Université de Montréal

L'hétérogénéité spatiale des microhabitats forestiers affecte-t-elle la délimitation des territoires de la paruline bleue (*Dendroica caerulescens*) et de la paruline couronnée (*Seiurus aurocapillus*)?

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L'hétérogénéité spatiale des microhabitats forestiers affecte-t-elle la délimitation des territoires de la paruline bleue (*Dendroica caerulescens*) et de la paruline couronnée (*Seiurus aurocapillus*)?

présenté par

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Sommaire

La configuration actuelle des paysages forestiers est le résultat de perturbations naturelles et anthropiques. L'hétérogénéité spatiale du couvert forestier se manifeste sous forme de lisières nettes (lisière forêt-champ par exemple) et de lisières floues (changements graduels entre des peuplements de structure et de composition différentes). Bien que l'effet des lisières nettes sur la taille et la répartition des territoires des oiseaux soit maintenant reconnu, peu d'études ont porté sur l'effet des lisières floues sur la localisation et la délimitation des territoires des oiseaux forestiers. L'objectif principal de la présente étude est de déterminer si les lisières floues caractérisant les microhabitats forestiers ont un effet sur la délimitation des territoires de la paruline bleue (*Dendroica caerulescens*) et de la paruline couronnée (*Seiurus aurocapillus*). L'étude a été réalisée durant l'été 1999 à la Station écotouristique Duchesnay, située à 40 km au nord-ouest de la ville de Québec. Les limites territoriales de dix parulines bleues et de 14 parulines couronnées ont été cartographiées sur une grille composée de 756 points équidistants de 25 m pour un total de 49 ha. L'échantillonnage de 34 variables caractérisant les microhabitats a été réalisé sur cette même grille. Les territoires des oiseaux ont été délimités à l'aide de la méthode de délimitation des domaines vitaux de *kernel* ainsi qu'à l'aide de l'algorithme de *lattice-wombling.* Les lisières caractérisant les microhabitats ont également été délimitées à l'aide de cet algorithme, puis le chevauchement spatial entre les deux types de lisières a été estimé à l'aide des statistiques de chevauchement. Les variables caractérisant les microhabitats où se retrouvaient les oiseaux ont été identifiées à l'aide de l'analyse de redondance (RDA). Les résultats de la RDA et des statistiques de chevauchement se sont avérés très contrastés. Il y avait un chevauchement direct significatif entre les frontières caractérisant les microhabitats et les limites territoriales des oiseaux selon 18 et 20 variables pour la paruline bleue et la paruline couronnée respectivement. Les limites territoriales de la paruline bleue étaient fortement associées, entre autres, avec les lisières caractérisées par le recouvrement des semis de conifères, celui de la strate herbacée et le recouvrement végétal total entre 0-2 m de hauteur. Les lisières caractérisées par l'intensité du bruit de la route, le recouvrement en roches couvertes et la diversité arbustive étaient les plus fortement associées aux limites territoriales de la paruline couronnée. Les oiseaux forestiers tiennent donc compte des discontinuités spatiales floues caractérisées par certaines variables des microhabitats lors de la délimitation de leur territoire. Les algorithmes de détection de frontières et les statistiques de chevauchement pourraient devenir d'excellents outils statistiques à utiliser dans les études portant sur les relations faune-habitat.

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Introduction générale

La sélection de l'habitat en période de nidification est vue comme un processus critique dans la vie de la majorité des oiseaux (Morse, 1985). Le choix de l'emplacement du site de nidification affecte le succès reproducteur et la survie des adultes (Rosenzweig, 1985). Jusqu'à présent, la majorité des études concernant la sélection de l'habitat chez les oiseaux ont été effectuées à des échelles correspondant aux territoires (par exemple, le peuplement forestier), ignorant ainsi les processus à fine échelle impliqués dans la localisation du territoire (Fretwell & Lucas, 1969; Klopfer et Ganzhorn, 1985; Morse, 1985; Orians & Wittenberger, 1991; Steele, 1992). En ce qui concerne les oiseaux forestiers, certains auteurs ont quantifié l'importance de caractéristiques locales de la végétation dans la sélection de l'habitat telles que la structure verticale ou horizontale (Shugart & James, 1973; Collins *et al.*, 1982; Morse, 1985; Steele, 1992; Haila *et al.*, 1996; Villard, 1999) et la composition (Holmes & Robinson, 1981; Rotenburry; 1985; Sherry & Holmes, 1985, Robichaud et Villard, 1999). Les caractéristiques habituellement utilisées afin de décrire la structure de la végétation sont le recouvrement de la strate herbacée, la densité et la hauteur de la strate arbustive ainsi que le pourcentage de recouvrement de la voûte forestière (DeGraaf *et al.*,1998). L'étude de De Graaf *et al.* (1998) a démontré que des variables de structure du peuplement expliquent davantage l'abondance des espèces d'oiseaux que d'autres variables telles que la classe d'âge des arbres ou le type de couvert végétal. À l'opposé, Holmes et Robinson (1981) ainsi que Rotenberry (1985) ont démontré qu'une partie importante de la variation dans la structure des communautés d'oiseaux s'explique par la composition végétale. Rotenberry (1985) nota que seulement 35% de la structure des communautés aviaires s'explique par des variations dans la physionomie verticale et horizontale de la végétation. Ces résultats ne concordent pas avec ceux de l'étude de Bersier et Meyer (1994), où la structure de la végétation expliquait la majeure partie de la variance à l'échelle grossière (i.e., où l'ensemble de la succession est prise en compte) mais où l'importance de la composition végétale augmentait localement (où seulement le dernier stade successionnel est pris en compte ; ex., proportion des différentes essences d'arbres matures). Selon ces auteurs, la composition taxonomique est un descripteur plus fin de la structure de la végétation à petite échelle que les variables décrivant la structure de la végétation elles-mêmes. Il s'avère donc crucial de tenir compte de l'échelle d'observation (grossière ou fine) utilisée dans l'interprétation des facteurs prédominants lors de la sélection de l'habitat.

En plus de l'importance de la structure et de la composition de la végétation, d'autres facteurs ont un grand rôle à jouer dans la sélection de l'habitat chez les oiseaux. En effet, de nombreux auteurs se sont interrogés sur l'influence de facteurs tels que le risque de prédation (Klopfer et Ganzhorn, 1985), l'âge des individus (Ficken & Ficken, 1967; Desrochers & Magrath 1993), le parasitisme (Paton, 1984) et les relations inter- et intraspécifiques (Rosenzweig, 1991). L'abondance de nourriture pourrait à elle seule, selon Klopfer & Ganzhorn

(1985), être indicateur d'un habitat propice pour certaines espèces. Ce critère serait plus limitant pour les frugivores que pour les insectivores, ces derniers pouvant compter sur une ressource relativement stable (Klopfer & Ganzhorn, 1985).

Il est important, cependant, de distinguer la sélection de l'habitat du choix de l'emplacement du territoire. Selon Haila *et al.* (1996), les oiseaux répondent à la structure de l'habitat en sélectionnant dans un premier temps le type d'environnement dans lequel ils choisiront, par la suite, l'emplacement de leur territoire. Un territoire se définit comme étant l'aire défendue activement, et ce, majoritairement par les mâles en période de nidification, contre toute intrusion par des rivaux (Kaufmann, 1983; Bailey, 1984). Lors du processus de défense du territoire, faisant suite au choix de l'emplacement de celui-ci, l'individu en choisit ses limites. On considère qu'un territoire doit contenir les ressources nécessaires pour la survie et la reproduction des individus, ce qui l'amène à être différent d'un site choisi aléatoirement dans la même localité (Klopfer et Ganzhorn, 1985; Steele, 1993). Différents facteurs sont reconnus comme ayant un effet sur le choix de l'emplacement du territoire. La présence de perchoirs pour le chant, de sites de nidification adéquats (Zimmerman, 1971; Calder, 1973; Holway, 1991) et l'abondance de proies (Stenger & Falls, 1959; Partridge, 1976) sont les critères les plus cités.

La majorité des études ayant été menées à ce jour concernant la sélection de l'emplacement du territoire chez les oiseaux visaient à comparer certaines caractéristiques de la végétation à l'intérieur et à l'extérieur des territoires (Smith & Shugart, 1987; Steele, 1992; Steele, 1993). Par exemple, Steele (1992) a démontré qu'il y a une différence significative entre les caractéristiques de la strate arbustive retrouvées à l'intérieur et celles retrouvées à l'extérieur des territoires de la paruline bleue (*Dendroica caerulescens*). Ces comparaisons entre les caractéristiques végétales à l'intérieur des territoires et celles que l'on retrouve dans la même localité permettent d'élucider les composantes recherchées par les oiseaux mais ne procurent aucune information sur les mécanismes de délimitation des territoires. Depuis longtemps, on considère que la délimitation des territoires est le résultat des interactions entre les individus voisins (Nice, 1937; Lack, 1954). Cependant, selon Klopfer & Ganzhorn (1985), la délimitation du territoire pourrait aussi résulter d'un processus en plusieurs étapes i.e., d'une échelle spatiale grossière à une autre plus fine. Ce processus serait basé sur des aspects visuels associés à la forme, la densité et la distribution de la végétation dominante.

