FIG. 2. Frequency of distribution of peatland areas in our sample. N = 63.

Bird censuses

We sampled bird populations within peatlands from June 4 to July 14, 1995, using both transect lines and fixed-radius point counts (Ralph *et al.*, 1993). Point counts were conducted using a 100-m radius and lasted 10 min, during which all birds seen or heard were recorded. Along transect lines, all birds seen or heard were recorded up to 100 m on either side of the line. The total length of transect lines in each peatland was proportional to peatland area, but sampled ratio was negatively related to area (Fig. 3), so sampling effort was proportionally lower in larger peatlands. Both transect lines and point counts were located at least 150 m from the peatland edge (% trees > 5 m exceeding 50%), leaving a 50-m wide buffer zone to avoid observation of birds in or near the edge of adjacent habitats.

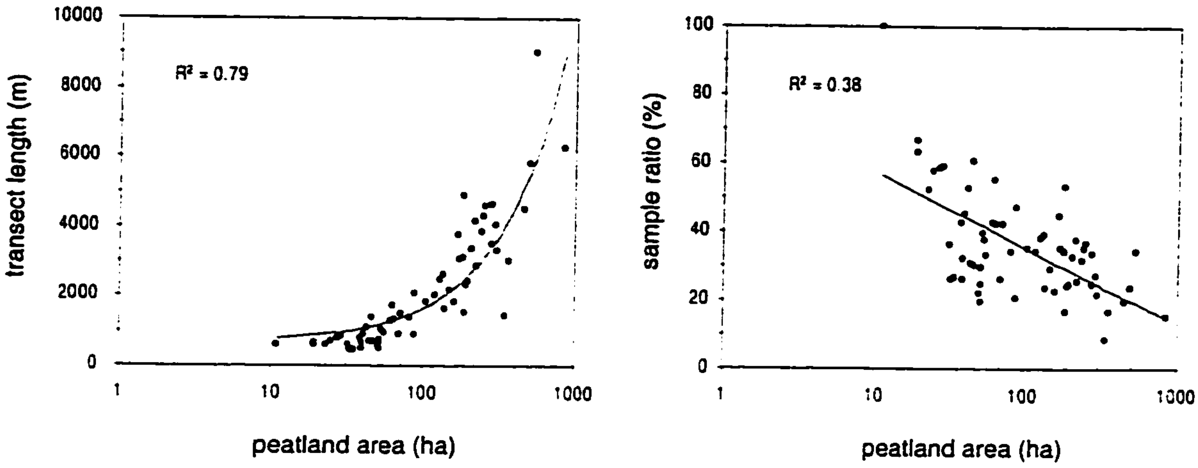

FIG. 3. The relationship between peatland area and length of transect (left graph) shows that absolute sampling effort increases with peatland size (n=63), but tends to decrease in relative terms (right graph).

A total of eighty-one bird species were detected, but only twenty-one were included in the analyses (Table 1). To restrict our analysis to species well associated with peatlands, we retained only species (1) that are known to breed in peatlands (Gauthier & Aubry, 1994), (2) for which the sampling methods were apropriate, (3) species breeding during the sampling period, and (4) species whose territories did not encompass the peatland and the surroundings. Aditional details can be found in Chapter II. Two rare species (Clay-colored

Sparrow, *Spizella pallida*, and Field Sparrow, *Spizella pusilla*) were included because their presence and territoriality had been confirmed at least two years at the same site (unpubl. data).

Vegetation mapping

We identifed ten types of microhabitats found in peatlands in the study area (Chapter II), based mainly on height and density of trees but also on spatial arrangement of trees in the case of clumps of black spruce (*Picea mariana* [Mill.] BSP). Two microhabitats with fen attributes reflected the presence of open water, and of more diverse vegetation. These two classes are rare in ombrotrophic peatlands, but can be found along edges where decomposition is higher, or in complex peatlands.

We mapped the ten types of microhabitats using recent 1:15000 aerial photographs with. Photo-interpretation was validated in the field by verifying whether both classification and limits between microhabitats were accurate. This step was crucial since interpretation is sometimes difficult due to the low height of the vegetation (often below 2 m). In the final step, maps obtained were digitized and analyzed using a Geographic Information System. We considered that optical distortion on aerial photographs was negligible for our purposes since we used as many photographs as possible, and because peatlands have little or no relief.

Quantifying peatland heterogeneity

Beyond the mere count of the number of habitat types, habitat spatial heterogeneity characterizes the composition and configuration of patches of different habitat types. Only a few studies have measured the effect of spatial heterogeneity in vegetation on bird species richness, with contrasting results. For instance, Wiens (1974) found no relationship between richness of grassland bird species and an index of heterogeneity based on evenness, whereas Roth (1976) also using evenness but with a different type of information, found that heterogeneity had a strong effect on bird diversity in various habitats. Li & Reynolds (1995) define heterogeneity «as the complexity and/or variability of a system property in space and/or time», which implies that several components are included in the same concept, and may explain why results vary according to measured variables.

TABLE 1. The twenty-one bird species considered for analyses, and their number of occurrence in the 63 peatlands studied.

Order	Species name	Species code	Species occurrence
Falconiformes	Northern Harrier *Circus cyaneus* (L.)	noha	23
Charadriiformes	Upland Sandpiper *Bartramia longicauda* (Bechstein)	upsa	4
	Common Snipe *Gallinago gallinago* (L.)	cosn	4
Passeriformes	Alder Flycatcher *Empidonax alnorum* (Brewster)	alfl	27
	Eastern Kingbird *Tyrannus tyrannus* (L.)	eaki	19
	Tree Swallow *Tachycineta bicolor* (Vieillot)	trsw	15
	Hermit Thrush *Catharus guttatus* (Pallas)	heth	45
	American Robin *Turdus migratorius* (L.)	amro	24
	Nashville Warbler *Vermivora ruficapilla* (Wilson)	nawa	57
	Magnolia Warbler *Dendroica magnolia* (Wilson)	mawa	14
	Yellow-rumped Warbler *Dendroica coronata* (L.)	yrwa	13
	Palm Warbler *Dendroica palmarum* (Gmelin)	pawa	56
	Common Yellowthroat *Geothlypis trichas* (L.)	coye	63
	Clay-colored Sparrow *Spizella pallida* (Swainson)	ccsp	1
	Field Sparrow *Spizella pusilla* (Wilson)	fisp	1
	Savannah Sparrow *Passerculus sandwinchensis* (Gmelin)	sasp	45
	Song Sparrow *Melospiza melodia* (Wilson)	sosp	27
	Lincoln's Sparrow *Melospiza lincolnii* (Audubon)	lisp	61
	Swamp Sparrow *Melospiza georgiana* (Latham)	swsp	11
	White-throated Sparrow *Zonotrichia albicollis* (Gmelin)	wtsp	59
	Red-winged Blackbird *Agelaius phoeniceus* (L.)	rwbl	12

