

Université de Montréal

**Influence de la structure du paysage sur les communautés de parasitoïdes de la tordeuse de  
bourgeons de l'épinette.**

**par**

**Olivier Pontbriand-Paré**

Département de sciences biologiques

Faculté des arts et des sciences

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## Résumé

Il est essentiel pour construire des modèles biologiques spatialement explicites et réalistes d'accroître notre compréhension de la relation liant la structure spatiale et les processus biologiques. C'est particulièrement vrai pour l'échelle spatiale à laquelle ces processus opèrent puisque cette information est généralement manquante dans la littérature. Les parasitoïdes associés à la tordeuse des bourgeons de l'épinette (TBE), un défoliateur important au Canada, offrent l'opportunité d'étudier un processus biologique (c.-à-d. le parasitisme) dans un contexte spatial. On retrouve présentement dans la région de la Côte-Nord au Québec, Canada, une grande zone de défoliation causée par la TBE. Cette zone a été utilisée dans ce mémoire pour étudier comment la structure du paysage peut influencer les taux de parasitisme de la TBE et à quelle échelle spatiale. Pour répondre à ces questions, 20 000 larves de TBE ont été échantillonnées dans la zone de défoliation et élevées en laboratoire pour calculer le taux de parasitisme dans différents sites. Dans ce mémoire, j'examine deux questions reliées à la variation spatiale des taux de parasitisme de la TBE. Premièrement, je m'intéresse à l'échelle spatiale à laquelle la communauté de parasitoïdes (dans son ensemble) répond à la structure du paysage. En deuxième lieu, j'explore comment cette échelle de réponse au paysage varie en fonction d'une caractéristique morphologique liée au vol (c.-à-d. la charge alaire) chez cinq espèces de parasitoïdes. Les résultats suggèrent que la communauté de parasitoïdes répond à la structure du paysage à une échelle correspondant à une zone de 2000-2500 mètres de rayon. À cette échelle, les variables explicatives les plus importantes sont l'hétérogénéité du paysage et l'âge de l'épidémie de TBE. Une plus grande hétérogénéité est liée à un taux de parasitisme plus élevé des stades larvaires de la TBE tandis qu'une zone ayant connue une défoliation sur plusieurs années mène à un taux de parasitisme plus élevé chez les chrysalides. J'émetts par la suite l'hypothèse que l'échelle spatiale de réponse varie selon la capacité de dispersion des espèces. Les événements de parasitisme ont donc été divisés en trois groupes selon la charge alaire des espèces impliquées (charge alaire légère, moyenne et lourde). Cette division a montré qu'une plus grande proportion de la variance des taux de parasitisme pouvait être expliquée dans des modèles basés sur un trait relié à la dispersion que dans un modèle regroupant toutes les espèces. De plus, le groupe ayant la plus faible charge alaire (c.-à-d. la plus grande capacité de dispersion) présente aussi la plus grande échelle spatiale de réponse, comme il était attendu. Les résultats présentés dans ce mémoire pourraient avoir des implications dans l'aménagement forestier en suggérant une structure et une échelle spatiale adéquate pour réduire l'impact des épidémies de TBE sur les forêts. De plus, ces résultats pourront aider les chercheurs à créer de nouveaux modèles spatialement explicites pour mieux comprendre le système complexe de la TBE.

Mots clés : Aménagement forestier, Charge alaire, Échelle spatiale, Épidémies, Forêt boréale, Hétérogénéité, Parasitoïdes, Structure du paysage, Taux de parasitisme, Tordeuse des bourgeons de l'épinette

## **Abstract**

Improving understanding on how spatial structure influences biological processes is essential to build realistic models and information on the spatial scale at which these processes operate is mainly missing in the literature. Spruce budworm-associated parasitoids offer a great opportunity to investigate the importance of scale on space-related processes. The Côte-Nord region of Quebec, Canada, is currently experiencing a SBW outbreak on a vast extent that had been used to study how landscape structure can influence the parasitism rates on SBW and at which spatial scale. To answer these questions, 20 000 SBW larvae were collected in this region and reared individually to calculate parasitism rates. In this thesis, I examined two specific questions pertaining to spatial variation in SBW parasitism. First, I investigated the spatial scale of response of the parasitoid community as a whole to landscape structure (Chapter 1). Second, I explored how the spatial scale of parasitoids' responses to spatial structure varies as a function of a morphological trait related to flight (i.e., wing load). I explore this relationship between wing load and scale of response using the five most common species of parasitoids (Chapter 2). The results from the first chapter suggest that the community of parasitoids is responding to landscape at a scale corresponding to buffers of 2000-2500 meters radius. At this scale, the most important explanatory variables are landscape heterogeneity and the age of outbreak. Greater heterogeneity was linked to higher level of parasitism rates in SBW larval stages whereas age of outbreak favoured parasitism in pupae. These results indicate that there exist important differences in how parasitoids respond to spatial heterogeneity and that the scale at which they respond may depend on the species. In my second chapter, I hypothesised that variation in the spatial scale of response could be related to varying species dispersal capacities. Parasitism events were therefore divided in three groups according to the wing load of the responsible parasitoid (i.e., light, medium and heavy wing load). This division showed that a greater proportion of variance in parasitism rates could be explained in models based on dispersal-related trait than in a model considering the community as a whole. Moreover, the group with the lightest wing load (and supposedly the greatest dispersal capacity) had the greatest spatial scale of response to landscape as expected. The results presented in this thesis could have implication in forest management to reduced SBW impact but also in other modelling researches where there is a general lack of empirical data to support model building.

Keywords: Boreal forest, Dispersal ability, Forest management, Heterogeneity, Landscape heterogeneity, Landscape structure, Parasitism rates, Parasitoids, Pest outbreaks, Spatial scale, Spruce budworm, Wing load

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## Liste des sigles

### Français :

- AP: Avant le présent (Before present)  
TBE : Tordeuse des bourgeons de l'épinette (Spruce budworm)

### Anglais :

- AIC: Akaike information criterion (Critère d'information d'Akaike)  
ANOVA: Analysis of variance (Analyse de variance)  
dbMEM: Distance-based Moren's eigenfunction maps  
ENN: Euclidean nearest neighbor distance (Distance euclidienne du plus près voisin)  
GIS: Geographical information system (Système d'information géographique)  
MEM: Moren's eigenfunction maps  
OLI: Operational land imager  
PCoA: Principal coordinate analysis (Analyse des coordonnées principales)  
PPV: Positive predictive value (Valeur de prediction positive)  
PPTP: Post-test probability of true positive (Probabilité post-test de vrais positifs)  
RDA: Redundancy analysis (Analse de redondance)  
RGB: Red-Green-Blue image (Image Rouge-Vert-Bleu)  
SBW: Spruce budworm (Tordeuse des bourgeons de l'épinette)  
SHDI: Shannon's diversity index (Indice de diversité de Shannon)  
TIR: Thermal infrared sensor (Capteur thermique infrarouge)  
USGS: United States Geological Survey  
VIF: Variance inflation factor (Facteur d'inflation de la variance)

## Liste des abréviations

cm :	centimètre (centimeter)
g :	gramme (gram)
km :	kilomètre (kilometer)
L1-L2-L3-L4-L5-L6 :	Stade larvaire de développement de la tordeuse (Spruce budworm larval stage)
m :	mètre (meter)
mL :	millilitre (milliliter)
mm :	millimètre (millimeter)
S1-S2-S3 :	Période d'échantillonnage (Sampling period)
Adj. R <sup>2</sup> :	Adjusted R squared

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## **Introduction**

### Écologie spatiale en milieu forestier

#### **La forêt boréale**

La forêt boréale canadienne représente un vaste écosystème qui s'étend de la côte Pacifique à la côte Atlantique et qui couvre plus de 567 millions d'hectares. Cette superficie représente 30% des forêts boréales à l'échelle mondiale, ce qui en fait un système d'une grande importance tant écologique que sociale et économique (Brandt et al. 2013). À travers son étendue, cet écosystème est affecté par une large variété de perturbations naturelles incluant les feux de forêt, les insectes ravageurs, les maladies, les perturbations climatiques (p. ex, sécheresse et réchauffement climatique) ainsi que des perturbations d'origine humaine comme l'exploitation forestière (Bouchard et al. 2007). Il en résulte une structuration de la forêt boréale qui se traduit par une mosaïque de différents patrons d'âge et de composition d'essences forestières à différentes échelles spatiales (Shugart 1984, Holling 1992). En plus de l'effet des processus biologiques sur les patrons spatiaux, il existe aussi un effet opposé des patrons spatiaux sur les processus biologiques. Dans ce cadre de réciprocité, les paysages complexes créés par les perturbations influencent les perturbations à venir telles que les feux (Parisien et al. 2011), l'aménagement forestier (Wallin et al. 1994, James et al. 2011) et les épidémies d'insectes (Su et al. 1996, Cappuccino et al. 1998, Campbell et al. 2008). Ainsi, on ne peut étudier les systèmes de perturbations présentes et à venir sans considérer les legs des perturbations passées (James et al. 2007). Il est cependant difficile de quantifier cette importance dans un modèle biologique considérant l'abondance de variables qui entrent en jeu.

#### **Les ravageurs forestiers**

La définition d'un ravageur forestier ne prend son sens que du point de vue humain (Berryman 1986). De la myriade d'insectes qui peuplent les forêts, seul un nombre très restreint nous préoccupe de par son impact sur nos activités économiques et récréo-touristiques (p. ex. l'industrie forestière). Ces espèces causent problème lorsque leur population croît de manière exponentielle, lors d'épidémies, car c'est à ce moment qu'elles portent préjudices à la ressource exploitable (p. ex. le bois).

Les ravageurs les plus importants de la forêt boréale sont des espèces indigènes qui ont évolué dans ce système depuis plusieurs milliers d'années telles que le dendroctone du pin, *Dendroctonus ponderosae* (Coleoptera : Curculionidae) (Raffa et al. 2008), la livrée des forêts, *Malacosoma disstria* (Lepidoptera : Lasiocampidae) et la tordeuse des bourgeons de l'épinette de l'ouest et de l'est, *Choristoneura occidentalis* et *C. fumiferana* (Lepidoptera : Tortricidae, TBE) (Berryman 1986) .

Non seulement les ravageurs ont un impact sur la structure du paysage, mais ils répondent aussi à cette même structure (Gauthier et al. 2008). Par exemple, le dendroctone du pin dans l'Ouest canadien connaît des épidémies plus importantes lorsque la proportion de pins tordus matures (Chapman et al. 2012) ainsi que la température (Raffa et al. 2008) sont élevées. Pour la livrée des forêts au Québec, la persistance des épidémies est quant à elle plus grande dans les forêts homogènes que dans les forêts fragmentées (Charbonneau et al. 2012). Les études reliant la structure de la forêt aux ravageurs permet ainsi de cibler les zones à risque et de mieux comprendre la dynamique de ces systèmes. Puisque la tordeuse des bourgeons de l'épinette est présentement en période épidémique dans l'est du Canada, les relations entre le paysage et ce ravageur sont d'actualité et font l'objet de ce mémoire.