La conversion accrue des forêts au profit de l'expansion agricole et urbaine ainsi qu'à celle de l'industrie forestière induit énormément de morcellement dans la matrice forestière. Ce faisant, les zones de contact entre les peuplements de structure et de composition différentes augmentent (Yahner, 1988). Ces zones de contact peuvent former soit des lisières bien définies (lisières nettes) ou des zones de transition graduelles (lisière floues) (Yahner, 1988). La majorité des études relatives à l'effet du morcellement de la matrice forestière sur le choix de l'emplacement du territoire ont porté sur les discontinuités abruptes, c'est-à-dire, les lisières nettes. Plusieurs chercheurs se sont interrogés sur l'influence des lisières nettes sur la taille (Ortega & Capen, 1999) et la répartition spatiale (King *et al.*, 1997; Villard, 1998) des territoires des oiseaux. Cet effet de lisière est maintenant reconnu comme étant négatif pour les espèces dites spécialistes des forêts profondes comme dans le cas de la paruline couronnée (*Seiurus aurocapillus*) (Wenny *et al.*, 1993; Van Horn *et al.*, 1995; Burke & Nol, 1998; Ortega & Capen, 1999). Cela pourrait être partiellement dû à l'augmentation des risques de prédation le long des lisières nettes (Temple & Cary, 1988). Par contre, d'autres espèces dites spécialistes des lisières nettes, tirent profit des milieux fragmentés. Ces lisières confèrent entre autres plus de perchoirs pour le chant et de sites d'alimentation pour ces espèces (De Graaf, 1992). La paruline bleue est considérée par certains auteurs comme étant associées aux lisières nettes (King *et al.*, 1997).

Il existe peu d'information relative à la manière dont les oiseaux perçoivent, au moment de la délimitation de leur territoire, l'hétérogénéité spatiale et les changements graduels de la végétation présents au sein même de la matrice forestière. Selon Rail *et al.* (1997), un facteur végétal d'importance pour les limites territoriales des oiseaux est la présence de lisières végétales abruptes, telles que celles rencontrées aux abords des champs, des chemins et des coupes à blanc. L'étude de De Graaf (1992) portant sur l'effet de sept types de lisières, classées selon le degré de contrastes (abruptes, intermédiaires et subtiles), a démontré que les assemblages d'oiseaux diffèrent seulement aux interfaces entre les peuplements matures et les peuplements composés de semis ou de jeunes arbres. Cela suggère que des zones de transition subtiles entre des peuplements de structure ou de composition différentes n'ont pas d'effet net sur la composition des communautés aviaires. Par contre, ce type de lisière pourrait être perçu par les espèces d'oiseaux forestiers lorsqu'elles sont considérées individuellement et avoir une importance dans le choix de l'habitat ainsi que dans le choix de l'emplacement et la délimitation de leur territoire.

L'objectif général de la présente étude est de déterminer si les oiseaux considèrent les discontinuités spatiales graduelles de l'habitat vus sous l'angle de la composition et de la structure des microhabitats, dans la délimitation de leur territoire. Afin de répondre à cet objectif, deux espèces d'oiseaux forestiers dont l'utilisation des microhabitats (structure verticale et densité du couvert végétale) est contrastée serviront de modèle: la paruline bleue et la paruline couronnée. Ces deux espèces sont migratrices et nichent en partie au sud ouest du Québec dans les forêts feuillues ou mixtes à dominance feuillue (Darveau, 1995; Drapeau & Darveau, 1995). Nous voulons également, par cette étude, déterminer si les caractéristiques des microhabitats ayant une grande importance lors du choix de l'emplacement du territoire sont les mêmes que celles ayant une importance lors de la délimitation du territoire (différents processus à échelle grossière ou fine). En effet, l'échelle spatiale considérée lors de la délimitation du territoire serait plus fine que celle considérée lors du choix de l'emplacement de celui-ci (selon le processus hiérarchique énoncé par Klopfer & Ganzhorn (1985)).

Les deux espèces à l'étude ont été choisies de façon à représenter deux modes d'occupation verticale de l'habitat forestier contrastés. La paruline bleue se nourrit d'insectes à une hauteur de 3 à 9 mètres (Steele, 1993) et niche à environ 1 mètre au dessus du sol (Holway, 1991). De fortes concentrations de parulines bleues ont été observées là où la strate arbustive est dense et où la voûte forestière est ouverte (Steele, 1992; Holmes *et al.*, 1996). À l'opposé, la paruline couronnée se nourrit au sol d'invertébrés caractéristiques des milieux humides (Smith & Shugart, 1987). Dans une revue de littérature sur la paruline couronnée, Blanchette et Larue (1993) notent que l'habitat optimal de cette espèce comporte un couvert arborescent de plus de 55%, un faible recouvrement des strates arbustives supérieure et inférieure ainsi qu'une prédominance de feuillus. Puisque ces deux espèces utilisent la forêt très différemment, il est peu probable qu'elles soient en compétition interspécifique. En effet, selon Klopfer et Ganzhorn (1985), différentes espèces de parulines ne se nourrissant pas dans la même strate de la végétation peuvent occuper le même habitat et former des assemblages stables d'oiseaux, c'est-à-dire, sans qu'il n'y ait présence de compétition interspécifique.

Les objectifs spécifiques de l'étude sont : 1) d'utiliser une nouvelle méthode statistique afin de cartographier les limites territoriales de la paruline bleue et de la paruline couronnée; 2) de caractériser les microhabitats utilisés préférentiellement par les individus; 3) de caractériser et de délimiter les frontières relatives à l'habitat et 4) de déterminer le degré d'association spatiale entre l'emplacement des limites territoriales des oiseaux et les frontières relatives à l'habitat (statistiques de chevauchement).

En ce qui concerne le dernier objectif, l'hypothèse nulle (H_0), stipulant l'absence de relation spatiale entre les limites territoriales des oiseaux et les lisières caractérisant les microhabitats forestiers, sera testée. L'hypothèse alternative considère qu'il y a une association entre les limites territoriales des oiseaux et les lisières caractérisant l'hétérogénéité spatiale des microhabitats.

La méthodologie employée dans cette recherche combine une approche comportementale ainsi qu'une approche reliée à l'écologie des paysages. En effet, l'écologie des paysages comprend des avenues très intéressantes pour les écologistes du comportement. Par exemple, cette discipline procure des outils pouvant aider à mieux comprendre comment l'hétérogénéité des habitats est perçue par un animal (Lima & Zollner, 1996). Elle nous permet, de plus, de mieux comprendre quelle information est disponible pour un animal et comment celle-ci est utilisée.

ARTICLE

Associations between microhabitat fuzzy boundaries and territory limits of two forest songbird species.

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Abstract

Agriculture, urbanization and forestry induce a lot of spatial heterogeneity in forests, leading to sharp and fuzzy boundaries. Although the effect of sharp boundaries on forest birds' territory size and distribution has been studied, the effect of fuzzy boundaries on territory delineation has not been investigated. We determined whether small-scale microhabitat heterogeneity has an effect on black-throated blue warbler (*Dendroica caerulescens*) and ovenbird (S*eiurus aurocapillus*) territory limits. The study was conducted during summer in amature deciduous forest near Quebec City (Canada). Territory limits of ten black-throated blue warblers and 14 ovenbirds, as well as 34 microhabitat variables were mapped using systematic surveys in a 49 ha grid with points 25 m apart (n = 756). We delineated bird territories and microhabitat boundaries with a lattice-wombling. Lattice-wombling territory limits corresponded well with limits of standard kernel home ranges. Furthermore, according to redundancy analysis, birds used different microhabitat characteristics for foraging vs. territory delineation. There was significant spatial overlap between microhabitat boundaries and territorial limits for 18 and 20 variables for black-throated blue warbler and ovenbird respectively. The strongest associations between microhabitat variables and birds' territory limits were with conifer seedling coverage, grass and total vegetation cover between 0-2 m high for black-throated blue warbler and with road proximity, vegetation-covered rocks and shrub diversity for ovenbird. This study illustrates the potential of boundary detection algorithms for investigations on habitat-wildlife relationships.

Key words: forest heterogeneity, songbirds, territory delineation, fuzzy boundaries, overlaps statistics, scale

Introduction

Agriculture, forestry and urbanization induce a lot of spatial discontinuity in forested landscape, leading to an increase in the proportion of sharp as well as fuzzy vegetation boundaries. Sharp boundaries are characterized by abrupt changes between forested and non-forested areas, whereas fuzzy boundaries are gradual transition zones between stands of different composition and structure (Yahner, 1988). These boundaries can have an important impact on wildlife (Andrén, 1994). A large number of investigations relative to the effect of sharp boundaries, i.e., edge effect, on the size (Ortega & Capen, 1999) and spatial distribution (King *et al.*, 1997; Villard, 1998) of songbird territories have been conducted by ecologists. When establishing their territory (i.e., defended area; Kaufmann, 1983), forest songbirds such as ovenbird (*Seiurus aurocapillus*) apparently avoid sharp forest edges (Wenny *et al.*, 1993; Van Horn *et al.*, 1995; Burke et Nol, 1998; Ortega & Capen, 1999) whereas others are generally associated with sharp forest edges, like black-throated blue warbler (*Dendroica caerulescens*) (King *et al.*, 1997). At a finer scale, sharp forest edges may also determine the location of territory limits because of movement constraints (Rail *et al.*, 1997).

Studies on the selection of breeding territories of forest songbirds usually compare what vegetation features and food abundance lie inside territories to what is available in the study area (e.g., Smith & Shugart, 1987; Steele, 1992;

1993). For example, black-throated blue warblers tend to locate their territories in dense shrub areas (Steele, 1992; 1993). While these studies contain important information about what general criteria are selected when songbirds are locating their territory, they provide little information about territory delineation *per se*. Following the pioneering work of Nice (1937) and Lack (1954), most ornithologists believe that interactions with conspecifics determine the location of territory boundaries. However, according to Klopfer & Ganzhorn (1985), the choice of a territory may follow a multi-step procedure, based on visual cues associated to the contents and the spatial distribution of the predominant vegetation first at the landscape, then at stand and microhabitat scales. The last step in territory choice, namely its delineation, remains little understood, partly because songbirds perception of habitat spatial heterogeneity (fuzzy boundaries) is not known. The lack of information concerning the effect of these subtle and gradual discontinuities on territory delineation may have arisen from the difficulty of delineating and quantifying this type of boundary. For example, edge width at two adjoining patches is highly subjective and may vary according to the nature of the adjoining patches (Yahner, 1988) and the variables measured (Fortin, 1997).