We computed statistics that characterize complexity in composition and configuration of patches in categorical maps (see Li & Reynolds, 1995) using the program Fragstats (McGarigal & Marks, 1993). Eighteen variables were selected, that characterized patch type and size, contrast, shape, and diversity within each peatland. Five of them were eliminated after testing for multicollinearity. The variables retained in the analysis were: largest patch index (LPI), number of patches (NP), patch density (PD), patch size standard deviation (PSSD), patch size coefficient of variation (PSCV), contrast-weighted edge density (CWED), mean edge contrast index (MECI), mean patch fractal dimension (MPFD), area-weighted mean patch fractal dimension (AWMPFD), mean proximity index (MPI), patch richness (PR), patch richness density (PRD), and contagion index (CONTAG). A discussion of the variables and mathematical definitions are provided by McGarigal & Marks (1993). A Principal Coordinates Analysis was performed after transformation and standardization of the variables to encompass as much spatial information as possible within one or several principal axes. We performed the analysis using the PCoord procedure of the R software (Legendre & Vaudor, 1991). The first axis in the Principal Coordinates Analysis explained 15.1% of the variance ($\lambda = 223.7$). It was significantly correlated ($\geq r \geq > 0.34$; $p < 0.01$) to eight of the thirteen landscape variables (Table 2). In particular, PSCV was almost perfectly correlated with the first axis. However, the other variables captured a different information.

TABLE 2. Coefficients of correlation (Pearson's r) of the first axis (A1) of the Principal Coordinates Analysis with thirteen landscape variables. Variables are ordered according to their correlation with A1, from the most negative to the most positive value. Levels of significance are into parentheses. Signification of abbreviations can be found in the text.

	PSCV	PSSD	NP	PR	PRD	MECI	MPI	AWMPFD	CONTAG	LPI	PD	CWED	MPFD
A1	-0.988 (<0.01)	-0.658 (<0.01)	-0.617 (<0.01)	-0.576 (<0.01)	0.486 (<0.01)	-0.388 (<0.01)	-0.379 (<0.01)	-0.295 (0.02)	-0.086 (0.50)	-0.085 (0.51)	0.096 (0.45)	0.102 (0.43)	0.336 (<0.01)

In subsequent analyses, the new coordinates of sites along the first principal axis were used as a measure of heterogeneity within peatlands. Note that increasing values along this axis indicated a decreasing heterogeneity, i.e., the higher the value for a site, the more homogeneous the site.

Measuring peatland relative isolation

Relative isolation of peatlands was measured as the inverse of the total area of peatlands present in a 10 km-radius around the approximate centroid of each peatland, excluding the area of sample peatland (< 0.03 % of sampled region). This measure does not take into account spatial arrangement of peatlands. However, it provides an estimate of the availability of the habitat regionally, and thus better reflects isolation of the habitat in the landscape than does the distance to the nearest patch (Vos & Stumpel, 1995), as the regional amount of habitat is thought to influence the rate of dispersal (Askins, Philbrick & Sugeno, 1987). Measurements were done with an electronic planimeter using recent aerial photographs.

Assessing the relationship between peatland metrics and species use

We used multiple regression to test the relationship between bird species richness, peatland area, isolation, microhabitat richness, and heterogeneity after correcting for sampling effort. Although we have already evaluated the relationships between species richness, sampling effort, peatland area, and microhabitat richness with a path analysis in Chapter II, the present regression analysis involved two new explanatory variables (isolation and peatland heterogeneity), and a smaller set of peatlands. The contribution of each variable to the model after the effects of all other variables have been factored out was assessed with type II sums of squares (Littell, Freund & Spector, 1991). To normalize variables and stabilize the variance, peatland area, sampling effort and relative isolation were log-transformed, while species and microhabitat richness were transformed by square root. The analysis was performed with the REG procedure of SAS software (SAS Institute Inc., 1989).

Relationships between bird species abundances and the variables that may influence their distribution (referred to as environmental variables) were investigated with canonical correspondence analyses (CCA; TerBraak, 1987). Environmental variables were peatland area, relative isolation, microhabitat richness, and heterogeneity. Four bird species with frequencies of occurrence lower than 10 % were not included in the analyses. They were Clay-colored

Sparrow, Field Sparrow, Upland Sandpiper (*Bartramia longicauda*), and Common Snipe (*Gallinago gallinago*).

Because individual bird species have different ecological requirements, we calculated their individual probabilities of occurrence in peatlands by logistic regression, with the same explanatory variables as mentioned previously. Logistic regression analysis was performed on eighteen species, after excluding omnipresent (Common Yellowthroat, *Geothlypis trichas*) and rare species (Clay-colored Sparrow, Field Sparrow). To isolate the effect of each variable, we used type III errors (Agresti, 1996). We selected the most important variables by setting the level of significance at $\alpha = 0.10$. We performed the analyses using the GENMOD procedure of SAS software (SAS Institute Inc., 1993).

Results and discussion

Role of area, isolation, heterogeneity and microhabitat richness on species richness

Area, sampling effort, heterogeneity, isolation and microhabitat richness jointly accounted for 54.8% of the variation in bird species richness (adjusted R^2). The z coefficient for the $\log S = c+zA$ relationship was 0.21 (95% confidence interval: 0.20 - 0.21), which is far from the value of 0.26 reported for true islands (MacArthur & Wilson, 1967). Explaining this pattern requires first to distinguish effects of peatland area, heterogeneity and microhabitat richness, which were strongly inter-correlated ($r = 0.70$; Fig. 4). However, peatland isolation, another key variable, was poorly correlated with other variables ($r = 0.20$), and thus allowed us to estimate its effect.

Bird species richness was significantly related to microhabitat richness and sampling effort, which explained 7.6% ($F_{1,58} = 4.77$, $p < 0.05$) and 6.3% ($F_{1,58} = 3.88$, $p < 0.10$) of the total variation respectively, all other effects being factored out. Our results thus support both the habitat diversity (Williams, 1964), and the passive sampling hypotheses (Connor & McCoy, 1979). Other factors such as peatland area, isolation and heterogeneity were relatively unimportant (all $F_{1,58} < 1.94$, $p > 0.10$). Stockwell (1994) also found vegetation diversity to be more important than area as an explanation of peatland bird species richness and abundance in eight peatlands in Maine, USA. It is likely that the species-area relationship within peatlands was due to high correlations between area and the two significant variables explaining species richness: microhabitat richness (r = 0.73) (Fig. 4) and sampling effort (r = 0.85) (Fig. 3). We thus support the view of Simberloff & Levin (1985) that if habitat diversity explains species richness, area *per se* is probably a secondary factor.