## **Système de la tordeuse des bourgeons de l'épinette**

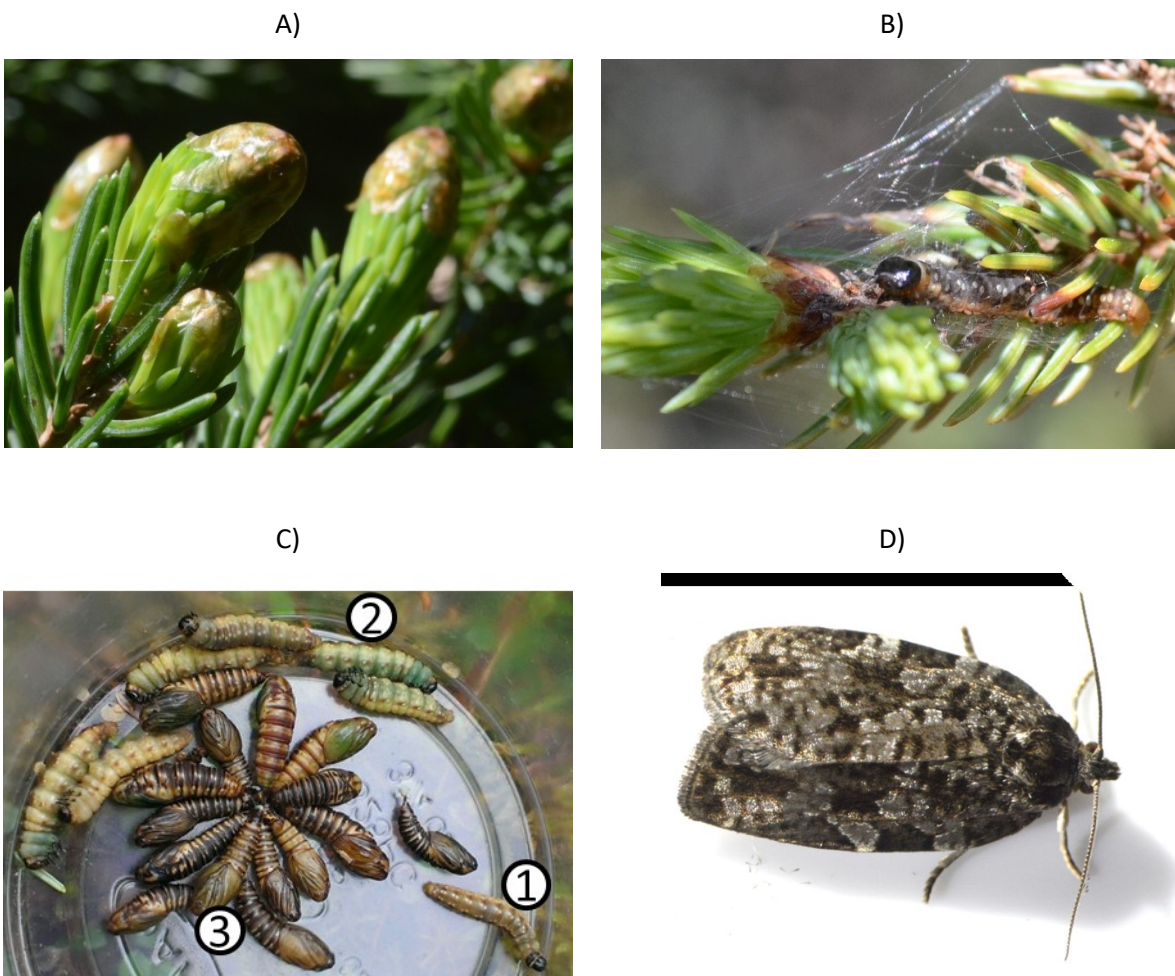
### Biologie

La tordeuse des bourgeons de l'épinette est une espèce éruptive de lépidoptère indigène d'Amérique du Nord. Il s'agit du ravageur causant le plus de dommages dans la forêt boréale de l'est du Canada. La TBE se nourrit des nouveaux bourgeons de conifères avec une préférence particulière pour, dans l'ordre, le sapin baumier (*Abies balsamea*) et l'épinette blanche, rouge et noire (*Picea glauca*, *P. rubens*, *P. mariana*) (MacLean 1980).

### Cycle de vie

La TBE est une espèce univoltine (c.-à-d. une seule génération par année). Au courant de l'été (de juillet à août selon les régions), les femelles pondent de 100 à 300 œufs sur leurs arbres hôtes. Une dizaine de jours plus tard, les œufs éclosent et les larves de stade 1 (L1) se déplacent vers le centre de l'arbre pour sélectionner un site d'hibernation dans une crevasse de l'écorce. Elles y tissent un hibernacle et muent en L2 afin de passer l'hiver en diapause. Au printemps suivant, les L2 émergent et se dispersent vers l'extrémité des branches où elles s'installent dans les nouveaux bourgeons de

l'hôte. C'est durant la période de croissance des stades L3 à L6 que la TBE défolie son arbre hôte en se nourrissant des bourgeons de la nouvelle année. Le dernier stade larvaire (L6) transite ensuite par la nymphose et émerge sous forme adulte de 10 à 12 jours plus tard (Figure 0.1) (Royama 1984). Après la reproduction, les adultes peuvent se déplacer localement ou monter dans la colonne d'air à plus de 100m d'altitude pour ensuite migrer à l'aide des vents. Ce vol passif leur permet de couvrir de grandes distances pouvant aller jusqu'à 450km (Greenbank et al. 1980, Sturtevant et al. 2013). Toutefois, il est difficile d'estimer la distance maximale considérant l'effet encore inconnu de facteurs comme les précipitations et le comportement de recherche d'hôte de la TBE une fois dans la colonne d'air (Sturtevant et al. 2013). Ainsi, il existe toujours un débat sur la capacité de vol et son rôle dans la dynamique des épidémies, dont leur synchronisme à l'échelle régionale (Régnière et al. 1995).



**Figure 0.1: Stades développementaux de la tordeuse des bourgeons de l'épinette.** A) Bourgeons tordus par les larves (L2-L4) se nourrissant à l'intérieur. B) Larve L6 se nourrissant sur plusieurs bourgeons depuis un abri de soie. C) L6 (1), pré-chrysalides (2) et chrysalides (3). D) Adulte. Photos de terrain.

## **Dynamique des épidémies**

Tous les 30 à 40 ans (Jardon et al. 2003), les populations endémiques de TBE connaissent une croissance exponentielle ayant pour conséquence une exploitation intense de leurs arbres hôtes pouvant mener à la mort de ceux-ci après plusieurs années de défoliation cumulative (Simard et al. 2011). Ces épidémies ont un long historique dans l'est du Canada (Royama 1984, Boulanger et al. 2012). En utilisant une approche par dendrochronologie, la série d'épidémies de TBE a pu être reconstruite pour les 400 dernières années (Boulanger et al. 2012) et des évidences d'épidémies plus anciennes encore ont aussi été trouvées pour le dernier millénaire (Simard et al. 2011). L'étude des fèces de tordeuse des bourgeons de l'épinette dans des carottes de sol dans des tourbières du Québec ont permis de remonter la série d'épidémie loin dans l'Holocène, jusqu'à environ 8200 AP (Simard et al. 2006). Cette étude conclue que les épidémies de TBE, bien que présentes, ont rarement été aussi ou plus intenses que les trois épidémies survenues dans les années 1900. Au tournant du 20<sup>e</sup> siècle, on observe un changement dans le type d'épidémies alors qu'elles se synchronisent au niveau suprarégional et prennent plus rapidement de l'expansion (Morin et al. 2007). Ces changements ont été mis en parallèle avec le changement de la structure de la forêt durant ces mêmes années, en partie en raison de l'exploitation de la forêt par l'homme (Blais 1983, Morin et al. 2007).

Avec la diminution de la fréquence des feux depuis la fin du Petit Âge Glaciaire, les épidémies de TBE assume un rôle prépondérant de perturbation dans la forêt boréale de l'est du Canada (Bergeron et al. 2001). L'accumulation de combustible dans les forêts suite à cette augmentation de l'intervalle de temps inter-feux n'a peut-être pas augmenté l'occurrence des grands feux (Johnson et al. 2001), mais elle a pu favoriser les grandes épidémies du XX<sup>e</sup> siècle par l'augmentation de la densité en arbres hôtes de la TBE (Bergeron et al. 2001).

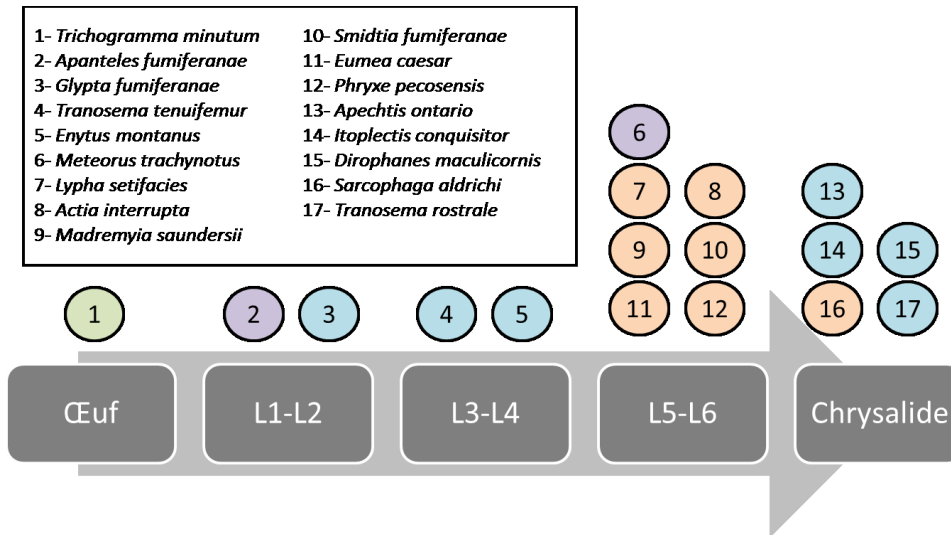
## **Impacts économiques**

Malgré le rôle écologique important que jouent les épidémies de tordeuses dans le système boréal, les préoccupations actuelles sont plutôt d'ordre économique. À la fin du siècle dernier, la mortalité induite par la TBE au Canada dans les peuplements de sapins et d'épinettes représentait 40% du volume total de pertes dues aux insectes chaque année (MacLean et al. 2000). Durant les trois épidémies du 20<sup>e</sup> siècle, la mortalité pouvait atteindre 100% dans les peuplements purs de sapins baumiers matures, mais elle avoisinait normalement 85% pour les sapinières et 35% pour les pessières (MacLean 1980).

Toutefois, avec les changements climatiques en cours, les dynamiques historiques pourraient changer; selon les prédictions, les épidémies de TBE dureront plus longtemps et seront plus intenses (Gray 2008). Ces changements pourraient affecter la stabilité à long terme de l'écosystème et amener des préoccupations environnementales alors que les changements sont déjà visibles sur le terrain où l'épidémie actuelle au Québec a débuté à une latitude plus nordique que durant les 100 dernières années.

## **Les parasitoïdes de la TBE**

Les parasitoïdes forment un groupe particulier d'insectes qui ont besoin d'un seul hôte pour compléter leur cycle de vie et qui, contrairement aux parasites, causent la mort de celui-ci durant leur développement. Les parasitoïdes de la TBE forment un vaste complexe d'ennemis naturels, ou guildes, de près de 180 espèces dont, chez les hyménoptères, 66 espèces d'Ichneumonidae (Bennett 2008), 31 espèces de Braconidae (Fernandez-Triana et al. 2010) et 68 espèces de Chalcidoidea (Huber et al. 1996). Les diptères regroupent une quinzaine d'espèces parasitoïdes chez les Tachinidae (O'Hara 2005). Malgré le nombre élevé d'espèces de Chalcidoidea dans le système, une grande partie sont des parasitoïdes secondaires ou tertiaires (c.-à-d. qui s'attaquent à d'autres parasitoïdes de la tordeuse) et seul *Trichogramma minutum* (Hymenoptera : Trichogrammatidae) est considéré comme un parasitoïde primaire important de la TBE dans ce groupe (Huber et al. 1996). À titre d'exemple, 66 espèces de parasitoïdes primaires ont été identifiées dans une même région pour une trentaine d'hyperparasitoïdes (Eveleigh et al. 2007). Ces espèces attaquent la TBE à différents stades de son développement (Figure 0.2) et peuvent causer une grande mortalité (Zebrowski 1998).



**Figure 0.2: Parasitoïdes communs et importants de la TBE ainsi que le stade auquel ils attaquent la TBE (Zebrowski 1998). *Chalcidoidea* en vert, *Braconidae* en violet, *Ichneumonidae* en bleu et *Tachinidae* en orange.**

### Biologie des parasitoïdes de la TBE

Selon le spectre d'hôtes, on regroupe les parasitoïdes en spécialistes (une ou très peu d'espèces hôtes) et généralistes (plusieurs espèces hôtes) (Coppel et al. 1977). La spécificité d'un parasitoïde influence son potentiel d'agent de lutte biologique. La théorie veut que les espèces spécialistes seraient les meilleures pour contrôler les ravageurs dans un système naturel puisqu'elles seraient mieux adaptées à leur hôte et qu'elles seraient plus à même de démontrer une relation densité-dépendante avec celui-ci. Toutefois, la proportion de spécialistes serait moins grande qu'initialement suggérée et la majorité des parasitoïdes serait plutôt généralistes (Coppel et al. 1977).