In this study, we investigate whether birds territorial boundaries are associated with microhabitat spatial discontinuities (fuzzy boundaries). To address this, we measured the spatial relationship between microhabitat boundaries defined by spatial variation in 34 microhabitat variables (biotic and abiotic), and territorial limits of the black-throated blue warbler and the ovenbird, based on recently-developed boundary delineation methods (Fortin, 1994). We also provide an analysis of relationships between the abundance of the microhabitat variables and the occurrence of both species. The latter analysis was used to determine which habitat variables are associated with territory location (core areas) and to compare variables important to territory location vs. territory delineation. Our main goal is to better understand whether habitat spatial heterogeneity provides cues or landmarks for territory delineation. Both bird species under study are neotropical migrants that breed in deciduous and mixed woods forests of southern Québec (Canada). Their life history is very different so we expected that they would use habitat cues differently.

Methods

Study area and plot establishment

The study was conducted at the Station écotouristique Duchesnay, near Québec City, Canada (Figure 1). Station écotouristique Duchesnay (47°42N, 72°48W) is located in the ecological zone of the boreal shield (Paquin, 1996), occupying a transitory position between the St-Lawrence plain and the Laurentian plateau. The elevation range of the study area is 270 - 390 m. Stands are dominated either by balsam fir (A*bies balsamea* (L.) Mill.) / yellow birch (*Betula alleghanensis* Britton), sugar maple (A*cer saccarum* Marsh.) / yellow birch and balsam fir / red spruce (*Picea rubens* Sarg.) associations.

Our study plot was a systematic sampling grid of 49 ha (700 m x 700 m) consisting of 756 points, 25 m apart. All points in the study plot were located inside mature stands. Each point was positioned with a stake, using a GPS receiver with real time differential correction (Figure 2). At each point, bird surveys were conducted and microhabitat data were recorded.

Bird occurrence mapping

Bird locations were mapped from 10 May to 23 June 1999, between 0500 and 1000 under weather conditions with no rain or strong winds. We used an adaptation of the point count method to map territories (Liverman, 1986; Villard, 1999). Ten territorial black-throated blue warbler males and 14 ovenbird males were captured and marked with unique combination of color bands for individual recognition. To map bird locations, a systematic survey routine was established so that each of the 756 points was visited three times during the 2 months survey period. Every morning, two observers covered one half of the study area by walking along transects 100 m apart. Five minutes counts were made at each sampling point, 100 m apart along transects. Transects were shifted by one grid point (25 m) on consecutive days, so that each point was visited once every 16 days. During the first three minutes of each count we recorded the presence or absence of black-throated blue warblers and ovenbirds and estimated their location. During the last two minutes, we used playback of conspecific songs of both bird species successively to increase sampling efficiency (Falls, 1981). Males that were coming in the direction of the speaker were identified. To reduce the chance of playback tape habituation, observers alternated every day between songs of three different conspecific individuals. We obtained a minimum of twenty accurate (± 12.5 m) locations for each male in order to map their territory.

Microhabitat measurement

Spatial information on microhabitat for each of the 756 points was collected from 5 July to 28 August (Table 1). We measured the following: canopy opening, maximal canopy height, slope, microrelief, road noise intensity and coverage of water. Because road proximity is a continuous variable (i.e., rates of change between points along the north-south axis are the same), we couldn't use it to compute boundaries. Therefore, we used road noise intensity as an index of road proximity. A quoted value proportional to road noise intensity was attributed at each sampling point (4 = very strong to 0 = null). We will therefore use the terminology *road proximity* in the results and discussion section.

Each of the 756 points was then divided into four quadrants in which we recorded: percentage cover of grass (0-2 m), shrubs (2-5 m and 5-10 m) and trees (taller than 10 m), coverage of bare rocks, covered rocks and logs. We also listed all trees (classified by species and DBH) and all shrub species. Five coverage classes were defined to facilitate the estimation and to minimize bias among the three observers (0 = 0%; 1 = 1-5%; 2 = 6-25%; 3 = 26-50%; 4 = 51-75%; 5 = 76-100%).

Relationship between bird occurrence and microhabitat variables abundance

To identify which microhabitat features were mostly associated with core areas within territories, the relationship between bird species occurrence and microhabitat was assessed using a redundancy analysis. The occurrence of black-throated blue warbler and ovenbird was calculated as the number of times each species was seen on each point of the study grid. RDA was chosen because canonical correspondance analysis (CCA), another ordination technique, is not suitable for extremely short gradients in which species abundance is a linear function of gradients (Palmer, 1993; Legendre & Legendre, 1998). In our case, therefore, only linear responses were obtained.

The data consisted in one matrix of grid points x 28 explanatory microhabitat variables and one matrix of grid points x two response variables (i.e., occurrence of each bird species).

Delimiting territory and microhabitat boundaries

We used two methods to delimit territories : lattice-wombling (Fortin, 1994; GEM 1997) and the kernel (Worton, 1989). Lattice-wombling algorithm computes rates of change for regularly spaced data for each set of four adjacent cells (quadrats) and provides an effective way to deal with territory and vegetation boundaries that vary greatly in sharpness. With lattice-wombling, the magnitude of rate of change is computed for the centroid location of each set of quadrats (Fortin & Drapeau, 1995). A rate of change is considered as a boundary element if it exceeds an arbitrary threshold. We defined as boundary elements (BEs) all instances where the rate of change was above the 85th percentile for a given vegetation variable or bird occurrence. This threshold was chosen to optimize the detection of birds territory limits and to avoid the detection of noise occurring with a more liberal threshold. Given that 840 rates of change were computed based on the 756 sampling points, we retained the most pronounced 126 BEs for each variable. However, in some cases, the 126th rate of change value was tied in magnitude with others. In such circumstances, only the rate of change values having a magnitude greater and equal than that at the 126th rank were kept as BEs. For example, for ovenbird occurrence, the magnitude of rate of change was the same between the 89th and 151st, so we selected 89 BEs for this variable.

The kernel method is widely used in studies of wildlife distribution (Worton, 1989) and therefore provides a good basis for comparison with the above method. Kernel home ranges are based on estimated positions to calculate contour lines for specified probabilities of occurrence. A probability of occurrence of 85 % was used in our study.

Measuring overlap between boundaries

The overlap between territory boundaries of both bird species (based on lattice-wombling) and those of each habitat variable was calculated using the overlap statistics of Jacquez (1995). The overlap statistics computed were *Os* and *Oxy*. *Os* is the direct spatial overlap, i.e., association, defined as the number of boundary elements (birds and microhabitat) that are at the same location (Fortin *et al.*, 1996). *Oxy* is the mean minimum distance between all birds and vegetation boundary elements. We tested the significance of overlap estimates with a randomization procedure ($n = 999$ randomizations). The significance of O*s* and O*xy* was assessed using one-tailed tests ($p \leq 0.05$), because we were interested only in overlap (not avoidance) between microhabitat and territory boundaries.

Results

Microhabitat inventory

Twenty tree species were identified in the study area. The proportion of deciduous and conifer tree species was respectively 91% and 9% (n = 28 412 trees). The most abundant deciduous species were sugar maple (*Acer saccharum* Marsh.) (46 % of the total number of deciduous trees), yellow birch (*Betula alleghaniensis* Britton) (15%) and american beech (*Fagus grandifolia* Ehrh.) (9%). We found also few red maple (*Acer rubrum* L.), bird-cherry (*Prunus pensylvanica* L.f.) and striped maple (*Acer pensylvanicum* L.). The most abundant conifer species were balsam fir (Abies balsamea (L.) Mill.) (58%) followed by spruce (*picea* sp.) (13%) and tamarack (*Larix laricina* (Du Roi) K. Koch) (10%). The shrub layer was composed of twenty species. Hobblebush (*Viburnum alnifolium* Marsh.) dominated (26%) followed by ground hemlock (*Taxus canadensis* Marsh.) (25%) and sugar maple (20%).

Relationship between bird occurrence and microhabitat variables abundance

RDA shows the relationship between bird species occurrence and microhabitat characteristics (Figure 3; acronyms defined in table 1). The first axis accounted for 62.4 % of the variation of the species and environmental data while the second accounted for 37.6%. The first axis of the RDA suggests marked differences between microhabitat use by black-throated blue warbler and ovenbird. Black-throated blue warbler was associated mainly with grass, high superior shrub layer coverage, deciduous seedlings, logs and road proximity. Slope, canopy height and decomposed logs and stumps were, among other variables, also associated with black-throated blue warbler occurrence. According only to axis I, bare rocks, high inferior shrub layer coverage, ground hemlock and total vegetation cover between 2-5 m were associated more with black-throated blue warbler than with ovenbird.

Ovenbird occurrence was associated with annual, deciduous tree density, ferns and trees coverage, as well as with shrub diversity, non-decomposed logs and stumps, canopy opening and microrelief (Figure 3). Other variables according only to axis I were more associated with ovenbird than with black-throated blue warbler: shining-club moss, conifer density, sphagnum as well as trails, water relative coverage, moss and conifer seedlings.

Territory boundaries and spatial relationship with microhabitat boundaries

Territory limits delineated by kernel and lattice-wombling methods coincided spatially, both for black-throated blue warblers (Figure 4; direct spatial overlap for 74% of BE and kernel territory limits locations) and ovenbirds (Figure 5; direct spatial coincidence for 89% of BE and kernel limits locations). Note that contrary to the kernel, lattice-wombling boundary elements do not necessarily form closed polygons. The spatial overlap between black-throated blue warbler and ovenbird boundary elements shows that the location of one species territory limits does not exclude the other species territory limits in the same area (Figure 6).