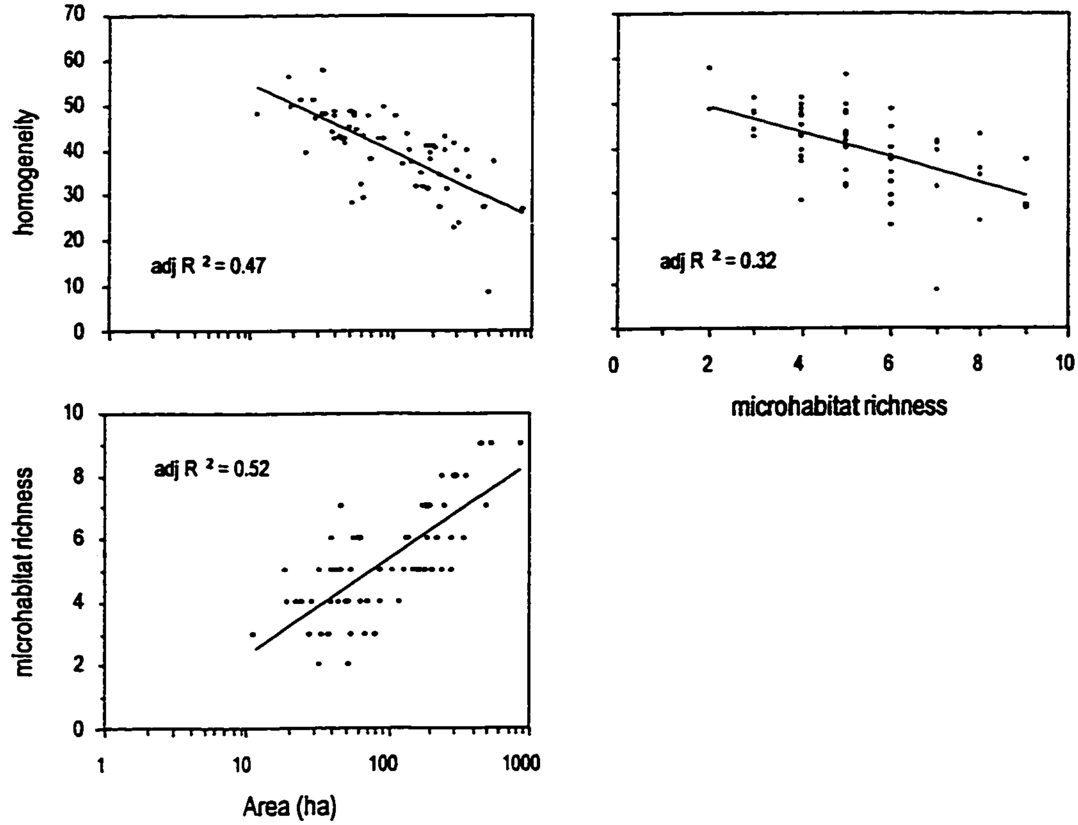

FIG. 4. Relationships between peatland area, microhabitat richness, and homogeneity (n=63). The term homogeneity was used for the upper panels instead of heterogeneity, because low values corresponded to more heterogeneous peatlands. R^2 values were adjusted for the number of variables entered in the models.

Heterogeneity, which expressed the complexity in composition and configuration of microhabitat patches within peatlands, was poorly correlated to the total number of species encountered in peatlands. It first seems contrary to previous findings in temperate forests (Freemark & Merriam, 1986; Boecklen, 1986), but heterogeneity in these studies was mostly based on vegetation composition and structure, not on patch sizes and arrangement. Also, vertical heterogeneity, an important component for explaining bird species diversity in forests, is low in peatlands (Stockwell, 1994).

Distribution of individual bird species

Results of analyses of bird species abundance and occurrence generally tallied, and will be discussed jointly. Peatland area and peatland heterogeneity were strongly and positively correlated with the first environmental axis in the CCA, whereas isolation was correlated with the second axis (Table 3). The first two environmental axes explained respectively 63% and 20% of the variance of the species-environment relationship. All environmental variables accounted for 15.6% of the variance in the model ($p<0.01$).

TABLE 3. Correlation matrix (Kendall's Tau) of the environmental variables with the first two environment axes in the Canonical Correspondance Analysis.

	Peatland area	Microhabitat richness	Amount of peatland habitat	Homogeneity
Axis 1	0.75	0.48	0.56	-0.87
Axis 2	0.43	0.23	-0.73	-0.21

Higher abundances of forest species appeared to be related to peatland homogeneity or to smaller peatland area, as all these species were on the left of axis 2 (Fig. 5). By contrast, species associated with humid or open habitats were on the right-hand portion of the graph, indicating a positive relationship with both peatland area and microhabitat richness. Large peatlands, which are also characterized by more heterogeneous and diverse microhabitats, tended to have fewer habitat available for forest species in relative terms, because they supported a smaller proportion of peripheral densely forested habitat. Thus, abundances of forest species tended to decrease with peatland heterogeneity or area. The converse was also true for abundances of species of open/humid habitats.

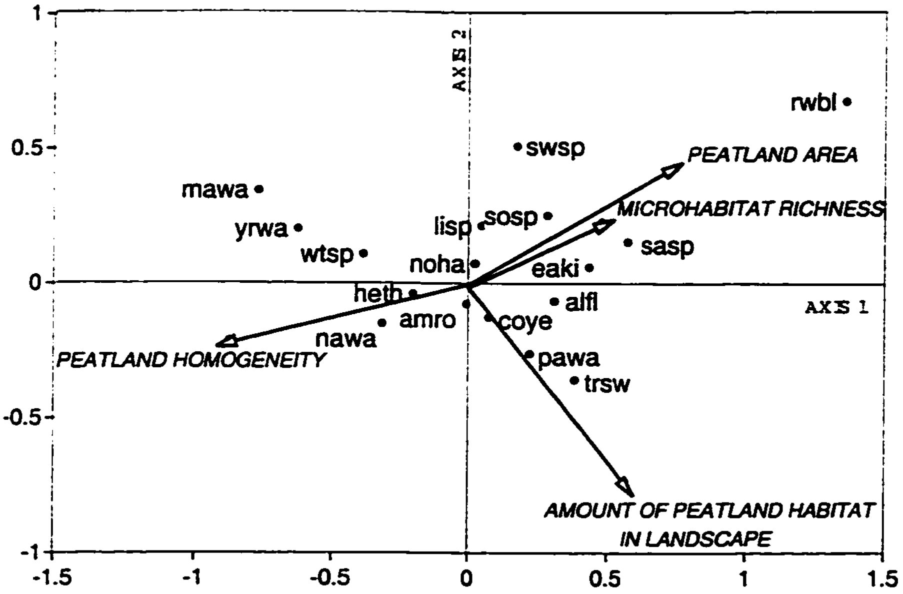

FIG. 5. Bird species ordination diagram obtained with abundance data in the CCA. Environmental variables are represented by arrows, which can be interpreted as axes in the diagram. Species codes are as in Table 1.