Toutes les espèces de parasitoïdes n'ont pas la même stratégie de parasitisme. Les femelles pondent leurs œufs soit à l'intérieur de l'hôte (endoparasitisme) ou sur l'hôte (ectoparasitisme) après l'avoir tué/paralysé (parasitoïde idiobionte) ou non (parasitoïde koinobionte) (Coppel et al. 1977). Lorsque plusieurs larves peuvent exploiter le même hôte, l'espèce est dite grégaire par opposition à solitaire. Puisque les hôtes constituent une ressource limitée, il existe une compétition pour y avoir accès. Le superparasitisme est une compétition entre plusieurs individus d'une même espèce et le multiparasitisme est une compétition entre des individus de plus d'une espèce. Dans les deux cas, le ou les individus qui émergent correspondent au parasitisme effectif et seul celui-ci peut être mesuré

(Coppel et al. 1977). La compétition entre les espèces et les individus réduit l'efficacité générale de la guildes de parasitoïdes pour contrôler les populations de TBE.

Outre la compétition, l'attaque de parasitoïdes par d'autres parasitoïdes (hyperparasitisme) freine aussi le développement des populations de parasitoïdes primaires (Muesebeck et al. 1926). Les hyperparasitoïdes sont pratiquement tous polyphages, ce qui leur permet généralement de se maintenir dans le milieu même lorsque les populations de parasitoïdes sont basses. Les parasitoïdes primaires avec un cocon exposé pour une longue période, comme *Glypta fumiferanae* (Hymenoptera : Ichneumonoidea) et *Apanteles fumiferanae* (Hymenoptera : Microgastrinae), sont plus à risque de se faire parasiter que les espèces qui finissent leur développement à l'abri comme *Smidtia fumiferanae* (Diptera : Tachinidae) (ex. dans le sol ou dans l'hôte) (Muesebeck et al. 1926). Selon les conditions et l'espèce, un parasitoïde primaire peut aussi être un parasitoïde secondaire et vice-versa. Il est toutefois ardu de faire la différence entre le multiparasitisme et l'hyperparasitisme car bien souvent seul le parasitisme effectif (c.-à-d. le parasitoïde qui gagne la compétition et atteint son stade adulte) est observable. Il existe aussi des parasitoïdes de troisième et quatrième niveau, mais ceux-ci sont plus rarement rencontrés (Muesebeck et al. 1926, Brodeur et al. 2000).

L'alimentation durant la phase adulte d'un parasitoïde affecte sa production d'œufs et sa longévité. L'ingestion de ressources protéiques sert à produire les œufs tandis que les sucres augmentent la longévité ainsi que d'autres fonctions telle que le vol. Il existe deux types d'alimentation : l'alimentation sur l'hôte (pour les protéines) et la recherche de sources végétale ou animal de sucre (Cappuccino et al. 1999). La consommation du liquide corporel de l'hôte au niveau du trou d'oviposition est un comportement très répandu autant chez les parasitoïdes que les hyperparasitoïdes (Muesebeck et al. 1926). Particulièrement chez les hyperparasitoïdes, ce mode d'alimentation peut causer la mort de l'hôte et ainsi diminuer le nombre de parasitoïdes primaires (Muesebeck et al. 1926). La seconde source d'alimentation regroupe le miellat produit par les pucerons et le nectar des fleurs. Dans la forêt boréale, l'abondance des fleurs sauvages est plus grande dans les peuplements mixtes ou ouverts (p. ex. une pessière à éricacées ou suite à un chablis) que dans une forêt de conifère dense (Simmons et al. 1975). Dans le système de la livrée des forêts, les taux de parasitisme par *Itopectis conquisitor* (Hymenoptera : Pimplinae) sont positivement corrélés à la proportion de fleurs sauvages dans le milieu (Leius 1967). On retrouve la même relation pour les petits parasitoïdes attaquant les premiers stades de la TBE dans une étude où certaines

zones étaient enrichies en solution sucrée (Cappuccino et al. 1999). Une des raisons avancée pour l'absence de cette relation chez les plus gros parasitoïdes de cette étude est qu'ils sont capables de chercher leur nourriture dans une région plus grande que les quadrats de 50m x 50m utilisés. Cette question d'échelle est une préoccupation centrale en écologie du paysage (Turner 2005) et elle sera abordée plus loin.

### **Utilisation en lutte biologique**

L'utilisation de parasitoïdes en lutte biologique se divise en deux catégories : l'introduction d'espèces exotiques et la manipulation d'espèces indigènes (Varty 1984). L'introduction de parasitoïdes dans une nouvelle région pour lutter contre des ravageurs (lutte biologique classique) est une action fréquente. À travers le monde, c'est plus de 4 300 espèces de parasitoïdes qui ont été introduites dans différents écosystèmes pour contrer près de 300 insectes ravageurs agricoles et forestiers (Waage et al. 1988). L'efficacité de cette méthode est hautement variable. Dans certains cas, l'espèce introduite n'arrive pas à s'établir ou bien, une fois établie, elle n'est pas aussi efficace que désirée ou change d'hôte. Des 135 espèces importées au Canada, seulement 12 se sont acclimatées et sont considérées comme un succès (Kelleher et al. 1984).

L'idée d'importer des parasitoïdes pour contrôler les populations de tordeuse apparaît relativement tôt à partir du moment où la TBE est considérée comme un problème pour l'industrie forestière. La première introduction d'une espèce en 1936, *Copidosoma geniculatum* (Hymenoptera : Encyrtidae), n'a cependant pas l'effet escompté et la population ne s'est jamais établie (Baird 1938). Entre 1944 et 1973, 18 autres espèces sont importées dans l'est du Canada depuis l'ouest canadien, le Japon et l'Europe sans beaucoup plus de succès (Varty 1984, Smith 1993).

Dans la catégorie de la manipulation d'espèces indigènes, on discerne deux approches : la production/ de masse suivie du relâchement ainsi que la manipulation *in situ*. La première consiste à élever une espèce déjà présente dans le système et de la relâcher en masse dans la nature comme agent temporaire de lutte (c.-à-d. lutte inondative). Le plus grand succès de cette méthode au Canada concerne la dispersion de 480 millions d'œufs parasités par *T. minutum* sur une superficie de 30 hectares en Ontario pour lutter contre la TBE. L'effet de ce traitement fut cependant limité dans l'espace et le temps (Smith et al. 1990, Bourchier et al. 1998). La manipulation *in situ* utilise des pratiques sylvicoles dans le cadre d'un plan d'aménagement forestier pour tenter de favoriser



l'impact des parasitoïdes indigènes. La méthode est détaillée plus bas dans la section « Concepts théoriques ».

### **Structuration densité-dépendante des communautés de parasitoïdes**

L'arrivée dans un écosystème d'une perturbation de l'ampleur des épidémies de TBE vient chambouler la structure et la stabilité du réseau trophique (Eveleigh et al. 2007). Plutôt que de voir un tel système comme un réseau statique, il serait plus approprié de le considérer comme une succession de réseaux qui varient selon la densité de l'insecte-hôte (c.-à-d. la TBE).

Dans les zones où la population de TBE est élevée (c.-à-d. en stade épidémique), on retrouve un plus grand nombre d'espèces de parasitoïdes. Cette agrégation d'ennemis naturels autour d'une ressource abondante (c.-à-d. l'effet de mangeoire) entraîne une diversification et une complexification de la communauté de parasitoïdes (Eveleigh et al. 2007). Alors que la densité de TBE augmente, plusieurs parasitoïdes généralistes vont changer d'un hôte alternatif vers la tordeuse. Cette augmentation des parasitoïdes primaires va aussi se refléter chez les hyperparasitoïdes généralistes et on observera plus de parasitoïdes de deuxième et troisième niveaux trophiques (Eveleigh et al. 2007). La structuration du réseau trophique se fait donc par le bas où la base du réseau (c.-à-d. la TBE) va déterminer la composition et les interactions des niveaux supérieurs.

Durant la phase de croissance d'une épidémie, la communauté de parasitoïdes ne semble pas être en mesure de freiner la TBE (Miller et al. 1976). Toutefois, elle semble jouer un rôle dans l'accélération du déclin de la TBE avec d'autres facteurs comme l'épuisement des ressources alimentaires de la tordeuse. Des espèces comme *G. fumiferanae*, *A. fumiferanae*, *S. fumiferanae* et *M. trachynotus* sont communes après le pic de l'épidémie et vers la fin. Cependant, elles ne semblent pas se maintenir dans le système de la tordeuse une fois l'épidémie terminée (Miller et al. 1976, Thireau et al. 1995).

### **Concepts pratiques liés à l'écologie du paysage**

Les systèmes écologiques sont d'une grande complexité considérant la foule de facteurs qui interagissent les uns avec les autres, dont l'organisation spatiale dans le paysage d'une multitude d'habitats différents (Urban et al. 1987). L'écologie du paysage s'intéresse à l'impact de cette structure (composition et configuration) du paysage sur les processus biologiques. Tandis que l'écologie traditionnelle étudie l'écosystème au niveau local, l'écologie du paysage considère une échelle spatiale supérieure et s'intéresse aussi à l'influence des écosystèmes voisins. En effet, il a été

démonstré que le type d'écosystème local n'est pas toujours suffisant pour prédire par exemple la présence et/ou l'abondance d'espèces et que les patrons spatiaux à des échelles supérieures jouaient aussi un rôle (Urban et al. 1987, Gustafson 1998, Mazerolle et al. 1999).

Dans bien des systèmes, les processus à l'étude opèrent sur de grandes régions comme c'est le cas des épidémies de TBE. Le développement des technologies de télédétection (imagerie aérienne puis satellitaire) et des systèmes d'information géographique (SIG) ont donc permis l'essor de l'écologie du paysage en permettant d'acquérir et de gérer la quantité de données nécessaires à l'étude de tels systèmes. Dans le cas de ce mémoire, des images satellites ont été utilisées à partir du satellite Landsat8 pour acquérir des informations sur la structure du paysage sur l'ensemble de la région de la Côte-Nord au Québec. Ces données sur une grande étendue ont permis d'explorer le système de la TBE et les processus biologiques qui s'y déroulent. Pour étudier l'effet du paysage sur de tels processus, il faut d'abord répondre aux questions : Qu'est-ce qu'on mesure? Et à quelle échelle?

### *L'échelle d'analyse*

Les différents habitats essentiels aux espèces pour subvenir à leurs besoins influence l'abondance et le comportement de celles-ci. Par exemple, le taux de parasitisme infligé par une mouche, *Leschenaultia exul* (Diptera : Tachinidae), à la livrée des forêts est favorisé par une forêt continue (Roland et al. 1997). De même, le taux de parasitisme du méligèthes du colza, *Meligethes aeneus* (Coleoptera : Nitidulidae), est lié à la proportion d'habitat d'hivernage (c.-à-d. un habitat présentant des sites d'hivernage pour le parasitoïde, comme des branchages et des souches) des parasitoïdes (Thies et al. 2003). Cependant, pour pouvoir utiliser de telles métriques du paysage, il faut tout d'abord savoir à quelle échelle les calculer.

Le choix de l'échelle d'analyse est inhérent au système à l'étude et devrait refléter l'échelle de perception de l'organisme étudié (c.-à-d. l'échelle spatiale à laquelle l'organisme peut interpréter son environnement). Cette échelle peut se restreindre à un arbre ou bien s'étendre à la forêt entière. Lorsqu'il s'agit d'une espèce animale mobile, l'échelle de perception est généralement contrainte par la capacité de dispersion de l'organisme (With 1994). Cependant, la capacité de dispersion est une mesure difficile à obtenir directement, particulièrement chez les insectes où il est pratiquement impossible de suivre un individu à la trace (Cronin et al. 2014). Il faut alors utiliser des méthodes indirectes pour évaluer l'échelle de perception et de là inférer la capacité de dispersion. Construire

des modèles utilisant des métriques calculées à différentes échelles permet ainsi de cerner l'échelle de perception de l'organisme en déterminant le meilleur modèle (Roland et al. 1997, Gustafson 1998, Schooley 2006).