To evaluate if there is a confounding effect between some microhabitat variables that could be strongly associated spatially (e.g., deciduous seedling coverage and total cover between 0-2 m), we have constructed a table that represents the number of boundary elements that were at the same location for each pair of variables (Table 3). According to Table 3, the pair of variables that had the highest number of boundary elements locations in common were: canopy opening – global canopy characteristics (99 BEs at the same location), canopy height – slope (99), microrelief – water (87), tree – global tree characteristics (90).

Eighteen of the 34 microhabitat variables significantly overlapped with black-throated blue warbler territory limits (Table 2). According to O_s and O_{xy} measures taken jointly, BEs most consistently associated with black-throated blue warbler territory limits were those defined by conifer seedlings (Figure 7A), deciduous seedlings, decomposed and non decomposed logs and stumps, grass, total cover between 0-2 m, microrelief and road proximity. None of these microhabitat variables had a strong confounded effect according to their number of common boundary elements location (Table 3). Although not significant according to O_{xy}, boundaries defined by bare rock, shrub diversity and tree coverage were among the five most significant predictors of black-throated blue warbler territory limits according to O_s.

Twenty of the 34 microhabitat variables significantly overlapped with ovenbird territory limits (Table 2). According to O_s and O_{xy} measures taken jointly, BEs most consistently associated with ovenbird territories were those defined by road proximity, covered rocks, logs, non decomposed logs and stumps and shrub diversity. The effect of these variables does not seems to be confounded according to their number of common boundary elements location (Table 3). Although not significant according to O_{xy}, boundaries defined by fern (Figure 8A), trail, total ground characteristics and slope were among the five most significant predictors of ovenbird territory limits.

Discussion

Forested landscapes are shaped by edaphic factors, natural disturbances and human activity. Current forestry practices induce a lot of spatial heterogeneity in forested landscapes, resulting in an increase in the proportion of sharp and fuzzy boundaries (Yahner, 1988). While the effect of sharp boundaries on bird territory size and location has been well studied in the past years (King *et al.*, 1998; Villard, 1998; Ortega & Capen, 1999), a shortage of efficient statistical techniques has limited our understanding of the ecological role of fuzzy boundaries on bird territory location delineation. Earlier work on edge detection algorithms and overlap statistics documented relationships between vegetation and abiotic factors (Fortin, 1994; Fortin & Drapeau, 1995; Fortin *et al.*, 1996). Our study now shows that, based on the strong overlap between territory limits defined by kernel and lattice-wombling, the latter method is appropriate to define bird territory limits. Furthermore, we provide, by the analysis of the overlap between microhabitat boundaries and birds territory limits, some of the first evidence on the effect of fuzzy boundaries on territorial birds. The possible ecological explanation of this effect is given at the end of this section.

Relationship between bird occurrence and microhabitat variables abundance

There were marked differences between both bird species according to their association with microhabitat variables, as was expected by their different life history (Smith & Shugart, 1987; Holway, 1991; Steele, 1992, 1993; Blanchette & Larue, 1993; Holmes *et al.*, 1996) (Figure 3). Black-throated blue warblers forage mainly 3-9 m above the ground (Steele, 1993) and usually nest 1 m above the ground (Holway, 1991), in contrast with ovenbird which forage and nest on the ground (Smith & Shugart, 1987).

The association between black-throated blue warbler occurrence and a high grass, superior shrub strata, deciduous seedlings, inferior shrub strata, and ground-hemlock coverage is consistent with most other studies which emphasized the role of the shrub stratum for this species (Steele, 1992; 1993). Black-throated blue warbler territories were also associated with road proximity. According to King *et al.* (1997), black-throated blue warblers might prefer sharp edges which provide an increase in the number of singing perches and foraging substrates (See also De Graaf, 1992; Yahner, 1983). Microhabitat variables that were most correlated with the occurrence of ovenbirds were low ferns, deciduous seedlings, annuals and non-decomposed logs and stumps coverage, again all at the shrub and lower strata, which are locations where ovenbirds spend most of their time during to forage and nest (Stenger & Falls, 1959; Smith & Shugart, 1987).

Territory limits could be influenced by the presence of conspecifics (Nice, 1937; Lack, 1954) and other species (e.g., Bourski & Forstmeier, 2000). However, evidence from our study, both in terms of territory contents and limits, was not consistent with direct interspecific competition (i.e., by social interference). A preliminary analysis using overlap statistics revealed no significant direct overlap between black-throated blue warbler and ovenbird boundary elements ($O_s > 0.05$). However, an experimental approach would be required to provide a conclusive assessment of interspecific relationships between our two study species. For the purpose of this study, no behavioral data on interspecific competition have been recorded.

Spatial relationship between territory limits and microhabitat boundaries

As it was expected from their different life history, black-throated blue warblers and ovenbirds perceived microhabitat boundaries differently. Also, the microhabitat variables that were significantly associated to territory limits did not have a confounded effect according to the number of their common boundary elements location. The association between black-throated blue warbler territory limits and conifer seedlings, deciduous seedling, grass and total vegetation cover between 0-2 m boundaries could reflect the importance of these characteristics in the territory delineation process. According to O_s statistics, bare rocks, shrub diversity and tree coverage were also important predictors of black-throated blue warbler territory limits.

While bare rocks importance was reflected by the RDA, shrub diversity and tree coverage were apparently not important for territory delineation by black-throated blue warblers. At the territory scale, shrub diversity could be an important factor taken into account by black-throated blue warbler. According to Rotenburry (1985), the importance of floristic components at small scale (within habitat) could be related to the amount of food and to the foraging behavior. Bersier & Meyer (1994) also reported the importance of floristic composition at small scale, whereas at larger scale, vegetation structure was more important in defining bird species assemblages. Our results show also that abiotic features such as bare rocks and microrelief can complement biotic features in the territory delineation process.

Ovenbird territory limits coincided mainly with boundaries defined by road proximity, shrub diversity, covered rocks, logs and non-decomposed logs and stumps. Ovenbirds is known to avoid sharp edges possibly because they correspond to a higher rate of nest predation and parasitism (Temple & Cary, 1988) and a diminution of food abundance and quality (Gibbs & Faaborg, 1990; Burke & Nol, 1998). The association between road proximity boundary and ovenbirds' territory limits could be explained by this fact. In addition to the above variables, ovenbird territory limits were associated with slope boundary elements, which support Reid & Weather's (1988) hypothesis on the importance of topological features in the territory delineation process. Our results contrast, however, to those found by Ortega & Capen (1999), where, among all the vegetation variables sampled, only ground coverage was found to be significantly higher outside than inside territories. Our study suggests that other factors than those usually cited in territory location have an effect on the delineation of ovenbird territories studies. For example, the coverage of logs and non-decomposed logs and stumps.

Different patterns-Different scales

The comparison between results obtained with RDA (a method traditionally used in territory location studies) and the overlap statistics is another demonstration that different patterns do occur at different spatial scales (coarse vs fine). As it was suggested by Klopfer & Ganzhorn (1985) and Sodhi *et al.* (1999), territory location can be viewed as a multi-step procedure, from the landscape level to the territory level, where the last step is the delineation of the territory. RDA shows which variables tend to be associated with birds relative occurrence (territory location) whereas the overlap statistics are a measure of the spatial relationship between microhabitat boundary and birds' territory limits (territory delineation). As Steele (1992) and Bersier & Meyer (1994) discussed some characteristics of the habitat could be important at a given scale, but negligible at the other. For example, microrelief and total cover between 0-2 m boundaries were significantly associated with black-throated blue warbler territory limits but were not prevalent within territories. Additionally, road proximity, shrub diversity and covered rocks boundary were strongly associated with ovenbird territory limits, but were not the major variables associated with the occurrence of this species.

Why do birds use fuzzy boundaries in territory delineation?

In undisturbed forest patches, boundaries are generally fuzzy due to subtle variations in leaf type, tree species composition and arthropod abundance (Sherry & Holmes, 1985). The fact that birds consider microhabitat fuzzy boundaries could be related to the optimization of territory shape, affected by differences in the amount or type of resource in patches that are present in heterogeneous environment. Eason (1992) and others argued that birds tend to optimize territory shape in spatially heterogeneous environment in order to reduce the costs associated to foraging efficiency and defense and to increase food availability and intruders visibility. While our study did not focus on the relation between territory shape and microhabitat features, we can infer from Eason's (1992) study that some of these factors associated with territory defense and foraging activity may also be important criteria for territory delineation as well. For example variables defining territory limits may represent important food sources (e.g., saplings; see Jokimaki *et al.*1998), singing posts or view points (Bamford, 1986), which may become the stage for encounters with rivals. Territory shape, and thus its limits, could be optimized in order to maximize intruder visibility (e.g., low ground coverage for ovenbird), having a direct effect on territory defense costs (Eason, 1992). When studying birds' territory shape, and probably also when studying their limits, we should consider foraging costs as well as defense costs (Eason, 1992).

According to Stamp *et al.* (1987), factors extrinsic to territories (e.g., the nature of habitat surrounding the territory) may have an effect on defense costs as important than intrinsic characteristics of territories. This reflects the importance of understanding which microhabitat features lies at the limits of territories and which one are considered by forest birds when they delineate their territories. Our study shows, thus, an innovative method that enable us to detect these specific microhabitat features for each species of interest.

Conclusion

This paper proposes an innovative approach to delineate birds' territories, i.e., lattice-wombling algorithm and to associate territory limits with vegetation boundaries (overlap statistics). Three main conclusions can be drawn from our study. First, boundary elements for the lattice-wombling coincided well with territory limits delineated with the kernel method, thus providing an alternative tool to detect birds' territory limits. Using this tool could be very interesting to associated birds territory limits with habitat features. Second, vegetation and abiotic features were associated not only with core areas within territories, but their gradients (boundaries) coincided with territory limits in ways consistent with their known habitat preferences, as was shown by the spatial overlap statistics. Third, associations between birds' territory limits and microhabitat boundary elements differed between ovenbird and black-throated blue warbler as it was expected from their different life history.