Of the 18 species for which probabilities of occurrence were calculated, only ten could be satisfactorily modeled by logistic regression, according to likelihood test (Table 4). None of the independent variables could explain the distribution of the following bird species: Upland Sandpiper, Common Snipe, Eastern Kingbird (*Tyrannus tyrannus*), Tree Swallow (*Tachycineta bicolor*), Magnolia Warbler (*Dendroica magnolia*), Savannah Sparrow (*Passerculus sandwichensis*), Song Sparrow (*Melospiza melodia*), and White-throated Sparrow (*Zonotrichia albicollis*). Heterogeneity was the factor most frequently related to species occurrence (six times), while area, isolation and microhabitat richness explained respectively four, three and two of these occurrences. Thus, factors related to the occurrence of individual species can differ totally from those related to total species richness, as is the case for heterogeneity.

TABLE 4. Variables predicting significantly (p = 0.10) the occurrence of ten peatland bird species in 63 peatlands, as calculated by logistic regression. The sign of the relation is given into parentheses.

Species name	Significant predictor	*P*-value
Northern Harrier	Heterogeneity (+)	0.04
	Isolation (+)	0.09
Alder Flycatcher	Heterogeneity (+)	0.06
Hermit Thrush	Microhabitat richness (+)	0.01
American Robin	Area (+)	0.002
	Heterogeneity (-)	0.01
Nashville Warbler	Heterogeneity (-)	0.03
	Isolation (-)	0.07
Yellow-rumped Warbler	Microhabitat richness (+)	0.02
Palm Warbler	Isolation (-)	0.06
	Area (+)	0.08
Swamp Sparrow	Area (+)	0.005
Lincoln's Sparrow	Heterogeneity (+)	0.09
Red-Winged Blackbird	Area (+)	0.05

We may expect species associated positively with heterogeneity to be generalists within peatlands. However, according to a previous study (Chapter II), all these species but Lincoln's Sparrow were found to exhibit strong preferences for particular types of microhabitat. In fact, Lincoln's Sparrow is a peatland specialist in the study area (Aubry & Gauthier, 1994; Chapter II), but its abundance (it was the second most common and abundant species after Common Yellowthroat) prevented us from finding occurrence patterns. Thus, it is more likely that heterogeneity created a broader range of available resources in a smaller area as suggested by Freemark & Merriam (1986).

Peatland area was positively related to the occurrence of Red-winged Blackbird (*Agelaius phoeniceus*), Swamp Sparrow (*Melospiza georgiana*), Palm Warbler, and American Robin (*Turdus migratorius*). According to CCA, peatland area and heterogeneity also explained patterns of abundance of three other species, namely Tree Swallow, Eastern Kingbird and Savannah Sparrow. It is noteworthy that Red-winged Blackbirds and Swamp Sparrows depend on the presence of fen areas in peatlands. Swamp Sparrows were exclusively found in rich fens (Stockwell, 1994; Chapter II). Red-winged Blackbirds were found in rich fens (Stockwell, 1994), but also in poor fens provided the presence of snags and proximity of sedges (S. Calmé, pers. obs.). Though we did not find a significant area effect for Upland Sandpiper, this species is also preferentially found in large peatlands that contain poor fen habitat (Calmé & Haddad, 1996). In Chapter II, we demonstrated that habitats were distributed in a nested manner among peatlands, and that large peatlands, not small ones, usually supported fens. The importance of area in the distribution of Red-winged Blackbirds and Swamp Sparrows species might therefore merely reflect the presence of their preferred habitats in larger peatlands. Similarly, Tree Swallows, Eastern Kingbirds and Savannah Sparrows were found in large open or semi-open habitat patches within peatlands, which are more likely to be found in large peatlands. The presence of these large patches is also reflected by two of the landscape variables, patch size standard deviation and coefficient of variation (PSSD and PSCV), that are strongly and positively correlated with heterogeneity (Table 2).

Palm Warbler's occurrence was negatively correlated with peatland isolation, and positively with peatland area. As Palm Warblers are strongly and almost exclusively associated with peatlands (Wilson, 1996; Chapter II), this result is consistent with MacArthur & Wilson's (1967) prediction that immigration rates should drop with increasing isolation in insular systems, while extinction should increase with decreasing island size. It is striking that the species most strongly associated with peatlands should also be the only one that shows both isolation and area trends consistent with MacArthur and Wilson's (1967) theory. However, behavioural work will be required to assess whether it is too costly for Palm Warblers to reach isolated, small peatlands or whether they simply avoid these habitats.

Conservation implications

Peatland bird assemblages were richest in peatlands presenting the greatest diversity of habitat types (Stockwell, 1994; Chapter II; this study), and habitat-rich peatlands tended to be large. This double correlation makes area a good predictor of species richness, though the causality was only partially direct (Chapter II) and the relationship did not seem linear.

Even though the distribution of peatland birds was consistent with that expected from a set of islands, our results do not support the use of the equilibrium theory of island biogeography as a tool for peatland conservation. As in Margules *et al.* (1982), many of the species found in habitat islands such as peatlands have important populations in surrounding habitats. As a matter of fact, among all the bird species we studied, only Palm Warbler and possibly Lincoln's Sparrows strongly prefer peatlands in the region. The distribution of Palm Warblers depended both on peatland area and the amount of peatland habitat available in a 10 km-radius around a peatland it was found in. However, even in the case of Palm Warblers, the area-isolation relationship seems too tenuous to warrant special conservation measures. For other species whose occurrence was related to peatland area, the presence of habitat features specific to large peatlands could probably explain the area-occurrence relationships. Besides, we showed elsewhere that species- and habitat-rich peatlands supported species and habitats not found in poorer ones, but the hypothesis that nestedness was caused by extinction was unlikely (Chapter II). As suggested by Stockwell (1994), microhabitat diversity within peatlands might thus be used as a simple indicator of peatland biological diversity, as it should reflect diversity both in plant and animal communities.

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CONCLUSION GÉNÉRALE

Cette étude sur les oiseaux des tourbières ombrotophes est la première à couvrir extensivement le Québec méridional, exception faite de l'Abitibi. C'est aussi la première étude à fournir un inventaire aussi intensif des oiseaux nicheurs des tourbières pour une région complète, en l'occurrence les Basses-Terres des Appalaches. Elle a de plus permis de mettre en lumière certains aspects de la distribution des espèces d'oiseaux des tourbières qui devraient permettre de soutenir l'effort de conservation que nécessite cet habitat.