Cette méthode a été utilisée dans plusieurs systèmes incluant des parasitoïdes et une grande variété d'échelles ont été trouvées. Par exemple, dans le système de la livrée des forêts, quatre mouches répondent respectivement au paysage à des échelles de 52, 212, 425 et 850 m (Roland et al. 1997). Chez les parasitoïdes du méligèthes du colza, c'est à une échelle de 1 500 m que les taux de parasitisme étaient les plus corrélés (Thies et al. 2003). Pour expliquer cette grande variabilité, il est généralement accepté que l'échelle de perception tend à augmenter avec la taille de l'organisme, elle-même corrélée à la capacité de dispersion (Tscharntke et al. 2004). C'est cette relation taille/échelle de perception qu'on retrouve chez les mouches parasitoïdes de la livrée des forêts (Roland et al. 1997). Outre la taille, d'autres caractéristiques morphométriques dont le rapport masse/surface alaire (c.-à-d. la charge alaire) chez les insectes volants peuvent contribuer à prédire leur capacité de dispersion.

À l'intérieur d'un même système, les espèces aux niveaux supérieurs du réseau trophique sont plus affectées par la structure du paysage que les niveaux inférieurs puisqu'elles sont dépendantes de chaque échelon du réseau sous elles (c.-à-d. plus grande instabilité) (Thies et al. 2003). Cela suggère que la réponse des parasitoïdes de la tordeuse des bourgeons de l'épinette à la structure du paysage serait donc plus forte en général que celle de leur hôte à ce même paysage. Il est aussi généralement admis que les espèces appartenant aux niveaux trophiques supérieurs ont un domaine vital plus étendu que celui des niveaux inférieurs (Tscharntke et al. 2004). Cette corrélation est en partie associable au fait que les espèces dominant la chaîne alimentaire sont en général plus grosses chez les prédateurs ce qui leur donne une plus grande mobilité. Ils ont aussi besoin d'avoir accès à une plus grande quantité de ressources que leurs proies. Les cas des parasitoïdes est particulier puisqu'ils sont généralement de la même taille ou plus petit que leurs hôtes. Cela expliquerait pourquoi ils n'ont pas nécessairement une échelle de perception plus grande que celle de leur hôte, voir plus petite (Thies et al. 2003). Ainsi, malgré la vaste étendue des épidémies de tordeuses, il est probable que les populations de parasitoïdes se structurent à une échelle plus fine.

## Concepts théoriques applicables au système de la TBE

### *Hypothèse sylvicole*

La TBE est un ravageur dont les épidémies peuvent être modulées par la structure de la forêt (Su et al. 1996, Cappuccino et al. 1998, Campbell et al. 2008). Cela implique que les différentes configurations de la forêt ont un impact soit positif soit négatif sur la TBE. En identifiant et appliquant ces configurations à l'aménagement forestier, il est donc théoriquement possible de diminuer l'impact des épidémies de tordeuse des bourgeons de l'épinette (c.-à-d. théorie sylvicole) (Miller et al. 1993). Cependant, malgré un siècle de recherche, les mécanismes biologiques qui lient la structure du paysage aux dynamiques de population de la tordeuse restent incertains.

Une hypothèse avancée liant la structure du paysage et les populations de TBE concerne la communauté de parasitoïdes de celle-ci. Il y est suggéré qu'une communauté de parasitoïdes généralistes pourrait être en partie responsable des niveaux endémiques de TBE sur de longues périodes entre les épidémies (Cappuccino et al. 1998). Ces parasitoïdes répondent eux-mêmes à la structure de la forêt et ils joueraient un rôle d'intermédiaire dans le lien entre la TBE et la structure du paysage. Le potentiel des ennemis naturels pour stabiliser le système de la TBE est reconnu depuis le début des années 90 (Smith 1993) lorsque l'interaction entre la structure de la forêt (c.-à-d. composition et configuration) et les communautés de parasitoïdes était déjà suspectée. Le système de la TBE est donc un excellent exemple de la réciprocité de la relation entre les processus biologiques et les patrons spatiaux puisque la TBE affecte le paysage forestier mais est aussi affectée par celui-ci par l'intermédiaire de ses ennemis naturels.

### *Hétérogénéité, biodiversité et stabilité*

L'hétérogénéité d'un paysage (c.-à-d. l'agrégation d'habitats différents dans un paysage) joue un rôle important dans la diversité biologique. Les paysages hétérogènes possèdent généralement une plus grande diversité d'espèces que les paysages homogènes (Steinmann et al. 2011). En effet, une plus grande diversité d'habitat apporte une multiplication des ressources et donc des niches écologiques

propices à différentes espèces. Dans le système de la TBE, on retrouve effectivement plus d'espèces de parasitoïdes dans les zones de forêt hétérogène (Eveleigh et al. 2007).

L'hypothèse des ennemis naturels stipule que les parasitoïdes et les prédateurs seront plus efficaces pour freiner l'explosion d'un ravageur lorsque le milieu est diversifié (Riihimäki et al. 2005). En effet, un milieu hétérogène offre une plus grande diversité de ressources pour les parasitoïdes (p. ex. sources d'alimentation, sites d'hivernage), particulièrement pour les généralistes qui doivent compléter leur cycle sur plusieurs espèces d'hôtes (Sheehan 1973, Eveleigh et al. 2007).

Dans les écosystèmes agricoles, où la plupart des études ont été menées, l'hypothèse des ennemis naturels est largement supportée alors que l'herbivorie est moins élevée dans les polycultures ou dans les cultures à proximité d'habitats naturels que dans les grandes monocultures (Zhang et al. 2011) et ce en partie grâce aux parasitoïdes (Marino et al. 1996, Thies et al. 2003, Gagic et al. 2011, Zihua et al. 2012). La question a été beaucoup moins abordée dans les systèmes forestiers où elle est tout de même supportée dans le système de la livrée des forêts (Charbonneau et al. 2012) et de la TBE (Su et al. 1996, Eveleigh et al. 2007).

## Objectifs & hypothèses

L'objectif général de ce mémoire est de décrire la relation entre la structure du paysage et les parasitoïdes de la TBE. Pour ce faire, le taux de parasitisme de la TBE dans une zone de défoliation de la Côte-Nord au Québec couvrant approximativement 27 000 km<sup>2</sup> a été étudié.

Les études sur les parasitoïdes de la TBE ont traditionnellement été conduites à une petite échelle (Eveleigh et al. 2007, Seehausen et al. 2014). Il n'existe donc pas de réponse claire quant à l'importance de l'hétérogénéité à l'échelle du paysage aux grandes échelles pour la répression de la TBE basé sur des données empiriques. En considérant la vaste étendue des épidémies de la tordeuse au Canada, il existe un besoin d'examiner la variation régionale et locale des taux de parasitisme dans différentes structures forestières.

Cet objectif général se divise en deux objectifs spécifiques qui font l'objet de deux chapitres distincts. Mon premier objectif spécifique tentera de répondre aux questions suivantes : À quelle échelle spatiale les parasitoïdes répondent-ils au paysage forestier et comment, à cette échelle, la

structure de la forêt (p. ex. l'hétérogénéité du paysage) influence-t-elle les taux de parasitisme? Je m'attends à ce que les taux de parasitisme soient plus élevés dans les forêts diversifiées (p. ex. en présence de trouées ou de peuplements ouverts) que dans les forêts homogènes (Eveleigh et al. 2007).

Les espèces de parasitoïdes, dont celles de la TBE, ne répondent cependant pas toutes au paysage à la même échelle et de la même manière. Ces différences découlent entre autres de leurs caractéristiques morphologiques. Ainsi, mon second objectif spécifique s'attardera à la question suivante : Comment l'échelle spatiale de réponse au paysage varie-t-elle selon les caractères morphologiques des parasitoïdes? Mon hypothèse est que les espèces ayant une capacité de dispersion plus grande (exprimée par une charge alaire plus faible) perçoivent le paysage à une plus grande échelle (With 1994). La taille en elle-même ne devrait pas être un bon caractère pour différencier l'échelle de perception des parasitoïdes puisque qu'elle ne reflète pas nécessairement la capacité de dispersion.

Mon mémoire représente un appui en science fondamentale sur l'échelle spatiale de réponse au paysage. Ces connaissances nouvelles pourront être intégrées dans les plans d'aménagement forestier pour tenter de réduire les impacts futurs des épidémies de TBE. Savoir à quelle échelle répondent certains types de parasitoïdes permettra de cibler l'échelle à laquelle modifier la forêt à travers l'exploitation forestière pour favoriser le parasitisme.

## **Chapitre 1: Parasitism rate respond to forest structure at multiple spatial scales**

Olivier Pontbriand-Paré<sup>1</sup>, Véronique Martel<sup>2</sup>, Patrick M. A. James<sup>1</sup>

<sup>1</sup>Université de Montréal, Département de sciences biologiques, 90 Vincent-d'Indy, Montréal, Qc, Canada, H2V 2S9

<sup>2</sup>Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Center, 1055 du P.E.P.S., P.O. Box 10380, Succ. Sainte-Foy, Québec, Qc, Canada, G1V 4C7

## **Abstract**

Improved understanding of how landscape structure affects ecological processes is essential to the long term and effective management of ecosystems. An important challenge involves a characterization of the spatial and temporal scales that are relevant to the processes of interest. The eastern spruce budworm (SBW) system is an example of a complex system within which different species experience their environment at different spatial scales. In this chapter, I identified which properties of forest composition regulate the impact of parasitoid on this pest and at which spatial scale. Parasitoids play an important role in maintaining the SBW at endemic levels and during the collapse of an outbreak. For this research, 20 000 SBW larvae were collected in the Côte-Nord region of Quebec in 2014. Larvae were reared individually and parasitism rates were calculated at different sampling periods and sites. Parasitism rate varied from 3.7% to 35.3%. The best scales to describe parasitism rates using landscape metrics were buffers of 2000-2500m radius. At those scales, 46% of parasitism rates can be explained with an RDA using the mean age of outbreak (i.e. cumulative years of defoliation) at each location and the diversity of habitats (expressed through the Shannon's diversity index) along with spatial variables (dbMEM). The importance of each metric varied according to the sampling period. Parasitoids reared from SBW pupae were more influenced by the age of outbreak whereas those from third to sixth larval stages were favored by forest diversity. That difference can be explained by the varying biological needs of species at different SBW developmental periods.

**Keywords:** Boreal forest, Forest management, Heterogeneity, Parasitoids, Pest outbreaks, Spruce budworm



## Introduction

The role of spatial heterogeneity on ecological processes such as dispersal remains poorly known and represents an obstacle to understanding population dynamics in real landscapes (Cronin et al. 2005, Pearce et al. 2006). To better understand the role of forest landscape structure (i.e., forest composition and configuration) on spatial and temporal variation in species communities, many studies have used host-parasitoids systems, largely because parasitoid-induced mortality can be easily assessed and has economic impacts (Marino et al. 1996, Roland et al. 1997, Cappuccino et al. 1998, Cappuccino et al. 1999, Casas et al. 2003, Hilszczański et al. 2005, Krewenka et al. 2011, Cronin et al. 2014). Moreover, parasitoids play an important role in the complex spatial population dynamics of many forest pest systems (Smith 1993), including economically important outbreak species such as the spruce budworm.

The influence of forest landscape structure on insect parasitoid communities at broad spatial scales is yet to be assessed (Roland et al. 1997, Cronin et al. 2005, Cronin et al. 2014). Indeed, most research on parasitoid community-forest structure interaction have been undertaken in small-scale field studies, largely due to the challenges associated with experimental forest manipulation at broad spatial scale (Simmons et al. 1975, Marino et al. 1996, Cappuccino et al. 1999, Eveleigh et al. 2007, Seehausen et al. 2014). Even though some work has examined the effect of broad scale landscape structure on parasitism rates (Thies et al. 2003, Cronin et al. 2014), there is a need for studies that would look at regional rather than local variation. It is particularly true for forest pest outbreaks considering the broad spatial scale at which they occur. The eastern spruce budworm (SBW; Tortricidae: *Choristoneura fumiferana*), affecting 27 000 km<sup>2</sup> in the Côte-Nord region of Quebec, MFFP 2015) is a good example of biological process at broad spatial scale. Undertaking such studies would serve to better understand the role of landscape structure on ecological stability and how it can be influenced by human activities through the logging industry.