In summary, earlier studies mentioned the importance of the presence of conspecifics (Nice, 1937; Lack, 1954), other species (e.g., Bourski & Forstmeier, 2000), and sharp boundaries (Rail et al., 1992) on territory delineation. From the results of our study, however, it is clear that fuzzy boundaries can affect territory limits, even though they may have no impact on bird species assemblages (De Graaf, 1992). The relation between microhabitat fuzzy boundaries and birds' territory limits could be due, in part, to the optimization of territory shape in relation to foraging activity and territory defense costs.

We believe that edge detection algorithms and spatial overlap statistics could become useful statistical tools for future studies on habitat-wildlife relationships. For example, to study animal distribution in reaction to spatial alteration in the structure and configuration of their habitat in a management and conservation perspective. By increasing our comprehension of the effect of sharp as well as fuzzy boundary (characteristic of heterogeneous environment) on animal behavior and distribution, we can improve largely our skills and knowledge for a better management of wildlife and their habitat.

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Conclusion générale

La structure spatiale des paysages forestiers actuels est le résultat à la fois des perturbations naturelles et anthropiques. Les populations animales présentes dans les paysages forestiers de plus en plus morcellés diminuent, à la fois par la réduction des habitats disponibles et possiblement par une hausse de la proportion des lisières dans les ilôts forestiers résiduels. L'hétérogénéité spatiale forestière se manifeste par une mosaïque de lisières nettes (interface forêt-champ par exemple) et de lisières floues (zones de transition graduelle entre des peuplements de structure et de composition différente). Bien qu'il y ait un effet des lisières nettes sur la distribution (King *et al.,* 1997; Villard, 1998) et la taille (Ortega & Capen, 1999) des territoires des oiseaux forestiers, peu d'information est disponible sur l'effet des lisières floues sur la localisation et la délimitation des territoires des oiseaux. Contrairement aux lisières nettes, les lisières floues sont difficiles à délimiter. Les algorithmes de détection de lisières permettent maintenant de remédier à ce problème, puisqu'ils ont la particularité de pouvoir détecter à la fois des changements abruptes ainsi que des zones de transition dans les paysages forestiers (Fortin & Drapeau, 1995).

L'objectif de la présente étude était d'évaluer l'effet de l'hétérogénéité spatiale du couvert forestier (lisières nettes et/ou floues) sur la délimitation des territoires des oiseaux forestiers à l'aide de l'algorithme de lattice-wombling. Nous avons utilisé deux espèces modèles, soit la paruline bleue (*Dendroica caerulescens*) et la paruline couronnée (*Seiurus aurocapillus),* afin d'optimiser l'information relative à l'utilisation verticale de l'habitat. La majorité des activités journalières de la paruline bleue s'effectuent dans les strates arbustives inférieure et supérieure (Steele, 1992; 1993) tandis que la paruline couronnée passe la majorité de son temps au sol (Smith & Shugart, 1987).

Par cette étude, nous proposions une nouvelle approche statistique, soit l'utilisation d'un algorithme de détection de frontière et des statistiques de chevauchement spatial, afin de délimiter les territoires des oiseaux, de détecter les lisières caractérisant l'hétérogénéité spatiale des microhabitats forestiers et d'évaluer la relation spatiale entre les deux type de lisière (limites territoriales et microhabitats). Afin de répondre à l'énoncé de Klopfer & Ganzhorn (1985) et Sodhi *et al.* (1999) stipulant que la sélection du territoire chez les oiseaux est un processus se manifestant à plusieurs échelles spatiales, nous avons de plus effectué une analyse de redondance (RDA). De cette façon, nous avons pu évaluer quelles caractéristiques des microhabitats avaient le plus d'influence sur l'occurrence des deux espèces, afin de comparer ces résultats avec ceux des statistiques de chevauchement.

L'analyse de redondance a confirmé en premier lieu que l'utilisation des microhabitats par les deux espèces était contrastée. La paruline bleue est associée, entre autres, à un fort recouvrement des strates herbacée et arbustive supérieure, un fort recouvrement des semis de conifères et billots au sol. Quant à la paruline couronnée, elle était davantage associée à un faible recouvrement de plantes annuelles, de semis feuillus et de fougères. Ces résultats correspondent à ceux retrouvés dans la littérature. En effet, la paruline bleue préfère des sites où la strate arbustive est dense (Steele, 1992; 1993; Villard, 1999b), et la paruline couronnée des sites où la strate herbacée est éparse (Blanchette & Larue, 1993).

La comparaison entre les résultats de l'analyse de redondance et ceux des statistiques de chevauchement démontre que différents processus se manifestaient à différentes échelles spatiales (grossière ou fine) lors du choix de l'habitat et de la délimitation du territoire. Les résultats des statistiques de chevauchement démontrent également que les deux espèces ne réagissaient pas de la même manière face aux différentes lisières caractérisant les microhabitats. Un total de 18 et 20 variables sur 28 avaient un chevauchement direct (O_s) significatif pour la paruline bleue et la paruline couronnée respectivement. La statistiques O_{xy} a permis d'appuyer la statistique O_s en démontrant une forte association entre les limites territoriales des oiseaux et les lisières caractérisant les microhabitats. Seulement huit et six variables dans le cas de la paruline bleue et de la paruline couronnée ont respectivement atteint une valeurs significative pour cette statistique. Les résultats des statistiques de chevauchement démontrent une forte association (où O_s et O_{xy} sont toutes deux significatives) entre les lisières floues caractérisées par le recouvrement en semis de conifères, le recouvrement de la strate herbacée et le recouvrement total entre 0-2 m et les limites territoriales de la paruline bleue. Les limites territoriales de la paruline couronnée étaient fortement associées, selon ces deux mêmes statistiques, avec les lisières floues caractérisant l'intensité du bruit de la route, le recouvrement en roches couvertes et la diversité arbustive. Les lisières incluses dans des habitats non perturbés (lisières floues) sont caractérisées par des variations au niveau de la quantité de nourriture disponible, du type de feuillage et de la composition en espèces (Sherry & Holmes, 1985). L'association entre les lisières caractérisant les microhabitats et les limites territoriales des oiseaux peut être reliée à l'optimisation de la forme du territoire, affectée par les différences dans la quantité ou le type de ressources disponibles. En effet, selon Eason (1992), la forme du territoire doit être optimisée de façon à augmenter l'efficacité de recherche de nourriture et la visibilité des compétiteurs ainsi qu'à diminuer les coûts reliés à la défense du territoire. L'association entre les différentes lisières caractérisant les microhabitats et les limites territoriales des oiseaux pourrait être reliée, de plus, à leur apport en arthropodes ou en perchoirs pour le chant.

Cette étude suggère que, pour le secteur étudié, les oiseaux forestiers (dans ce cas-ci la paruline bleue et la paruline couronnée) considèrent les discontinuités floues des microhabitats lors de la délimitation de leur territoire. Les algorithmes de détection de lisières ainsi que les statistiques de chevauchement représentent des outils statistiques pouvant devenir très intéressants lors d'études portant sur les relations faune-habitat. Dans une perspective de conservation, par exemple, de telles statistiques pourraient être utilisées pour déterminer l'effet de l'hétérogénéité spatiale de l'habitat sur la répartition et les mouvements des espèces. En ce sens, et en vue d'une meilleure gestion des espèces animales et de leur habitat, l'intégration des notions ayant trait à l'écologie comportementale avec les outils et concepts relevant de l'écologie du paysage s'avère extrêmement prometteuse.

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ANNEXE 1

Tables

Table 1. Acronym description of all variables measured for each of the 0.03 ha within the study area with their respective number of kept^{+++} boundary elements (BEs) based on a 15% threshold.

Code	Description	BEs
Annu	% cover of annuals	105
BaRo	% cover of bare rocks	105
BTBW	Black-throated blue warbler	108
CaHe	Approximate canopy height	325
CaGlo	Canopy characteristics (CaHe; CaOp)	105
CaOp	% opening of the canopy	106
CoDe	Conifer trees density	107
CoRo	% cover of covered rocks	104
CoSe	% cover of conifer seedlings	104
DeDe	Deciduous trees density	105
DeSe	% cover of deciduous seedlings	104
Ferns	% cover of ferns	104
Grass	% cover of grass	104
GrassGlo	Global herb data (Annu; CoSa; DeSa; Ferns; GrHe; LostDc; LostNdc; Moss; ShCMo; Spgn)	104
GrHe	% cover of ground-hemlock	104
GroundGlo	Ground characteristics (BaRo; CoRo; MiRe; Trail; Water; Slope)	104
InSh	% cover of inferior shrub strata	104
Logs	% cover of logs	108
LostDc	% cover of decomposed logs and stumps	107
LostNDc	% cover of non-decomposed logs and stumps	116
MiRe	Microrelief	124

Moss	% cover of moss	106
Oven	Ovenbird	89
RoPr	Road proximity	137
ShCMo	% cover of shinning-club moss	104
ShDi	Shrub diversity	104
ShrubGlo	Global shrub data (ShDi; SuSh; InSh)	220
Slope	Inclination of the slope	104
Spgn	% cover of sphagnum	79
SuSh	% cover of superior shrub strata	104
T0-2*m*	Total 0-2*m* vegetation cover	104
T2-5*m*	Total 2-5*m* vegetation cover	104
Trail	% cover of trails	104
Tree	% cover of trees	106
TreeGlo	Global tree data (CoDe; DeDe; Tree)	104
Water	% cover of water or active water bed	132

[+++] See explanation in the Analyses section

Table 2. Spatial overlap statistics for territories of black-throated blue warbler and ovenbird in association with microhabitat boundaries. O_s is the percentage of direct overlap between microhabitat boundary elements (BEs) and territory BEs. O_{xy} is the mean distance between territory and microhabitat BEs. Statistical significance is based on 999 randomizations.