Dans le premier chapitre, j'ai pu montrer que les tourbières supportaient des assemblages d'espèces d'oiseaux qui variaient selon les régions et la structure de l'habitat. L'apparition de grandes mares, dans la Basse-Côte-Nord surtout, favorise la présence d'une avifaune très distincte. De plus, les assemblages d'espèces d'oiseaux des tourbières diffèrent de ceux des habitats environnants, et ceci particulièrement dans le sud, dans les régions naturelles des Basses-Terres du Saint-Laurent et des Appalaches. Dans ces régions, l'avifaune des tourbières se distingue particulièrement par la présence de deux espèces montrant une nette préférence pour cet habitat, la paruline à couronne rousse et le bruant de Lincoln. Il a été possible de mettre en évidence que dans les paysages agroforestiers du Québec méridional situés au sud du 48$^{\text{ème}}$ parallèle, les tourbières pouvaient servir de refuge pour certaines espèces. Fait encore plus intéressant, la probabilité de la présence de la paruline à couronne rousse augmentait avec l'abondance des tourbières dans un rayon de 5 km.

Le deuxième chapitre, plus théorique, a néanmoins des implications très claires pour la conservation de l'avifaune des tourbières. En effet, j'ai trouvé que les assemblages d'espèces d'oiseaux étaient très fortement hiérarchisés dans les tourbières des Basses-Terres des Appalaches. J'ai montré également que les assemblages de microhabitats étaient hiérarchisés dans ces tourbières et que cette hiérarchisation pouvait être à l'origine de celle des assemblages d'espèces d'oiseaux, par le biais des associations entre les espèces d'oiseaux et les microhabitats. Les tourbières les plus grandes et les plus riches en microhabitats supportaient donc les assemblages non seulement les plus riches, mais aussi les espèces d'oiseaux et les microhabitats les moins fréquents.

Finalement, dans le troisième chapitre, j'ai déterminé que les facteurs les plus importants pour la richesse en espèces d'oiseaux étaient d'abord la richesse en microhabitats, suivie de la superficie des tourbières. Comme ces deux variables étaient fortement corrélées et que la superficie des tourbières explique aussi une portion de la richesse en espèces par échantillonnage passif, la taille des tourbières était le facteur apparent le plus important. Cependant, quoique conforme à la prédiction de MacArthur et Wilson (1967), ce résultat n'apporte pas de support direct à leur théorie, mais plutôt à celle de la diversité de l'habitat (Williams, 1964). Enfin, l'étude des facteurs déterminant l'occurrence des espèces d'oiseaux dans les tourbières a révélé que ces facteurs pouvaient être très différents de ceux prédisant la plus grande richesse totale en espèces. En effet, l'hétérogénéité s'est avérée la variable la plus souvent significative pour prédire l'occurrence des espèces. Enfin, j'ai pu confirmer les résultats du premier chapitre pour la paruline à couronne rousse, puisqu'elle était négativement affectée par le degré d'isolement des tourbières et positivement par leur superficie, dans un rayon de 10 km.

L'ensemble de l'étude permet de distinguer trois points importants à considérer pour la conservation des tourbières du Québec méridional, au moins du point de vue de leur avifaune:

1) *Donner la priorité aux tourbières du sud*

Les tourbières situées au sud de Québec présentent les assemblages d'oiseaux les plus distincts des milieux environnants. Dans cette région, les tourbières forment de véritables enclaves d'avifaune nordique. Comme c'est aussi la région où la pression exercée sur cet habitat est la plus forte, un effort de conservation devrait en premier lieu y être dirigé.

2) *Favoriser les grandes tourbières diversifiées*

Les tourbières présentant une grande variété de microhabitats, qui sont aussi parmi les plus grandes, supportent des espèces rares avec des besoins de conservation comme la maubèche des champs (voir Calmé et Haddad, 1996). Elles supportent aussi de nombreux couples d'espèces spécialistes des tourbières comme la paruline à couronne rousse, ce qui devrait limiter les extinctions régionales dues à des variations stochastiques (May, 1994).

3) *S'assurer de conserver un réseau de tourbières*

Mes résultats indiquent que l'isolement pourrait constituer un obstacle à la recolonisation des tourbières par la paruline à couronne rousse. En effet, la probabilité de la présence de cette espèce diminuait significativement dans les tourbières isolées et de moindre superficie. Une étude des fragments naturels isolés de tourbières en exploitation en arrive d'ailleurs à la même conclusion (Delage, 1998). De plus, Desrochers et al. (1998) ont montré que les parulines à couronne rousse ne recolonisaient généralement pas les sites perturbés par l'exploitation puis revégétés. La disparition ou la perturbation de plusieurs sites pourraient donc éventuellement mener régionalement à la disparition de l'espèce, surtout si sa dynamique suit celle d'une métapopulation (voir May, 1994). La conservation de la paruline à couronne rousse dans le Québec méridional passe donc par la préservation de plusieurs tourbières naturelles voisines et de superficies intéressantes.

De futures recherches devraient donc s'orienter vers l'étude des patrons de dispersion des parulines à couronne rousse. Puisque l'espèce présente la particularité de nicher exclusivement dans les tourbières et qu'elle est sensible à l'isolement de son habitat, il serait intéressant de savoir si la composition du paysage a une influence sur ses capacités de dispersion et s'il existe des seuils critiques d'isolement au delà desquels la dispersion est compromise. Il serait aussi approprié de mesurer les taux de colonisation et d'extinction locales des populations de parulines à couronne rousse afin d'évaluer leur persistance face aux aléas de leur environnement. Enfin, le suivi d'individus marqués permettrait peut-être de déterminer, à la lueur des autres informations recueillies, si les parulines à couronne rousse forment une métapopulation.

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Annexe

Peatlands: A new habitat for the Upland Sandpiper, *Bartramia longicauda*, in Eastern Canada

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Calmé, S., and S. Haddad. 1995. Peatlands: A new habitat for Upland Sandpiper, *Bartramia longicauda*, in Eastern Canada. Canadian Field Naturalist.

Although there have been reports of Upland Sandpipers breeding in peatlands of northwestern Canada, our study is the first to demonstrate widespread use of peatlands in other parts of the species range. In the summer of 1995, while conducting a study on the breeding birds of Québec's peatlands, we recorded a total of 11 pairs of Upland Sandpipers, in five peatlands in a small region on the south shore of the St. Lawrence River. In the previous year, four pairs had been observed in two of the same peatlands. These peatlands were the largest in the region (160 ha to 496 ha), and consisted mainly of open treeless habitat. The mean density of breeding pairs in 1995 was 0.59 per 100 ha. The availability of large open areas, a low predation rate, and unfrequent human disturbance indicate that peatlands could constitute a suitable habitat for the species.