The eastern spruce budworm system offers an excellent opportunity to investigate the scale at which parasitoids respond to landscape structure. The SBW is a native lepidopteran defoliator of North American forests that affects forest structure at broad spatial scale (MacLean 1980). Outbreaks every 30-40 years lead to the death of thousands of hectares of coniferous forest in Canada (Simard et al. 2011). The SBW favoured host is balsam fir, *Abies balsamea*, but will also attack white, red and black

spruce, *Picea glauca*, *P. rubens* and *P. mariana* (MacLean 1980). Along with wildfires, it is the most important forest disturbance in eastern Canada (Bergeron et al. 2001). As such, outbreaks of SBW drive important ecological processes such as forest succession and the development of forest structure from stands to landscapes (Baskerville et al. 1975, Déry et al. 2000, Bouchard et al. 2007).

In addition to altering forest structure, the dynamics and consequences of SBW outbreaks are shaped by existing forest structure, which itself represents the legacies of previous disturbance – succession interactions (Wallin et al. 1994, James et al. 2007). The three outbreaks that occurred during the 20<sup>th</sup> century were more intense than previously detected (Blais 1983). It has been suggested that changes in forest composition and configuration due to human activities were partly responsible for the increasing extent and intensity of outbreaks (Blais 1983, Miller et al. 1993). This hypothesis, known as the silvicultural hypothesis (Miller et al. 1993), also suggests that forest management could be used to reduce the impact of SBW outbreaks. Despite a century of research, mechanisms linking forest structure and SBW population dynamics remain however uncertain (Pureswaran et al. 2016).

The community of generalist parasitoids has been hypothesised to be a main driver to control SBW populations (Royama 1984) and is affected by forest landscape structure (Royama 1984, Cappuccino et al. 1998, Eveleigh et al. 2007). This community, through its effect on the SBW, would contribute to the correlation between SBW dynamics and landscape structure (Cappuccino et al. 1998). The potential of parasitoids to stabilize the SBW system has been acknowledged since the beginning of the 90's (Smith 1993) but not conclusively demonstrated. This present chapter, by putting in relation parasitism rates and forest structure, investigates the scale at which parasitoids respond to landscape and the strength of this response.

The SBW-related parasitoid community is complex and is composed of close to 180 species on multiple trophic levels (O'Hara 2005, Bennett 2008). However, just over a dozen of them are responsible for most parasitism (Zebrowski 1998). This community is also highly temporally variable (O'Hara 2005). Within a season, each SBW developmental stage (i.e., eggs + six larval stages + pupae) is attacked by an array of different species, producing a succession of parasitoids communities throughout a single season. Among seasons, the community also changes over the course of an outbreak (i.e., ~10 years) with different species found during the rise, peak, and collapse of a SBW population (Eveleigh et al. 2007). Adding to this temporal variation in species composition, spatial variation might also occur as the SBW outbreak is moving northward in black spruce dominated

boreal forests where ecological dynamics might be different from southern regions (Pureswaran et al. 2015) and parasitoid communities might differ.

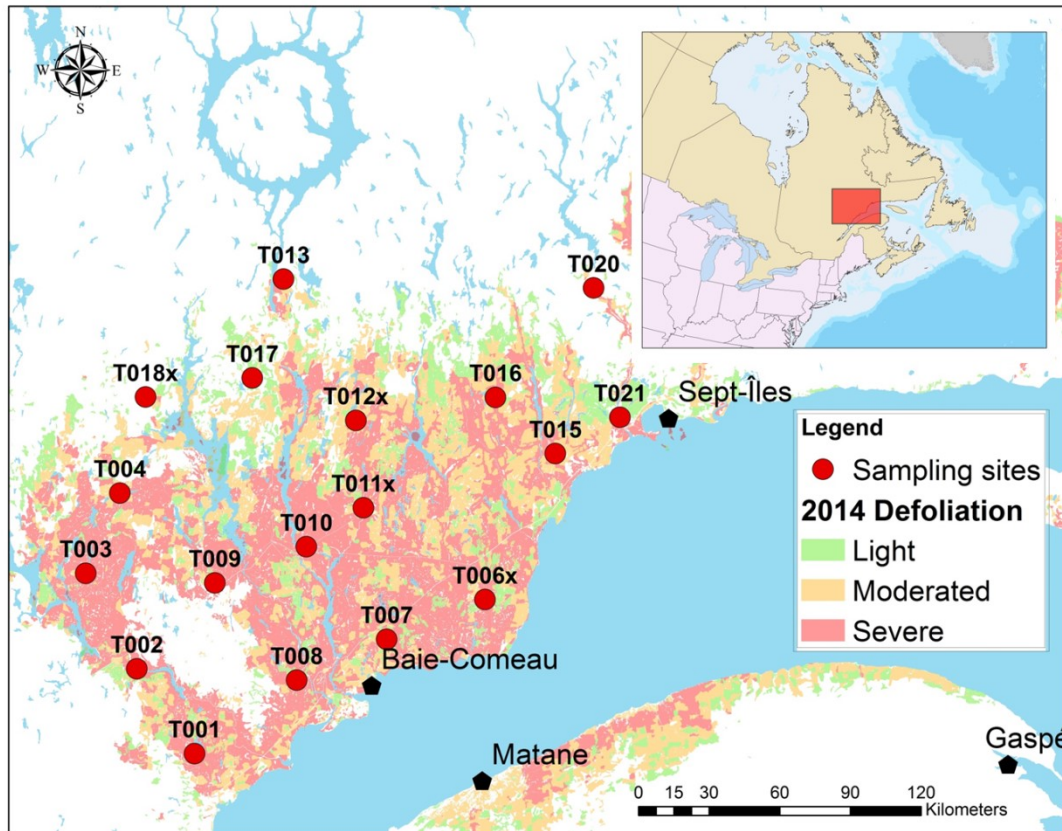
In this chapter, I examine how parasitism rates vary spatially and temporally within a single season over a large, heterogeneous region currently experiencing a SBW outbreak in the Côte-Nord region of Quebec, Canada. More specifically, I ask the following two questions: 1) Which attributes of forest landscape structure (e.g., stand diversity, forest type composition) influence spatial variation in SBW-associated parasitoid attack rates; and 2) at what spatial scales do these attributes affect parasitism? For the first question, I hypothesize that landscape diversity of stands should support higher parasitism rates by offering a diversity of habitats and alternate hosts (Cappuccino et al. 1998, Gagic et al. 2011, Charbonneau et al. 2012). Concerning the second question, I hypothesize that some spatial scales should capture parasitism rate variation better than other because they may reflect the parasitoids spatial scale of response to landscape. The answer to both of these questions would represent a great leap forward in our comprehension of the SBW system and how forest structure can be used to alter SBW outbreak impacts.

## **Methods**

### Study area

Samples were collected in the summer of 2014 in the Côte-Nord region of Quebec (Figure 1.1). In this region, 74% of forests are dominated by softwood stands. Stands are characterized by spruce-moss forest communities in the northern regions and balsam fir-white birch forest communities in the south (De Grandpré et al. 2008). Based on the severity of the defoliation and their proximity to access roads, 18 sites were visited across the region within the current SBW defoliation zone (Figure 1.1). Sites were separated by at least 30 km. Because different parasitoid species attack the SBW at different developmental stages within a season (Bennett 2008), I sampled three times throughout the summer to get the full suite of associated parasitoids: (S1) Larval stages 3 and 4 (L3-L4); (S2) L5-L6 and (S3) pupae. SBW eggs and early larval stages parasitism was not investigated due to field work limitations. Timing of sampling was determined using predictions made by the BioSim phenological model (Régnière et al. 2013). This software uses information on local degree days and up to date weather data to predict SBW development stage at a given location and time. For each sample period, I aimed to collect 500 individuals per site. At each sites, individuals were manually collected at

different heights in the canopy (mid-crown and eyes level) and evenly distribute when possible between available mature fir and spruce trees. In total, 7891 L3s-L4s, 6220 L5s-L6s and 5905 pupae were collected.



**Figure 1.1:** Sampling sites within the defoliation area in Côte-Nord region, Qc. Insert in upper right indicates continental context. Defoliation data taken from *Ministère de la Faune, de la Flore et des Parcs* (MFFP 2015).

Collected SBW larvae were individually reared in 25mL portion cups on synthetic diet (McMorran 1965). Larvae were monitored for the emergence of parasitoids every few days. Adult parasitoids were kept dry in 1.5 mL microcentrifuge tubes at  $-80^{\circ}\text{C}$  before being mounted on pins for identification. Parasitism rates were calculated over all sampling periods as well as per site. Multi-parasitism and hyperparasitism were considered in the same manner as if the SBW death was caused by a single parasitoid. In total, 3132 parasitoids were reared and identified to species under a stereoscopic microscope using identification keys developed specifically for SBW parasitoids (O'Hara 2005, Bennett 2008, Fernandez-Triana et al. 2010). Spatial variation in parasitism rates by the

different species at the different sampling periods was modelled with forest-related spatial variables acquired through remote sensing.

### Remote sensing data

#### *Ground cover map*

Remotely sensed forest data was used to characterize landscape structure around sampling sites and to model spatial and temporal variation in measured parasitism rates. Remotely sensed data for the study region were obtained through the USGS operated Landsat8 satellite in summer 2013 and 2014 (USGS 2015). Raw spectral bands were assembled in a RGB564 color composite image in PCI Geomatica software. Ground cover type was divided in 20 forest classes at 15m resolution based on individual pixel spectral signatures and using 909 verification sites (Appendix I).

These data were then reclassified into three categories relevant to SBW-associated parasitoids. The first group, coniferous forest, consists of SBW-host conifers. The second group, open/mixed habitats, represents all the patches of sub-optimal and non-favourable SBW habitat (i.e., mixed forest, open coniferous forest, deciduous forest, meadows and lower vegetation types) that nonetheless contain parasitoid resources such as alternative/alternate hosts and feeding sources (e.g., nectar). The last group, non-forest habitats, includes water, bare ground, or burnt soils that are considered inhospitable (i.e., landscape matrix) for both the parasitoids and their host. The accuracy of the final map was asserted using three indices: 1) sensitivity (i.e., proportion of verification sites in a given class that are correctly classified); 2) positive predictive value (i.e., proportion of sites that are mapped as part of a given class that are actually of that class) and 3) post-test probability of true positive value (i.e., the overall probability of a site of being correctly classified).

#### *Landscape pattern metrics*

Landscape structure surrounding each sampling location was quantified using landscape pattern metrics calculated using Fragstats (McGarigal et al. 1994). Three metrics were chosen to describe landscape structure for the SBW habitat and the open/mixed habitat land-cover classes. These metrics were: proportion of the ground cover class in the landscape, mean patch size, and edge density of each stand in the landscape. Shannon's diversity index (SHDI) was also computed on the

primary 20-classes ground cover map to quantify landscape diversity without *a priori* assumption regarding which habitat type is most relevant to parasitoids. Each of the three landscape metrics was computed for each site using 15 different circular landscapes centred on the site. The circular areas increased in size ranging from 100 to 10 000 meters radius (i.e., 100; 250; 500; 750; 1000; 1250; 1500; 1750; 2000; 2500; 3000; 4000; 5000; 7500; 10 000m).

### *Outbreak status*

I quantified SBW outbreak status at the site and regional level for use as model predictors. First, I quantified regional outbreak age at multiple spatial scales surrounding each focal site as above using cumulative remotely sensed data. Outbreak age was computed using a cumulative defoliation map (presence/absence) assembled from eight annual defoliation maps beginning when the outbreak was first detected in the region (2007) to the year of my study (2014). These data are freely available on the Quebec governmental website (MFFP 2015). For each sample site and scale, the mean age of outbreak was weighted by the surface area of each defoliation patch.