Code	***Black-throated blue Warbler***		***Ovenbird***	
	O_s	O_{xy}	O_s	O_{xy}
Annu†	7	81.81	8	52.30
BaRo	23***	51.87	15**	62.17
CaHe	18***	59.76	10*	50.80
CaGlo	12	57.20	9	46.20
CaOp	12	54.14	9	44.76**
CoDe	9	77.03	6	71.45
CoRo	17***	51.91	14***	48.38*
CoSe	20***	43.23***	12*	55.69
DeDe	7	70.33	6	64.67
DeSe	13*	48.87*	9	47.63
Ferns	10	71.61	18**	50.19
Grass	19***	49.56*	13**	44.56
GrassGlo	12	68.90	8	62.44
GrHe	18***	51.95	8	56.21
GroundGlo	20	58.90	16***	52.09
InSh	14*	60.70	13**	58.00
Logs	16**	52.31	13*	45.93**

LoStDc	15**	45.34**	14**	47.61
LoStNDc	13**	49.06*	13*	46.36*
MiRe	15*	44.08**	8	51.98
Moss	12	55.56	11*	59.28
RoNo	15*	48.71*	22***	37.10***
ShCMo	6	87.11	13*	62.23
ShDi	19***	55.93	14**	43.01***
ShrubGlo	13	61.06	11	52.51
Slope	10***	54.23	16*	55.24
Spgn	5	60.74	11	77.95
SuSh	13	62.89	13*	48.69
T0-2*m*	18***	46.39**	13*	47.30
T2-5*m*	8	63.51	9	58.17
Trail	12	89.51	17*	65.71
Tree	19***	56.29	11*	56.54
TreeGlo	15**	58.64	9	58.11
Water	13	78.51	14	60.71

†Refer to Table 1 for microhabitat acronym description.
*p • 0.05
** p • 0.01
*** p • 0.001

Table 3. Number of boundary elements having the same location for each pair of variable.

	Annu	BaRo	CaHe	CaGlo	CaOp	CoDe	CoRo	CoSe	DeDe	DeSe	Ferns	Grass	GrassGlo	GrHe	GroundGlo	InSh	Logs	LoStND	LoStD	MiRe	Moss	RoNo	ShCMo	ShDi	ShrubGlo	Slope	SpGn	SuSh	T0-2m	T2-5m	trail	Tree	TreeGlo
BaRo	11																																
CaHe	51	55																															
CaGlo	31	9	53																														
CaOp	31	9	48	97																													
CoDe	44	7	45	21	19																												
CoRo	27	18	45	21	22	35																											
CoSe	23	18	50	24	23	34	26																										
DeDe	26	18	55	15	16	38	10	19																									
DeSe	14	12	46	19	19	11	17	22	11																								
Ferns	23	4	39	30	31	18	17	18	19	11																							
Grass	13	15	58	21	20	18	20	18	10	19	17																						
GrassGlo	35	5	47	20	19	19	20	20	14	10	36	27																					
GrHe	14	11	56	15	14	10	16	12	12	14	11	32	27																				
GroundGlo	26	42	45	25	25	32	73	28	11	12	15	20	15	12																			
InSh	9	18	66	14	12	9	7	13	18	11	15	16	16	26	8																		
Logs	19	15	59	23	21	17	20	16	19	18	11	15	12	11	22	19																	
LoStND	16	18	46	20	21	16	16	13	23	19	15	17	19	13	13	17	21																
LoStD	19	21	54	16	17	16	17	10	25	23	21	9	15	10	15	19	18	49															
MiRe	24	15	51	29	32	17	31	19	18	25	24	19	26	19	33	17	15	10	10														
Moss	31	15	49	21	20	35	52	31	18	18	19	15	26	14	50	13	18	14	13	31													
RoNo	28	16	66	16	16	15	16	10	15	18	27	20	24	19	12	16	21	25	26	17	21												
ShCMo	15	8	33	18	16	4	4	6	10	15	13	20	29	13	5	18	20	20	9	20	9	22											
ShDi	20	13	58	17	18	16	12	19	19	10	21	18	11	14	15	11	19	15	9	20	18	21	9										
ShrubGlo	10	14	52	20	21	9	21	11	18	19	15	20	19	17	17	50	14	11	16	20	19	14	18	22									
Slope	31	35	99	39	39	41	42	26	39	18	31	31	31	24	40	38	36	39	38	36	41	33	25	27	36								
SpGn	34	3	28	32	34	39	33	21	23	39	21	9	20	5	31	4	12	9	11	34	31	10	10	14	11	25							
SuSh	14	11	42	20	22	11	24	11	13	23	14	20	20	16	19	17	14	19	11	20	17	15	20	21	67	26	10						
T0-2m	22	7	46	30	31	13	22	29	13	13	48	42	54	41	17	18	13	16	15	28	21	23	14	17	21	30	17	16					
T2-5m	16	14	54	19	17	8	18	11	15	13	16	18	16	20	14	35	19	10	12	23	15	21	18	14	37	33	10	29	20				
trail	27	31	58	22	19	20	25	22	12	15	14	20	23	12	50	14	20	9	7	25	31	25	16	19	17	43	18	15	20	16			
Tree	19	17	54	16	15	19	10	15	24	12	11	11	11	16	11	16	19	19	20	15	14	12	14	23	22	36	13	24	10	20	16		
TreeGlo	24	17	49	15	15	28	11	15	35	24	9	11	12	13	12	15	21	19	22	15	15	13	13	21	22	35	17	24	10	20	14	90	
Water	34	17	58	37	40	22	41	20	17	35	31	17	21	21	44	17	19	16	19	87	37	28	19	25	20	50	43	17	29	20	34	15	16

ANNEXE 2

Figures

Figure captions

Figure 1. Location of Station écotouristique Duchesnay, Québec, Canada.

Figure 2. Sampling grid (n = 756; 25 apart).

Figure 3. Ordination plot of bird occurrence and microhabitat variables after RDA analysis (axis I and II explain respectively 66.2% and 33.8% of the variation) (refer to Table 1 for habitat acronym description).

Figure 4. Ten territory limits of black-throated blue warbler according to kernel (black lines) and lattice-wombling (grey triangles) methods.

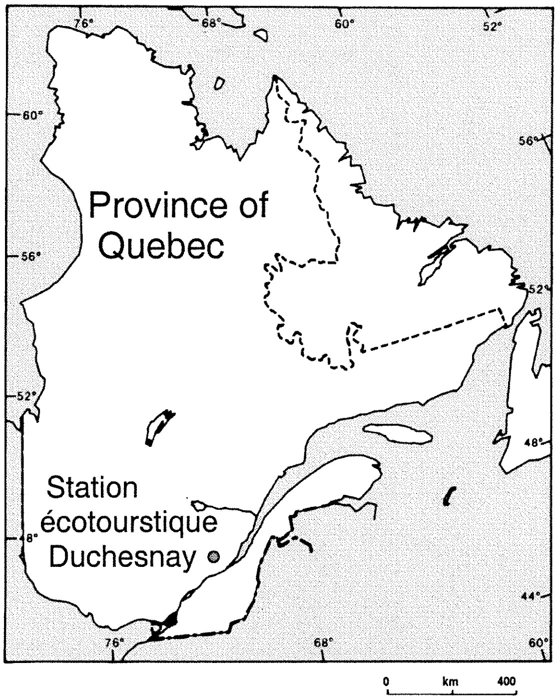
Figure 5. Fourteen territory limits of ovenbird according to kernel (black lines) and lattice-wombling (grey circles) methods.

Figure 6. Spatial overlap of black-throated blue warbler (black triangles) and ovenbird (grey circles) boundary elements.

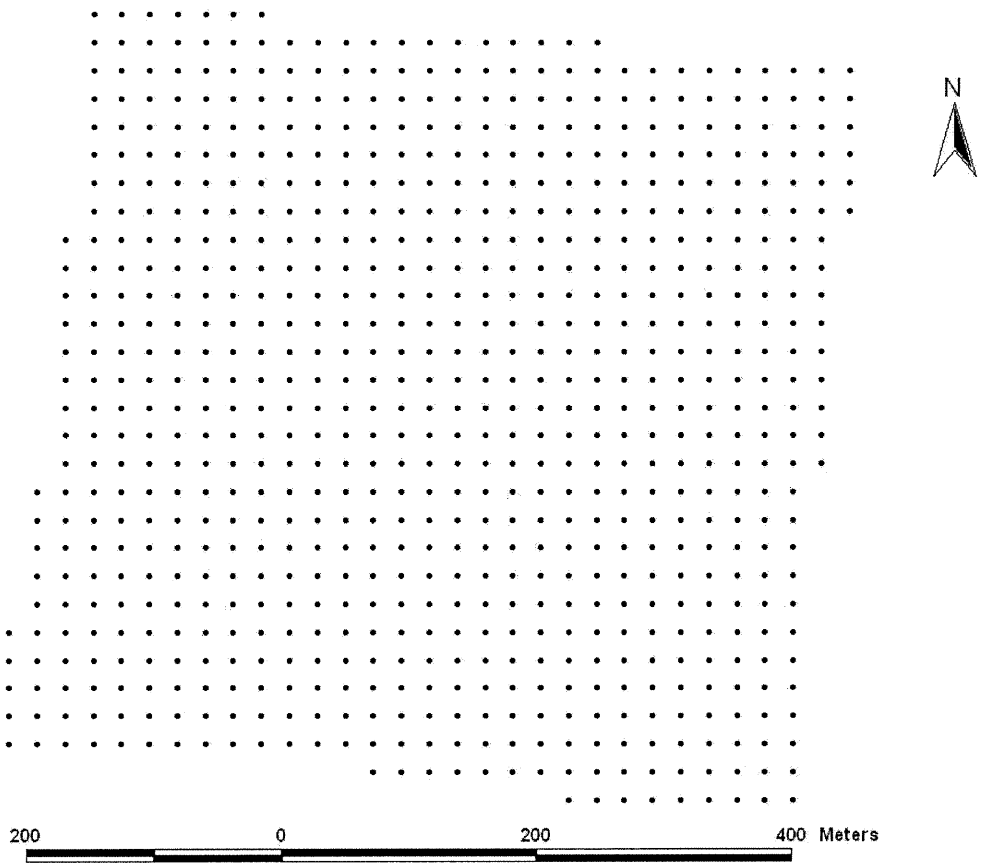
Figure 7. Spatial overlap between territory boundaries of black-throated blue warbler (black triangles) and boundaries defined by a) conifer seedlings (grey squares), and b) road proximity (grey circles).