Bien que des mentions de nidification de maubèche des champs aient été rapportées dans les tourbières du nord-ouest canadien, la présente étude démontre pour la première fois l'utilisation de cet habitat par l'espèce dans l'est de son aire de distribution. Au cours de l'été 1995, lors d'une étude sur les oiseaux nicheurs des tourbières du Québec, 11 couples de Maubèche des champs, ont été observés dans cinq tourbières localisées dans une petite région de la rive sud du fleuve Saint-Laurent. L'année précédente, quatre couples avaient été observés dans deux des mêmes tourbières. Ces tourbières, les plus grandes de la région (160 ha à 496 ha), étaient principalement constituées d'habitat ouvert dépourvu d'arbres. La densité moyenne de couples nicheurs était de 0.59 pour 100 ha en 1995. La disponibilité de grandes surfaces ouvertes, un faible taux de prédation, ainsi qu'un niveau de perturbation humaine presque inexistant pourraient faire des tourbières un habitat convenable pour l'espèce.

Key words: Upland Sandpiper, *Bartramia longicauda*, peatland, grassland, open habitat.

The Upland Sandpiper (*Bartramia longicauda*) is a species of the American grasslands, scarcely and locally distributed in much of its range (Peterson 1994). It usually inhabits grassland pastures, tall-grass prairies, blueberry barrens, airport runways, and recently burned or mowed areas (Askins 1992). In the Northwest, Upland Sandpipers are occasionally observed in clearings in spruce muskeg (Palmer 1967), on montane grasslands (Gabrielson and Lincoln 1959), and even in peatlands (Godfrey 1986).

Like many North American game species, it experienced near-extinction at the turn of the century. This decline was halted around 1920, with the help of the " Migratory Bird Convention ", (Osborne and Peterson 1984), as no open season has since been declared for this species. In spite of a period of recovery marked by the apparent westerly expansion of the species range, the number of Upland Sandpipers began to decline again in almost every northeastern and central region. For instance, its numbers in Illinois decreased by approximately 95% between 1956-1958 and 1978-1979 (Anonymous, cited in Askins 1992). In the New England states, the species became uncommon to rare, and it is still a species of special concern in many of these states (Vickery 1992). Moreover, the Upland Sandpiper was on the Blue List from 1975 to 1986 (Tates 1986), and is one of the species classified as threatened on its breeding grounds (Thompson et al. 1992). However, the results from the Breeding Bird Survey (BBS) show a positive trend of the species population in its entire area of distribution between 1966 and 1994 with a mean percent of annual change of 2.0% ($p \leq 0.001$). Most of this increase seems to have taken place before 1980, as the recent BBS trend (1980-1994) indicated a rate of annual change of 0.2% (non-significant). In Québec, for the same period, this mean percent of annual change reached -3.0%, though this value was non-significant (Sauer et al. 1995). A recent summary on shorebirds based on documented data and surveys indicates a possible general decline of the Upland Sandpiper throughout Canada with the current population estimated at 2 000 individuals (Morrison et al.1994). Therefore, while some studies show encouraging signs for the species, the overall status of the Upland Sandpiper warrants further attention.

In this paper we report on recent observations of Upland Sandpipers in peatlands. We discuss these findings in relation to previous knowledge of the species, while emphasizing their importance in regards to Upland Sandpiper's present status.

Methods

Study sites

This study was conducted in 1994 and 1995, between 5 June and 14 July. In 1994, we visited 137 peatlands, roughly distributed along the Saint Lawrence River lowlands, between the Québec/Vermont border and Havre-Saint-Pierre on the North Shore. In 1995, 72 peatlands were sampled south and west of Quebec City (Figure 1). In 1995, we also counted birds in open habitats, i.e., mostly hayfields (41) and pastures (10), abandoned farmlands (7), recent clearcuts (4), grain crops (6), fields of clover (3), food crops (2), cranberry farms (1), and young plantations (1).

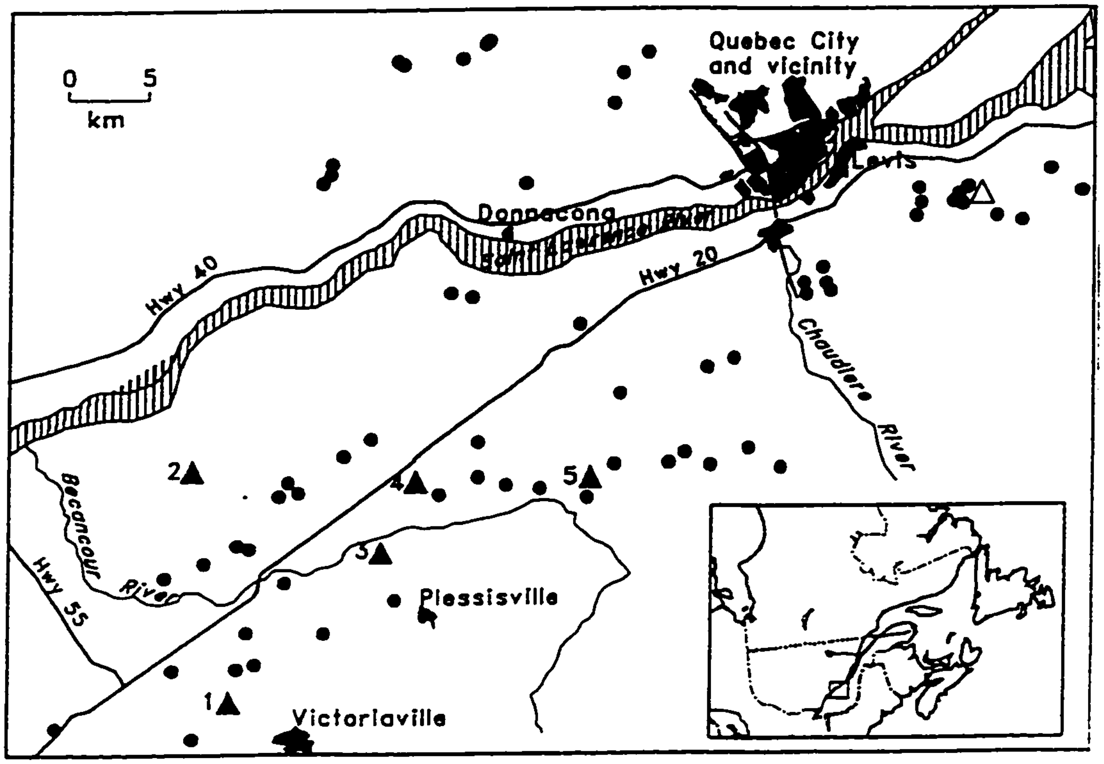

FIGURE 1. Study area in 1995. The peatlands with Upland Sandpipers are indicated by solid triangles (▲), while solid circles (●) indicate other peatlands sampled, and the empty triangle (Δ) represents the field with three observed pairs. Numbers correspond to the locations in Table 1. On the inserted map, the northern limit of distribution of Upland Sandpiper in Québec is indicated by the dotted line (.....), and the study area is represented by the small rectangle.