To quantify site-level outbreak status, I used direct measurements of SBW larval density. SBW density for every site was estimated during the first sample collection. SBW density was calculated as the mean proportion of budworms per bud on a branch (i.e., number of SBW larvae per number of current year buds) from ten 45 cm branches collected at mid-crown height at each site (Sanders 1980).

### Statistical analysis

#### *Spatial correlation*

To capture unmeasured spatial structure that would follow spatial patterns or gradients, I employed distance-based Moran's eigenvector maps (dbMEM) functions. MEMs are eigenfunctions from a principal coordinate analysis (PCoA) on a matrix of distances between sites. Those eigenvectors express spatial correlation at different scales and can serve as additional explanatory variables that represent latent spatial structure (Legendre et al. 2012). As the matrix of distances in a dbMEM can represent non-geographic distances, I used least cost path distances between sites based on a resistance surface in which topography and hydrography acted as constraints to parasitoids'

movement (Zeller et al. 2012). To construct the resistance map, each cell had a base value of 1 to which was added either the slope declination (i.e. the positive value of slope in degree) or a value of 5 if covered by water. This process of building the resistance surface reflects the hypothesis that parasitoid dispersal is affected by landscape topography. Moreover, instead of connecting all sites to one another, connectivity between sites was expressed in a Delaunay's triangulation to avoid connection between sites too far apart. From the ten positive MEM functions produced, only the first and last three (respectively broad and small scales MEMs) were retained arbitrarily to maintain the number of spatial explanatory variables as low as possible while keeping information at broad and fine spatial scales.

### *Model building*

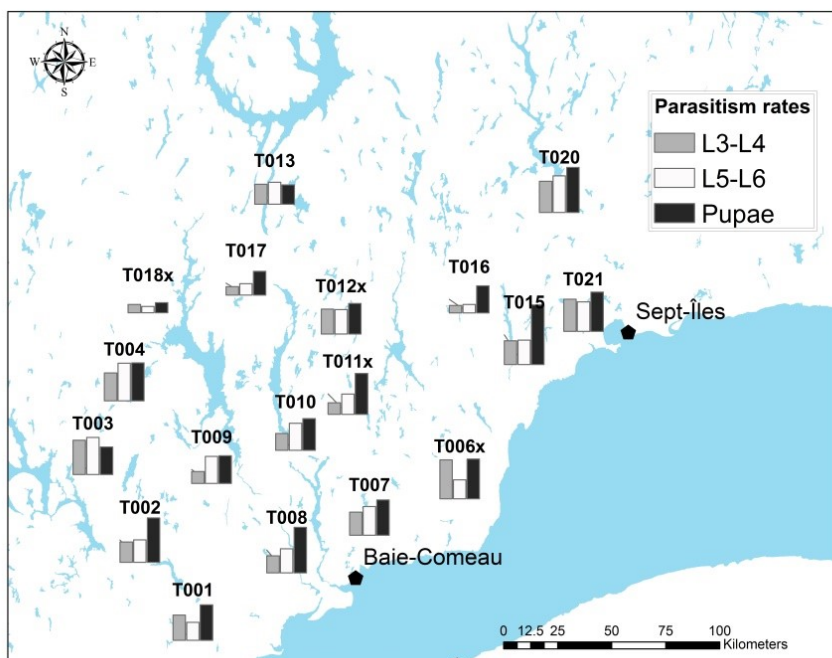
Redundancy analysis (RDA) was used to model variation in parasitism rates. Throughout this chapter, the different sampling periods have always been modelled together as a matrix of multiple response variables. Interpretations on single sampling period were made using the graphical representation (i.e., triplot) of the best RDA (i.e., the model explaining most of the parasitism variation). The parasitism rates were explained in the models as a function of local and regional SBW outbreak status variables (i.e., SBW density and age of outbreak), forest structure (i.e., proportion of open/mixed habitats and SHDI) and a set of variables representing latent spatial structure (i.e., two groups of three MEMs each). The model that includes all of these variables represents the "complete" model that I sought to improve through model selection. Multicollinearity among explanatory variables was checked prior to analysis by making sure that each variable has a variance inflation factor (VIF) not exceeding 10 (Legendre et al. 2012).

To obtain the most parsimonious models describing parasitism at each of the 15 scales examined, a two-way stepwise selection procedure based on the Akaike Information Criterion (AIC) was used (Legendre et al. 2012). For each step of the automated model selection procedure, the method compared the loss of information when a variable was added or removed from the initial complete model and stopped when it reached the lowest value. The objective here was to build models at each scale that maximize variance explained (i.e.,  $R^2$ ) but contain as few explanatory variables as possible. The models with the lowest AIC were considered as the "best" models and were henceforth referred to as the "reduced models". Once the reduced models were identified for each scale, their quality was evaluated and compared among scales using the adjusted  $R^2$ .

## Results

### Parasitism rates

Parasitism rates varied greatly between sites and sampling periods and ranged from 3.7% to 35.3%. Parasitism rates were greater in pupae (20%) than in larvae (13% and 14%; Figure 1.2 and Table 1.1) (ANOVA,  $F=9.042$ ,  $p<0.001$ ). Five species accounted for 92% of all specimens collected: *Glypta fumiferanae* (33%), *Smidtia fumiferanae* (24%), *Dirophanes maculicornis* (22%), *Apanteles fumiferanae* (10%) and *Meteorus trachynotus* (3%). The remaining 8% is composed of 37 rarer species. Species assemblage and species occurrence patterns also changed through sampling periods (Figure 1.2). For example, a species as abundant as *G. fumiferanae* in L4-L5 (66%) was almost entirely absent from pupae (0.5%), whereas *D. maculicornis* is absent from L4-L5 (0.002%) but broadly present in pupae (52%).



**Figure 1.2:** Spatial variation in parasitism rates of SBW during collection at three different developmental stages. Values represented by the height of the bar. See table 1.1 for precise values.



**Table 1.1:** Parasitism rates (%) per site per SBW stage of collection

<b>Site</b>	<b>L3- L4 (%)</b>	<b>L5-L6 (%)</b>	<b>Pupae (%)</b>
T001	15	11	21
T002	12	13	26
T003	20	22	16
T004	16	22	23
T005	23	11	24
T006X	14	17	21
T007	10	14	27
T008	7	16	16
T009	10	16	19
T010	7	12	24
T011X	15	14	18
T012X	12	13	11
T013	14	15	35
T015	4	5	16
T016	5	7	14
T017	5	4	6
T018X	18	22	27
T020	19	17	23
T021	13	14	20
<b>Mean</b>	<b>15</b>	<b>11</b>	<b>21</b>

#### Ground cover classification

Sensitivity of the ground cover classification was 68%, 62% and 72% for the coniferous forest, the open/mixed habitats and non-forest ground cover, respectively. Positive predictive value, in the same order, was calculated as 55%, 73% and 71%. As an indication of overall accuracy, post-test probability of true positive was 50%, 76% and 70%.

Uncertainty associated with these classifications stems from several practical challenges to classifying satellite imagery largely related to the scale of discretization of continuous spatial variation. The 15 meters pixel extent (the satellite resolution) can make the difference between a patch of bare ground and a patch of deciduous forest. Therefore, a verification site can be classified very differently depending on the observer's position. Second, merging neighbouring ground cover classes into a single 15x15m pixel affected its spectral signature and biased its classification. However, those neighbouring sites were not included in the characterization of the spectral signature of each ground

cover class and would therefore not have biased the making of the ground cover map, leading to a more accurate map than suggested (Appendix I).

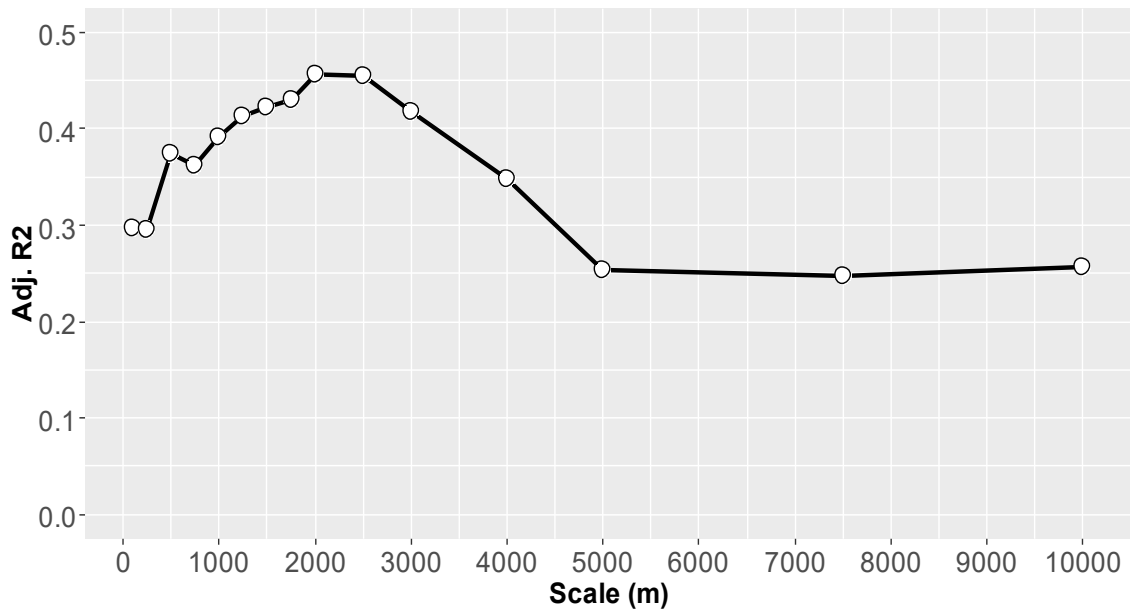
### Landscape pattern metrics

Coniferous forests and open/mixed habitats were the dominant ground covers in the landscape and were strongly correlated in their relative proportion ( $r = -0.91$ ). Open/mixed habitats were less common in the boreal forest (mean proportion in the landscape: 30%) than coniferous forest (mean proportion in the landscape: 56%). Open/mixed habitats also had a greater coefficient of variation (0.33 against 0.17). For those reasons and to avoid large VIFs (i.e., explaining more variation in the model than they should due to explanatory variables correlation), only the open/mixed habitats were used in our models with the biological assumption that the open/mixed habitats were the limiting factor in the landscape.

Landscape metrics are often correlated with one another (McGarigal 2015). In our study, edge density was highly correlated to Shannon's diversity index ( $r = 0.76$ ) and mean patch size for open/mixed habitats was correlated to the proportion of the same habitats in the landscape ( $r = 0.72$ ). Once again to keep VIFs below 10 and because they were more easily interpreted biologically, SHDI and proportion of open/mixed habitats were retained for use as predictors in the models and I omitted the predictors edge density and mean patch size.

### Scale of response to landscape

I computed the Adj.  $R^2$  for each reduced model describing parasitism rates as a function of landscape structure and SBW status at a series of 15 different spatial scales. This series of Adj.  $R^2$  values associated with these different spatial scales resulted in a unimodal curve (Figure 1.3). At small scales, the proportion of variance explained in the reduced models started off at 30% at 100m and increased with the scale. The best reduced models captured most of the variance (explaining 45-46% of parasitism rates variation) at scales of 2000 to 2500 m. At broader scales, a decrease can be observed with a low point of 25% at 10 000 m. The unimodal curve is important as it indicates, with multiple values, that there is an optimal scale at which parasitism rates will respond effectively to landscape properties.



**Figure 1.3:** Adjusted R<sup>2</sup> of each reduced models for each spatial scale.

#### Factors influencing parasitism rates

The models at very small spatial scales (i.e., from 100 to 750 m) were the only ones at which spruce budworm density and proportion of open/mixed habitats were useful in predicting parasitism rates (Table 1.2). In models at 1000 to 5000 m, the same four variables were selected (i.e., age of outbreak, SHDI, large and small scale MEMs). The only difference between the models within that interval was the spatial scale at which the age of outbreak and the SHDI were computed (MEMs been constant throughout all scales). That is, the variation due to scale was the only varying factors between models. That difference in the scale resulted in both the best (2000 m; R<sup>2</sup>=0.46) and the worst (5000 m; R<sup>2</sup>=0.25) models.