Figure 8. Spatial overlap between territory boundaries of ovenbird (black circles) and boundaries defined by a) conifer seedlings (grey squares), and b) road proximity (grey circles).

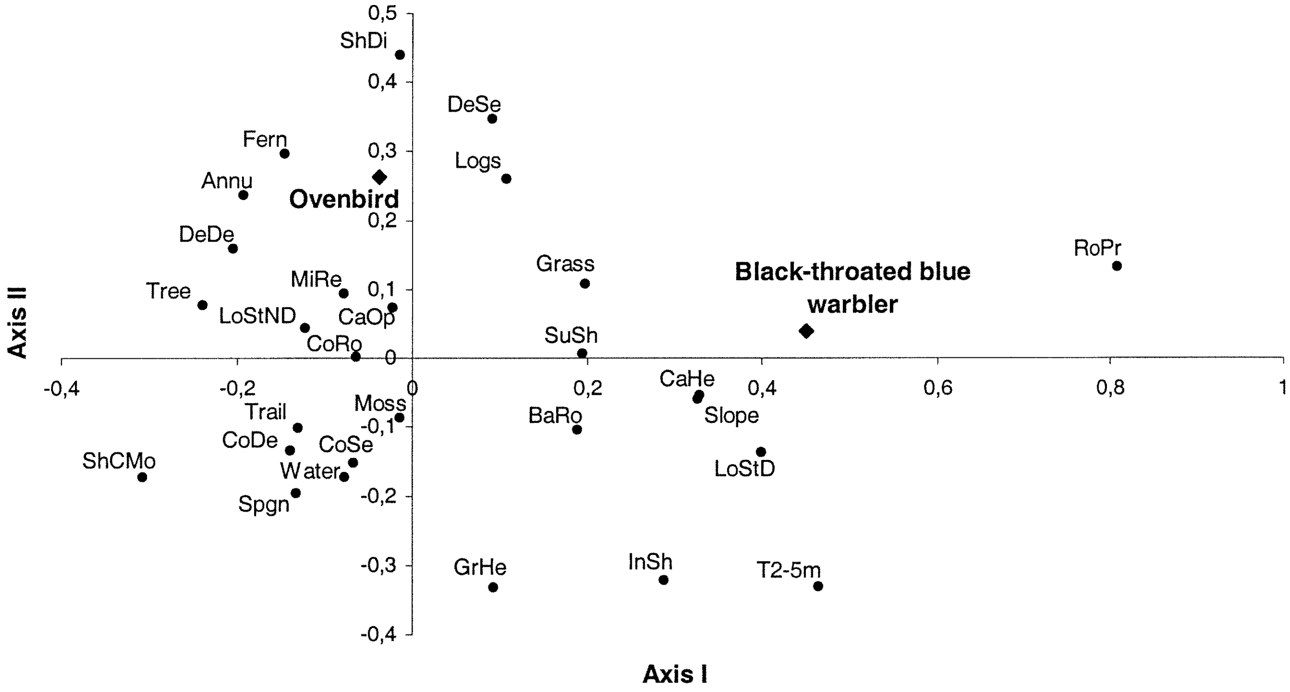
***St-Louis et al.**, Figure 1*



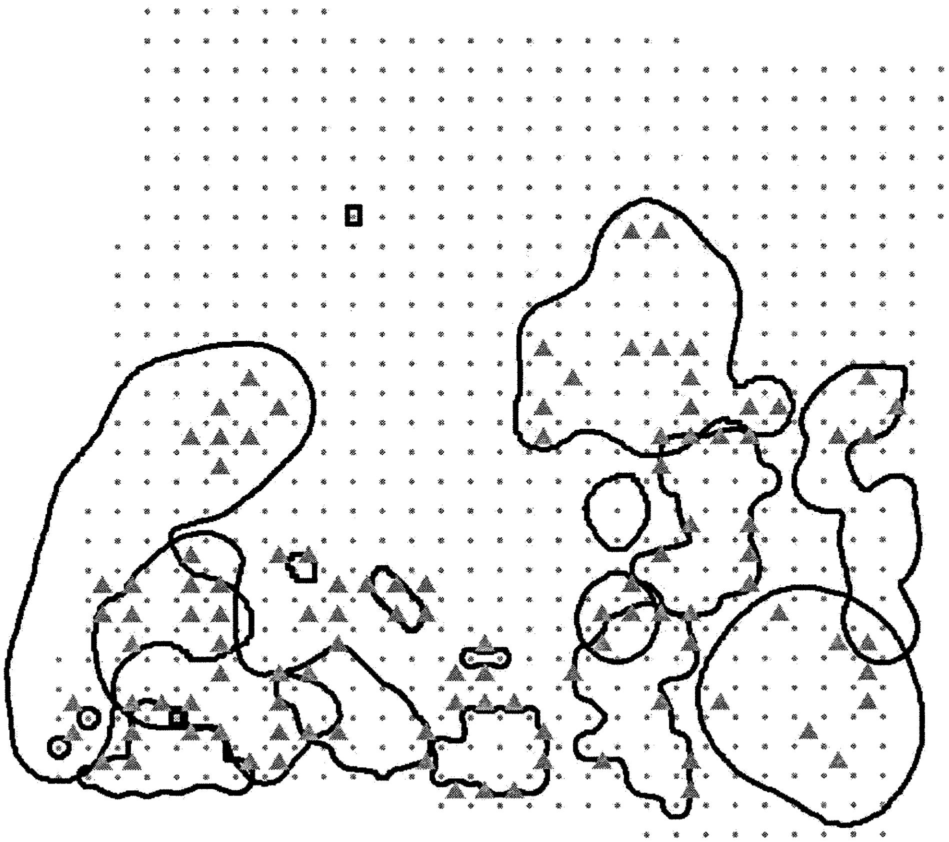
St-Louis et al., *Figure 2*



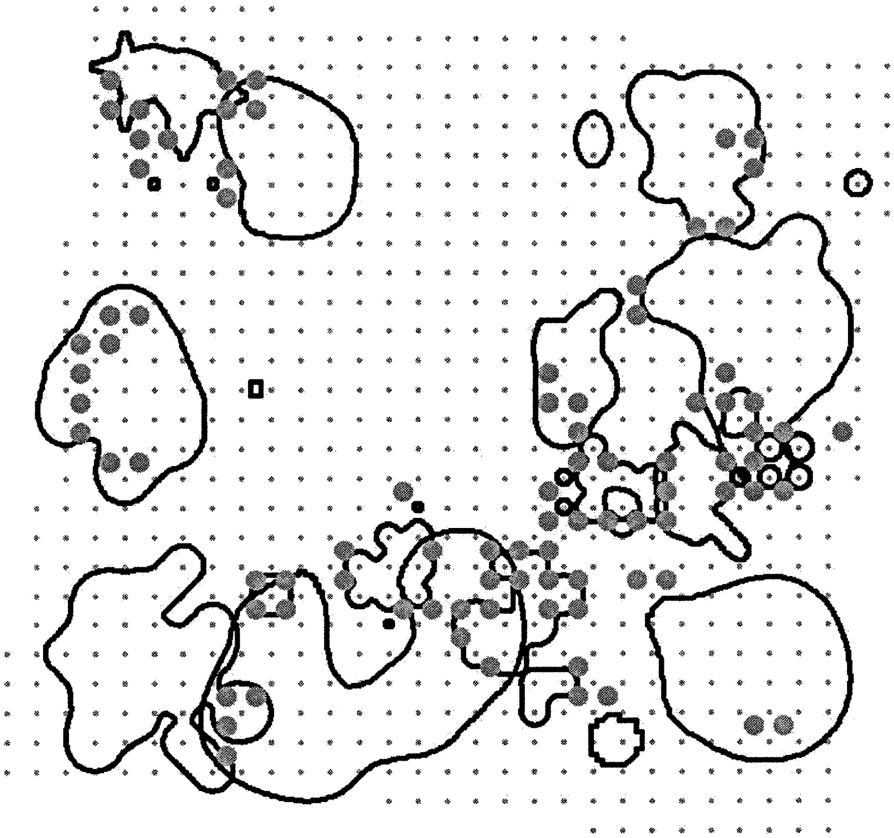
St-Louis et al., *Figure 3*