Sampling methods

In 1994 the fixed-radius point-count was used to measure species diversity. One 10-min observation period was carried out in each of the 137 peatlands, where all birds seen or heard within a radius of 100 m were recorded. When peatlands were large enough, a second point count was conducted at a distance of at least 1 km from the first point count. Plots were located at least 150 m from the peatland's edge. Vegetation was sampled in each circular plot by visually estimating the percentage of the different vegetation types, as well as the percentage of open water. Vegetation types consisted of the following strata: forbs, ericaceous shrubs, trees < 2 m, trees between 2 and 5 m, and trees > 5 m.

In 1995 the point-count technique was again used. We placed one count in each distinct habitat type in the peatland; thus their number depended on the peatland's heterogeneity. In the surrounding open habitats we used single point-counts. In the peatlands, birds were also sampled along 200-m wide transect strips. We recorded the positions of all birds seen or heard in the strips. All transect lines were situated at least 200 m from the peatlands edge and 300 m from each other. The total area sampled in each peatland represented a minimum of 30% and a maximum of 67% of its surface. Each peatland was surveyed once during the breeding season. Like many other shorebirds, Upland Sandpipers are mostly silent during incubation. However, we considered that failure to detect breeding Upland Sandpipers was unlikely since our surveys started around the first week of June. By this date, the main incubation period is completed and chicks begin to leave the nest in southern Québec (Yank and Breton 1995).

To determine whether the area of the peatland had a possible influence on the presence of Upland Sandpipers, the peatlands sampled in 1995 were divided into two groups, with and without Upland Sandpipers (n=5 and n=27, respectively). We assume that the peatlands without Upland Sandpipers used fot the analysis, had similar open habitat, based on the presence of the Savannah Sparrow (*Passerculus sandwichensis*), a species characteristic of open habitats, the habitat structure, and the interpretation of aerial photographs. We digitized 1:15 000 aerial photographs of the peatlands to measure peatland area. We used a two-tailed t-test to compare the two groups of peatlands.

Results

In 1994, four pairs were observed in two separate but neighboring peatlands (Table 1 and Figure 1). In 1995, 11 pairs were recorded in five peatlands (Table 1 and Figure 1), and three others in a hayfield (Figure 1). The peatlands with Upland Sandpipers were situated in a small region characterized by a mixture of lands dedicated to agriculture and forestry. Typically, these peatlands were the largest in the surrounding region, and they consisted mainly of open habitat. The vegetation was dominated either by ericaceous shrubs such as *Ledum groenlandicum* and *Kalmia angustifolia* or forbs such as *Carex* sp. Shrubs were scarce and usually found on peatland edges known as fen lags. Trees, mainly Larch (*Larix laricina*) and/or Black Spruce (*Picea mariana*), were rather rare and scattered: the overall tree cover rarely exceeded 15% (Table 1).

TABLE 1. Sites of observations of Upland Sandpipers in peatlands in Quebec, and number of territories found in 1994 and 1995.

Locality	No.	Location	Area (ha)	Vegetation cover in observation sites (%)					Number of territories	
				eric.	forb	>5m	2-5m	<2m	1994	1995
Saint-Valère	1	46°04'N; 72°06'W	160	90	2	0	3	2	–	1
Sainte-Marie-de-Blandford	2	46°19'N; 72°11'W	338	35	65	5	1	1	–	1
Notre-Dame-de-Lourdes	3	46°19'N; 71°49'W	418	70	15	5	5	1	2	4
Villeroy	4	46°23'N; 71°53'W	496	15	40	3	10	8	2	4
Sainte-Anastasie	5	46°22'N; 71°35'W	463	7	80	0	0	1	–	1

The results from the Student t-test show that the two groups of peatlands were significantly different ($t = 4.999$, $p < 0.0001$). The mean areas of peatlands used by the Upland Sandpipers was 375 ± 134 ha ($n = 5$) compared to 122 ± 98 ha ($n = 27$) for unused peatlands in the same region.

The birds were usually heard whistling before they became aware of us; as we approached their territories the sandpipers were visibly disturbed by our presence (Figure 2). They flew around us, calling repeatedly. These alarm calls often attracted other individuals, up to five. In peatland 4 (Figure 1), on 14 June, we also observed a chick, while an adult was performing a distraction display.

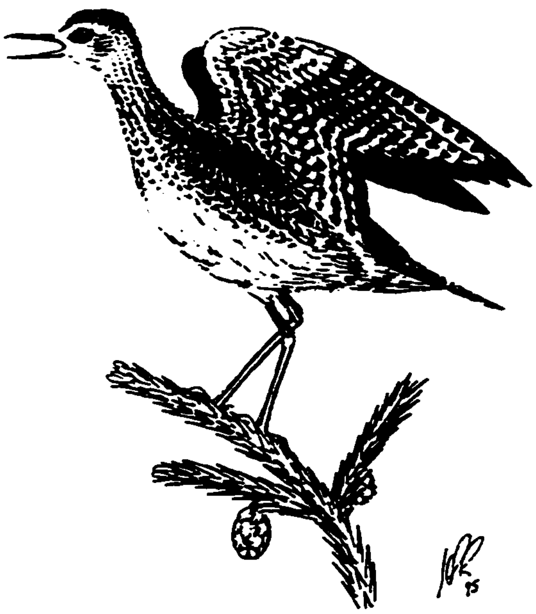

FIGURE 2. An Upland Sandpiper perched on a spruce, its wings semi-erect in an unstable position.

Discussion

In 1995, the mean population density in the peatlands was 0.59 pairs / 100 ha. This latter value could be higher if we considered only the type of habitat used by the Upland Sandpipers, thus eliminating " islands " of denser vegetation. To our knowledge, no other data are available concerning population densities in Québec. Despite the small sample size, the population density in our study was lower than the 1.1 nest / 100 ha found for Upland Sandpiper in a twenty-year study conducted in Illinois (Buhnerkempe and Westemeier 1988). According to Osborne and Peterson (1984), an ideal habitat could support up to eight pairs / 100 ha. That value was supported by a study in the Wisconsin prairies in which two Upland Sandpiper pairs had territories of 8.1 and 12.1 ha (DeGraaf and Rudis 1987).

The results show that Upland Sandpipers preferred large peatlands. The smallest peatland in which an individual was observed (160 ha) was of intermediate size, but the four other peatlands were the largest ones in the region studied in 1995. Area-sensitivity by Upland Sandpiper is not limited to peatlands: in Missouri and Illinois, Upland Sandpipers were not found in grassland habitat of less than 10 ha and 30 ha, respectively (Samson 1980, Herkert 1991). Closer to eastern Canada, Vickery et al. (1993) found a relationship between the presence of Upland Sandpipers and the area of grasslands in eastern Maine. The species was very rare in patches of habitat smaller than 50 ha, and reached an incidence of 50 % in grasslands of more than 200 ha.

As with many other grassland specialists (Askins 1992), the continued loss and fragmentation of habitat may be the major cause of the Upland Sandpiper decline. On breeding grounds, urban and surburban development, afforestation on abandoned farmlands (see Askins 1992), as well as changes in agricultural practices, contribute to the loss of suitable nesting habitat. In Québec, the disappearance of traditional family-owned farms, and the extensive cultivation of corn have both been related to the decline of the species (Yank and Breton 1995).