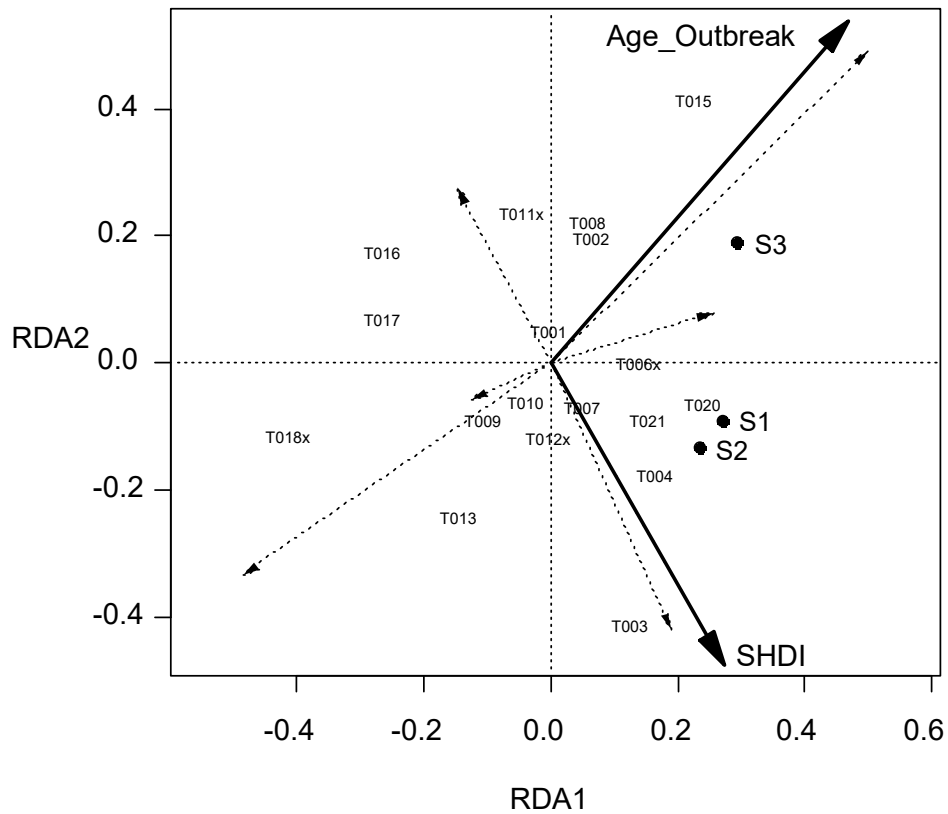
**Table 1.2:** Retained variables in reduced models following a stepwise variable selection. Shaded line indicates the scales whose model had the highest  $R^2$ .

Scale (m)	Adj. R2	Variables*					
		Local SBW density	Regional age of outbreak	Proportion of open/mixed habitats	SHDI	Large scale MEMs	Small scale MEMs
100	0,30	-	X	X	-	X	-
250	0.30	X	-	X	-	X	X
500	0.38	-	-	X	X	X	X
750	0.36	-	-	X	X	X	X
1000	0.39	-	X	-	X	X	X
1250	0.41	-	X	-	X	X	X
1500	0.42	-	X	-	X	X	X
1750	0.43	-	X	-	X	X	X
2000	0.46	-	X	-	X	X	X
2500	0.45	-	X	-	X	X	X
3000	0.42	-	X	-	X	X	X
4000	0.35	-	X	-	X	X	X
5000	0.25	-	X	-	X	X	X
7500	0.25	-	-	-	X	X	-
10000	0.26	-	-	-	X	X	-

\* Variables marked with an "X" were retained in the model at the corresponding scale based on two-way, AIC-based step-wise selection.

The scale specific models that captured the greatest variation in parasitism rates were at a scale of 2000 – 2500 m and included the age of outbreak, SHDI, as well as both broad and small scale MEMs (

Table 1.2). In these best models, the age of outbreak and the SHDI index were not correlated (Figure 1.4). Parasitism rates of the larval stages (i.e., L3-L4 and L5-L6) responded similarly to the variables in the reduced models. Moreover, higher parasitism rates for these stages can be observed in more heterogeneous habitats whereas parasitism rate in pupal stage was higher in later years of SBW outbreak (Figure 1.4).



**Figure 1.4 :** RDA triplot of reduced model at 2500m (only slightly different from the model at 2000m). The parasitism rates of varying sampling periods are shown in relation to selected explanatory variables. Dashed arrows represent MEMs eigenvectors, S1, S2 and S3 correspond to sampling periods. This figure indicates how the parasitoid community for each sampling period responds to forest diversity (SHDI) and when they are the most effective during an outbreak.

## Discussion

The objective of this study was to describe parasitism rate at the regional level and to describe how forest landscape affected parasitism and at which spatial scale. I answered these questions using field data for parasitism rate and remotely sense data for landscape characteristics. SBW outbreaks are both ecologically and economically important process and studies like this one are essential to understand the relation linking landscape structure to biological processes.

### Parasitism rates

Parasitism rates in the Côte-Nord region of Québec (13-20%) were similar with what had been previously reported during SBW outbreaks in New-Brunswick (Miller 1963). Parasitism rates tend to be lower in epidemic than in endemic SBW populations because parasitoids struggle to keep up with the rapidly increasing number of host (Miller 1963). During periods of lower SBW density between outbreaks (i.e., the endemic period), parasitism reached up to 77% in the Montmorency forest, Quebec, in 2011 (Seehausen et al. 2014). The Côte-Nord region differs from the regions aforementioned in its SBW history and forest composition. The Côte-Nord has only experienced SBW outbreaks since the end of the 20<sup>th</sup> century whereas both other regions are known to have been affected by outbreaks for at least the last two centuries (Blais 1983). While New-Brunswick and Montmorency forest are dominated by balsam fir and paper birch, the Côte-Nord region, particularly at the northernmost areas sampled, is mainly composed of black spruce forest.

The major parasitoid species identified (i.e., *G. fumiferanae*, *A. fumiferanae*, *S. fumiferanae*, *D. maculicornis* and *M. trachynotus*) are broadly distributed in Canada and are known for their importance during SBW outbreaks (Zebrowski 1998). Less common species such as *Itopectis conquisitor* that are important in other regions affected by SBW were also present in our study but at a lower frequency (Zebrowski 1998). *Smidtia fumiferanae*, although ranking as one of the most common parasitoids in some regions of western Canada, was believed to be rare or less common in eastern Canada where it has been released in New Brunswick, Newfoundland, Quebec and Ontario (Coppel et al. 1957). However, it is the most important parasitoid of SBW pupae (35%) in the Côte-Nord region. Those differences in regional abundance of species could be caused by varying species spatial distribution and forest structure.

### Scale of response to landscape

When describing the spatial scale at which a species responds to landscape structure, it is important to differentiate between a species simply reflecting the intrinsic spatial structure of the region under study, and the situation in which the species responds at a unique scale of its own. To distinguish between these two possibilities, I quantified the spatial scale structuring the landscape independently of parasitoid response using 822 reference points in the study region. Using RDA, I modelled the scale

at which the proportion of open/mixed habitats and the Shannon's diversity were structured using MEM eigenfunctions and a two-ways stepwise selection based on AIC (Legendre et al. 2012). Using these MEMs, I found that the dominant scale at which forest was structured, of the 15 scales tested, was 10km. Because the parasitoid scale of response that I identified was between 2000-2500m, it seems likely that this different scale reflects parasitoids biology and life-history, such as dispersal behavior, and is not an artefact of the underlying scale of forest landscape structure.

Based on my results, it seems that spatial scales greater or less than 2000 – 2500 m can explain little variation in parasitism rates whereas parasitism rates are well described by forest structure at this scale. I suspect that this scale was determined by the average on community level of a suit of species-specific morphological and behavioural characteristics of parasitoids such as dispersal capacity and foraging habits. The unimodal shape of the series at increasing scales (Figure 1.3) suggested three categories of scales. The first was a cluster of scales too small where parasitoids can easily search through and beyond for hosts and resources. Around 2000-5000m, a higher proportion of variation in parasitism explained (i.e., increased  $R^2$ ) suggested that the information captured by landscape metrics was relevant to parasitoid biology and could provide a mean to approximate their scale of foraging or habitat selection behaviour. In the third category, the spatial scale was beyond the perceptual or dispersal capacity of the parasitoids and therefore did not capture any additional variation in parasitism rates.

#### Factors influencing parasitism rates

The best models to explain parasitism rates (at a spatial scale of 2000 – 2500 m) contained information on how selected explanatory variables affected parasitism rates at different developmental stages (Figure 1.4). It had been previously demonstrated that budworm parasitoid communities change over the course of an outbreak (Zebrowski 1998, Eveleigh et al. 2007). In my study, parasitism of larval stages (S1 and S2) was greater in sites where defoliation was more recent (1 to 3 years). Indeed, *G. fumiferanae*, a very common parasitoid in sampling period S1 (66%) had been shown to be more abundant during the outbreak and before the increase of Tachinidae species later on (Zebrowski 1998). Parasitoid species of larval stages were also positively associated with greater habitat diversity (expressed by SHDI) as shown in the literature (Cappuccino et al. 1998,

Eveleigh et al. 2007). Greater diversity suggests a higher number of different habitats with various resources. It also suggests a more diverse community of alternative hosts for the parasitoids.

Females of *G. fumiferanae* and *A. fumiferanae* can live in their adult form for ~20 days if supplied with sugar (honey) but only a few without (Stairs 1983, Elliott et al. 1987). How *G. fumiferanae* and *A. fumiferanae* use natural sugar sources (e.g., honeydew, nectar) is unknown. It had been suggested that these species tend to choose honeydew over nectar because of the low density of wildflower nectar in coniferous stands that make it not worth exploiting (Elliott et al. 1987). However, in more diverse landscapes, parasitoids can potentially exploit habitats with high wildflowers density such as meadows and open coniferous forest while moving from one patch of coniferous forest to the other.

I also found that parasitism of the pupal stage was mainly a result of *D. maculicornis* (52%) and *S. fumiferanae* (35%) and both are more common toward the end of outbreak (McGugan et al. 1959). These species do not seem to respond to diverse landscape (SHDI) according to my results. Studies have shown that late stage SBW-associated Tachinidae, such as *S. fumiferanae*, do not respond to increased sugar availability (Cappuccino et al. 1999) which may explain why they did not strongly respond to SHDI in this study.

Surprisingly, the proportion of open/mixed habitats was not included in the final selected models of parasitism. I hypothesised that open/mixed habitats would influence: 1) the presence of alternative hosts that would lead to a more diverse and effective guild of parasitoids, and 2) the presence of feeding habitats for the parasitoids. The fact that proportion of open/mixed habitats was not retained in reduced models might be due to the reclassification that was undertaken and the resulting land-cover types included in this category. Deciduous and mixed forest covers, as well as shrubs are far more common than wildflower abundant habitats (e.g., meadows and Labrador tea field) in the open/mixed habitats category. Deciduous-related habitats were included in the open/mixed category because they represent a source of alternate hosts for parasitoids that have more than one generation per year (i.e. bivoltine or multivoltine). However, such parasitoids only make up for less than 11% of all reared parasitoids. Thus, information contained in open/mixed habitat variable holds little importance to the other 89% of univoltine parasitoids that can complete their life cycle on the SBW only. Shannon's diversity index, because it is computed on 20 ground cover classes, was potentially sufficient to express true feeding habitats availability.



This study showed once more the importance of landscape structure for parasitoids but its singularity relies on the scale at which it was examined. Indeed, most research on parasitoids did not even compute spatial structure metrics at the scale of the best models in this study (Leius 1967, Marino et al. 1996, Cappuccino et al. 1998, Cappuccino et al. 1999, Eveleigh et al. 2007, Holzschuh et al. 2010, Gagic et al. 2011, Zihua et al. 2012) and the only one to my knowledge to match this study was in an agricultural system (Thies et al. 2003). Therefore, this chapter suggests that landscape metrics that play a role at smaller scales, such as landscape heterogeneity, are also effective at broader scale. There is however a limit at which an organism can respond to landscape and using extremely broad scales enable me to identify these scales which are too broad to have meaning for the organism concerned.