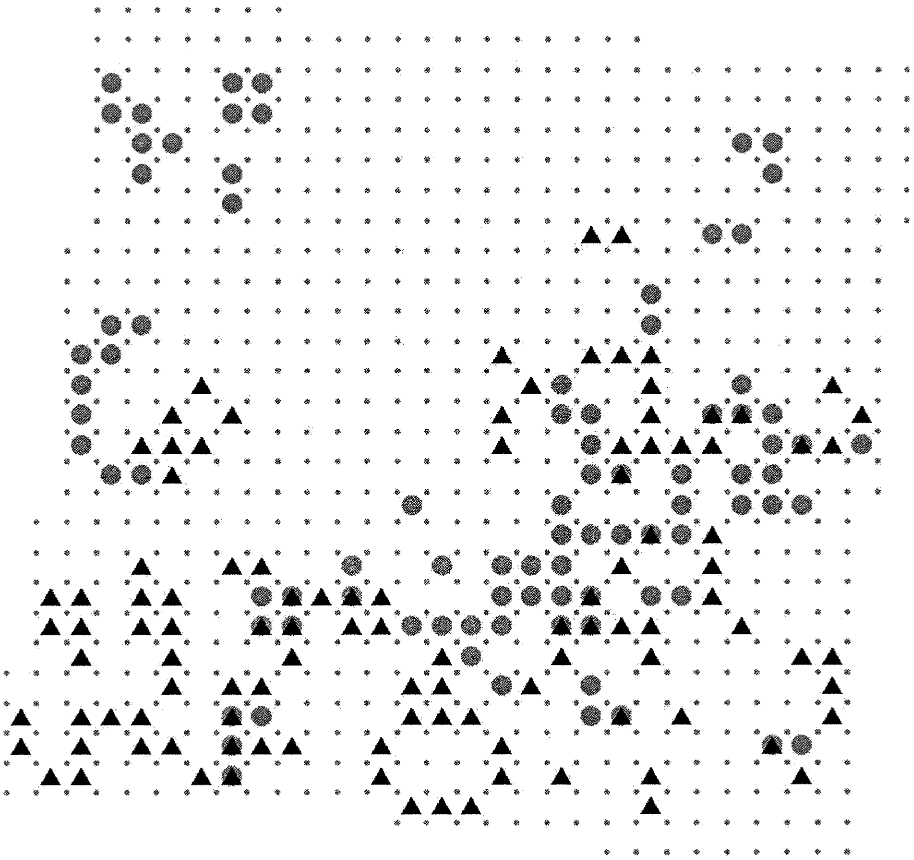
St-Louis et al., *Figure 4*



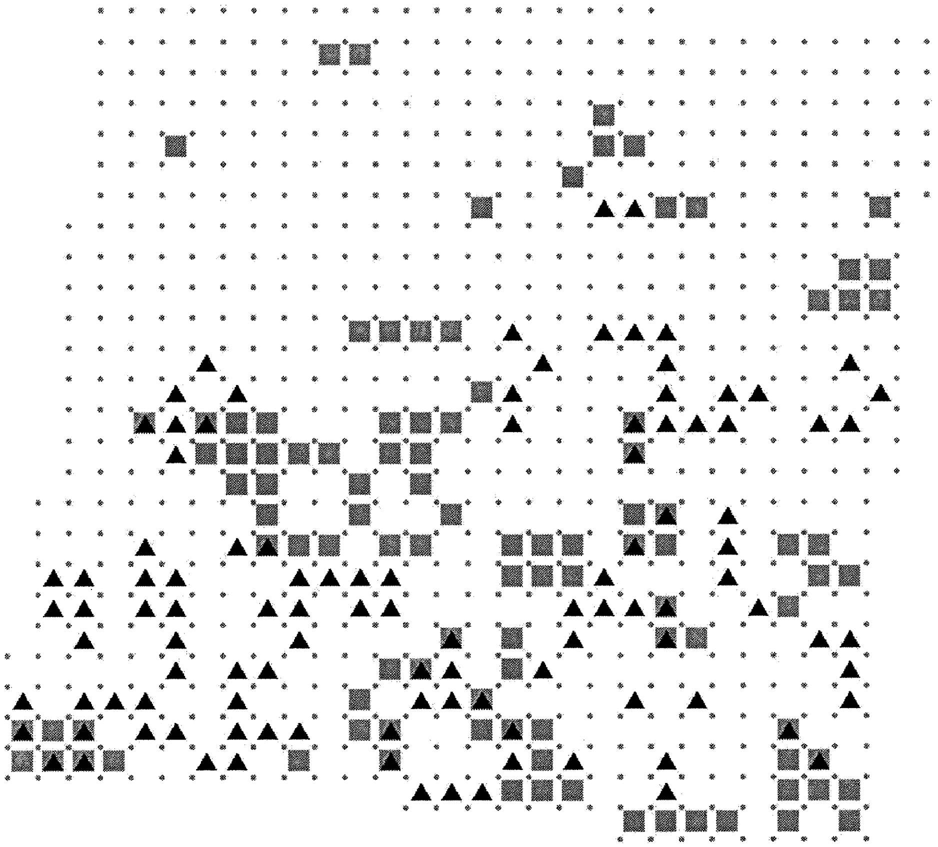
St-Louis et al., *Figure 5*



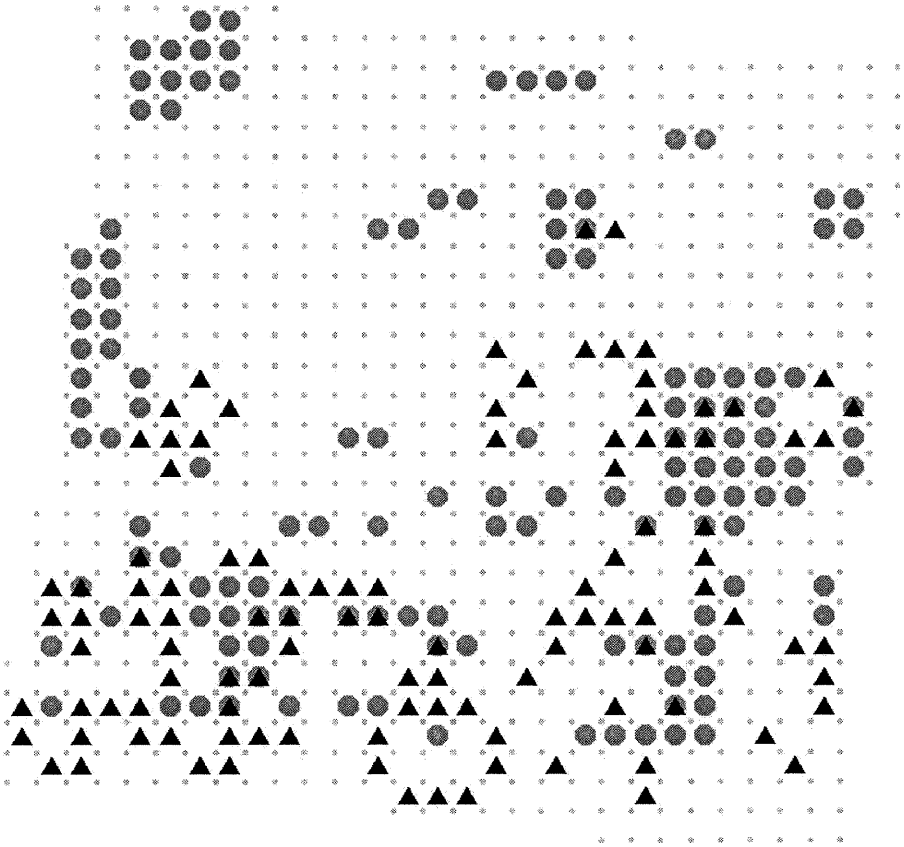
St-Louis et al., *Figure 6*



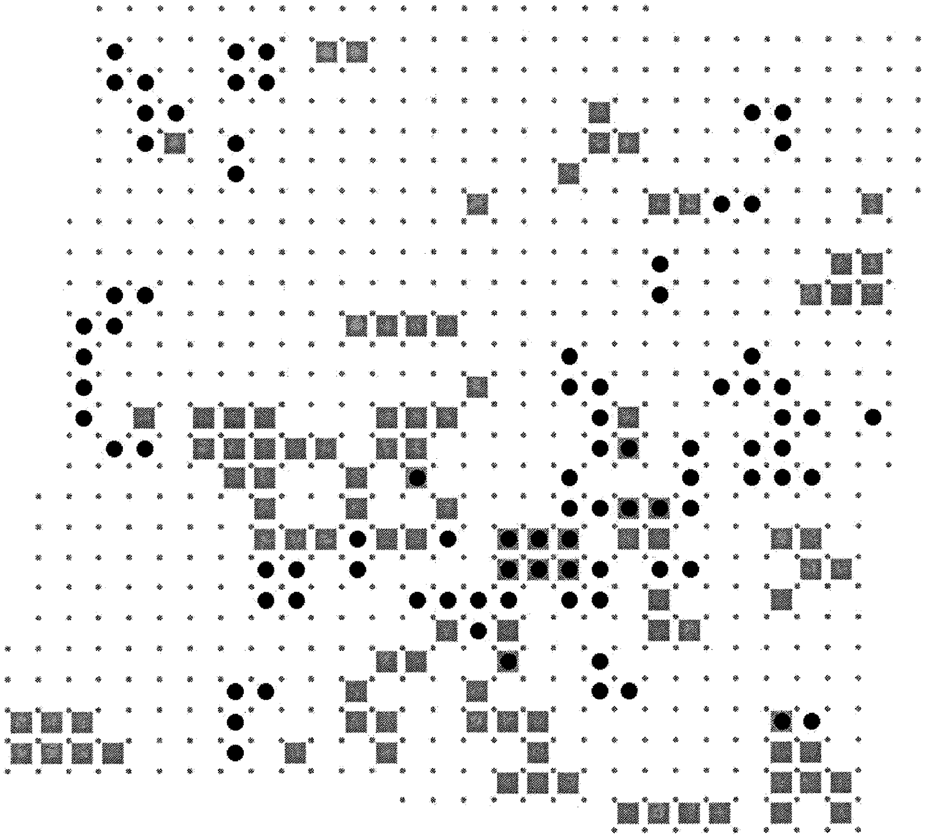
St-Louis et al., *Figure 7a*



St-Louis et al., *Figure 7b*



St-Louis et al., *Figure 8a*



St-Louis et al., *Figure 8b*