Threats to the species are not restricted to its breeding grounds; the Upland Sandpiper also faces a important reduction of its main wintering habitat, the South American pampas. Like the North American Great Plains, the Argentinian and Urugayan pampas have been replaced by extensive crops of corn and wheat. The region's natural ecosystem has become so scarce that the outlook for its avifauna seems even more pressing than the situation of tropical forest species (Terborgh 1989).

The presence of a breeding bird may be a good indication of the suitability of a site. However, breeding success is a guarantee of its quality (Van Horne 1983) and the most important obstacle to breeding success is often nest predation (Martin 1988). Here, we experimentally measured nest predation with artificial nests in 6 large and relatively open peatlands of the region previously described, including Villeroy, Sainte-Anastasie and Sainte-Marie-de-Blandford. The apparent predation rate on nests averaged 12% (n = 114), with no obvious effect of distance from edge (unpublished data). This value is similar to results found by Burger et al. (1994). In their study, the rate of predation on artificial nests averaged 16.2% (n = 216) for six prairie fragments larger than 130 ha in Missouri. Our results thus suggest that peatland habitat is as suitable as grassland habitat for breeding Upland Sandpipers in Québec.

Two hypotheses may explain the lack of previous observations of Upland Sandpipers in peatlands. First, until recently, peatlands have been relatively overlooked by ornithologists and this could explain the absence of documented observations of the species in peatlands. Nevertheless, the Upland Sandpiper call and behavior make it readily detectable even by non-ornithologists. A second hypothesis is that the Upland Sandpiper has recently found new sites, along with a new suitable habitat. This plasticity would be highly valuable for the species, given the scarcity of its " traditional " habitat in northeastern America. In peatlands, disturbance by humans or predators seems rare, and there is no risk for the brood to be destroyed by farm machinery, as is often the case in fields (Ehrlich et al. 1988).

These observations, based on only two years of data, give a limited picture of the situation of the Upland Sandpiper in eastern peatlands, even though geographic coverage was wide. Consequently, they should be considered as a starting point for more investigations on the potential of peatlands for sustaining Upland Sandpiper populations, and possibly those of other grassland species.

Acknowledgments

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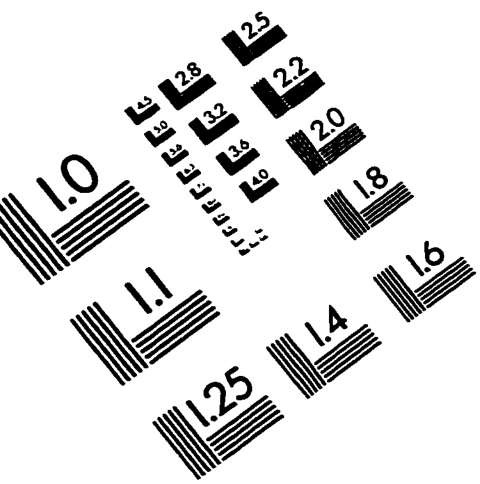

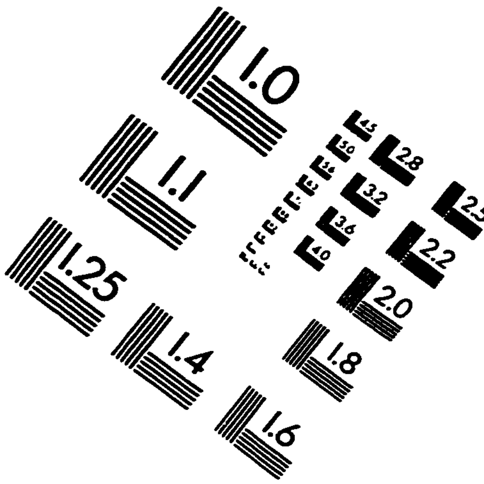

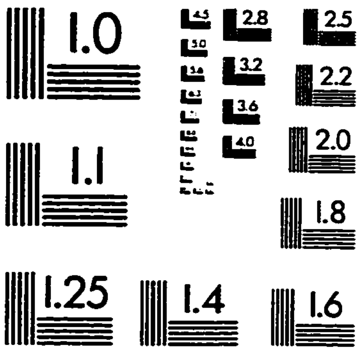

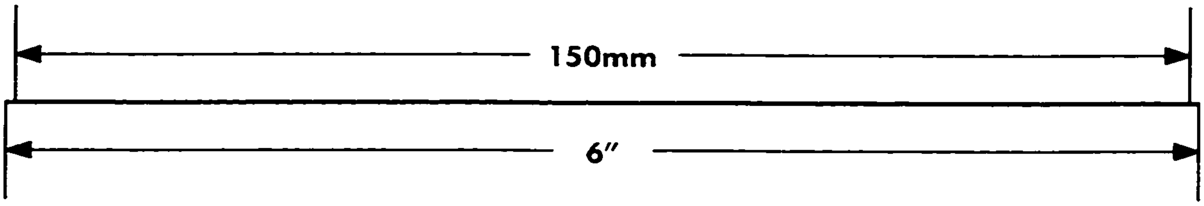

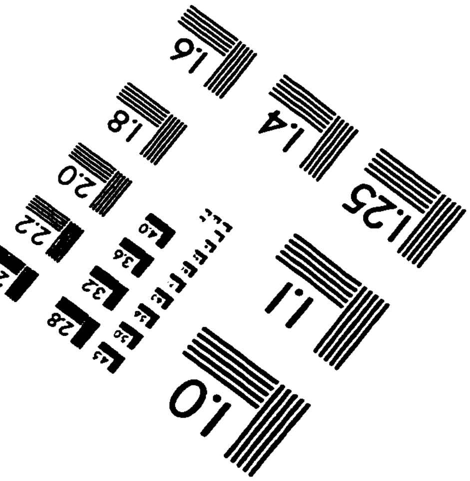

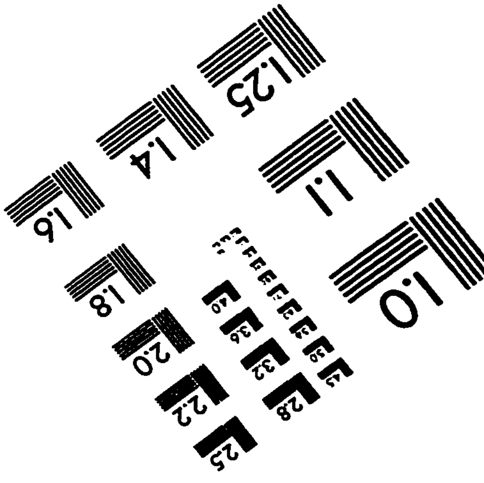

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