## **Conclusion**

The silvicultural hypothesis suggests that it is possible to reduce SBW impact on forest by managing its structure and altering the community of natural enemies (Miller et al. 1993). However, the scale at which we should modify the forest structure to obtain this effect was unknown. In this study, I identified the scale(s) at which forest diversity and spruce budworm outbreak status influenced spatial variation in spruce budworm parasitism. I found that parasitism was most influenced by landscape structure at a scale of 2000 – 2500m.

These findings suggest that, in order to influence parasitism, forest could be managed to produce a landscape structured to have a scale of 2000 – 2500 m through the creation of contrasting patches (e.g., open and intact forest areas) of roughly 13-20 km<sup>2</sup>. It is unlikely that those changes will lead to the collapse of an outbreak through the effect of parasitoids only, but the scale of the SBW outbreak is such that any modification that would lessen the forest susceptibility would represent a great amelioration. However, because species of parasitoids from different developmental stages respond differently to landscape structure, the spatial scales identified for the entire community of parasitoids may not reflect the ideal scale of forest spatial structure for individual species. Spatial scale of response to landscape may vary at the species level based on morphological traits and that possibility will be investigated in my second chapter. Studies such as this one are important because knowledge of the scale at which parasitoid seem to respond to landscape can be useful in guiding forest management planning (e.g., spatial scale of forest patches) and further studies on the spatial patterns of biodiversity associated with this complex and species rich dynamic irruptive system.

## **Acknowledgements**

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## **Appendix I: Remote sensing**

### **Satellite imagery**

Open access data on ground cover in the study region went back to 2000 with the latest governmental ecoforest inventory (MFFP 2014). I therefore made a new map from recent (2013-2014) data to characterize the actual forest composition. Satellite imagery used to quantify the forest landscape structure in the Côte-Nord region of Quebec were obtained through the United States Geological Survey (USGS) operated Landsat8 satellite. This satellite gravitates on a polar orbit around the Earth permitting the complete coverage of the planet in 16 days. Any region on Earth is photographed approximately 22 times per year. The satellite is equipped of two sensors: a multi-spectral sensor referred to as the Operational Land Imager (OLI) and a thermal infrared sensor (TIRS). Only the data from the OLI sensor were used for this project (Irons et al. 2012).

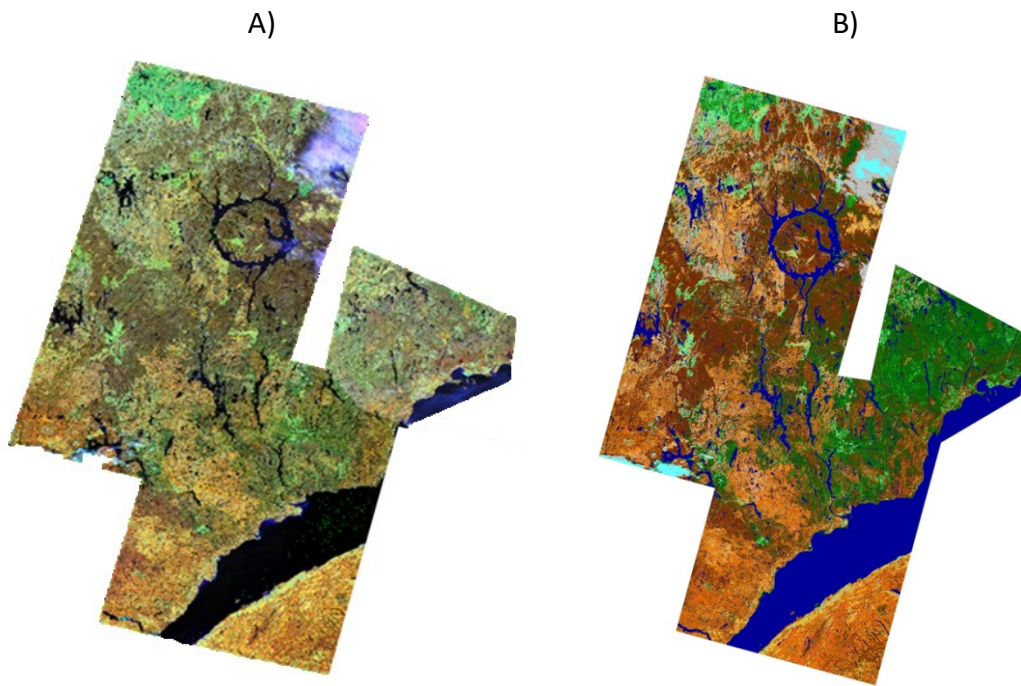
The OLI sensor is constantly recording data. The light reflected on the Earth surface is afterward captured by the telescope lens and then decomposed in nine spectral bands covering from the infra-red to the visible light. Each band has a ground resolution of 30 meters, except for the panchromatic band which has a 15 meters resolution. Data from the Landsat8 satellite are available freely online in 185 x 180 km tiles within 24h of their acquisition on the USGS website, [www.usgs.gov](http://www.usgs.gov) (Irons et al. 2012).

Decomposed spectral bands are reassembled in a geographical information system (GIS; e.g., PCI Geomatica) to create RGB (red, green, blue) composite images. Depending on the bands used and their order, it is possible to accentuate different ground properties such as burned soils, the kind of crop or the vegetation type cover. Indeed, each ground cover has its own spectral signature. These spectral signatures can then be used to differentiate hardwood from softwood forest as well as finer scale classification (e.g., tree species) in these broader categories (Madry 2013).

### **Ground cover mapping**

Five tiles were needed to cover the study region. Four of them were taken in 2014 and one in 2013 due to cloud cover in the area in 2014. All operations on tiles (i.e., assembling, color balance, pan sharpening and assisted classification) were undertaken using PCI Geomatica (2015). The first step

was to assemble each homologous band from the different tiles to create a single layer. To obtain a flawless merging, color were balanced using the superposing areas. The map resolution was thereafter enhance from 30 to 15 m using the panchromatic band. The last step was to create a composite image with the fourth, fifth and sixth bands under the RGB564 form. This image was used to assess ground cover type (Figure S1.5; A).

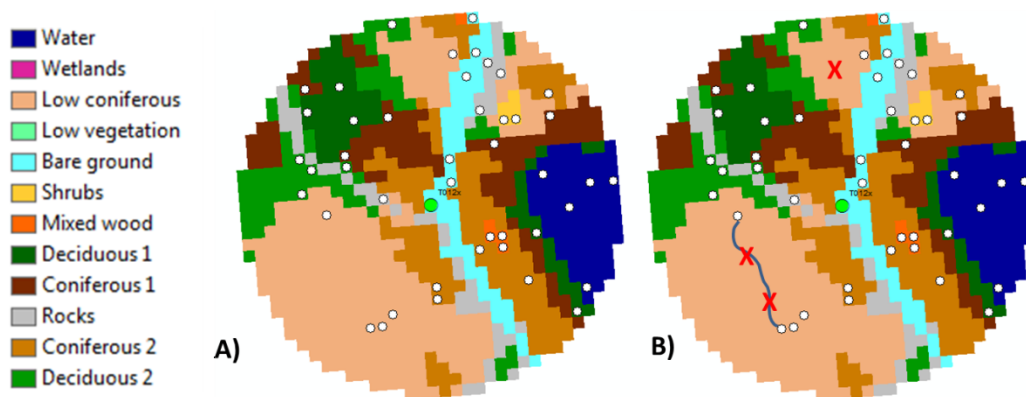


**Figure S1.5:** A) RGB564 composite image and B) first assisted classification with 12 ground cover classes.

Ground cover classification was done using supervised classification. In this method, the user draw polygons corresponding to the different ground cover classes on the RGB564 composite image based on the color shown (e.g., brown for coniferous forest or purple for bog). Once all ground cover are represented, the software computes the spectral signature for each ground cover based on the pixels within each polygon. Each pixel of the study zone (more than 524 millions) is thereafter associated to a ground cover class based on its similarity with its own spectral signature. This first classification was made of 12 ground cover classes: bare ground, low vegetation, low coniferous, shrubs, mixed forest, rocks, water, wetlands, 2 types of coniferous forest and 2 types of deciduous forest (Figure S1.5; B). The resulting map was simplified by eliminating objects of 1-4 pixels ( $225 - 900 \text{ m}^2$ ) considered as

noise in the data (using Sieve algorithm with 8 pixels neighborhood rule in PCI Geomatica). This filtering was undertaken on all maps.

Map classification accuracy was ground-truthed in summer 2015 with 909 verification points distributed in 24 clusters over all the study area (Figure S1.8). 11 of those clusters were centered on our sampling sites and 13 were areas presenting rarer ground cover of interest (e.g., burned soils or wetlands). Each cluster represented a circular area of 250 m radius. In this area, verification sites were chosen according to a stratified sampling design per ground cover class. Up to five sites were selected randomly per ground cover class and were at least 15 meters apart (i.e., the distance between two pixels). Each site geographical position was corrected to correspond to the center of the pixel it fell within. By doing so, I was able to use the pixel as sampling unit and sampling size (15m x 15m) to assess ground cover. In the field, ground cover classes were detailed in 20 more precise new classes (Table S1.3). In addition to randomly chosen sites, other sites were added when a well-defined ground cover class was identified over a broad area (Figure S1.6).



**Figure S1.6:** Map of verification sites. A) Stratified sampling plan per ground cover classes. B) Red crosses represent additional verification sites that were added while in the field between random sites.

With the new knowledge acquired from the verification sites, new sets of polygons were drawn for the 20 new ground cover classes. I used these new polygons to reclassify the data with the same method as describe above. The final product was a ground cover map of 20 classes describing 118 025km<sup>2</sup> (7.6% of the whole province of Quebec) at a resolution of 15 meters. This map was used to compute landscape metrics at different spatial scales.

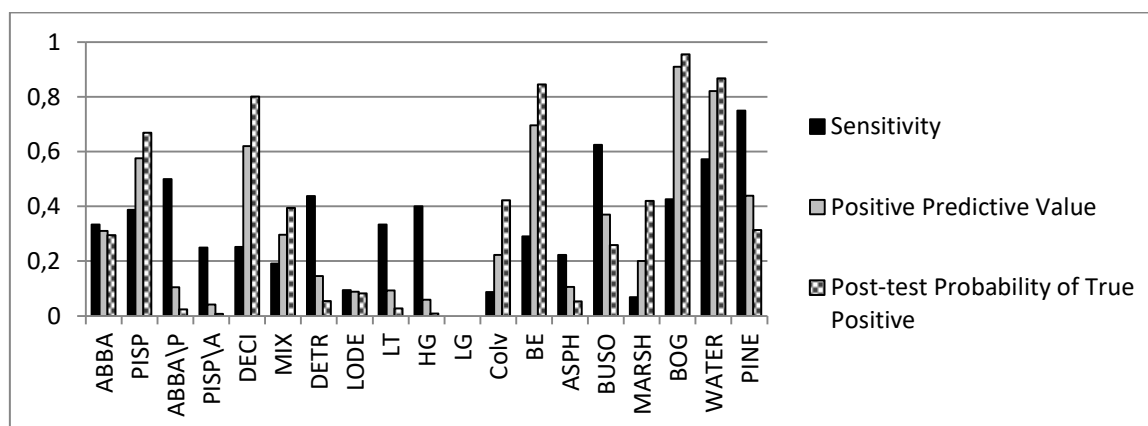
**Table S1.3:** Ground cover classes. When 80% of a verification site corresponded to the description, it could be part of a given ground cover class.

Symbol	Description
	<b>Mature forest</b>
ABBA	Balsam fir forest
PIMA	Spruce forest
ABBA-S	Balsam fir dominated forest with spruce
PIMA-B	Spruce dominated forest with balsam fir
DECI	Deciduous forest
PINE	Pine plantation
MIX	Mixed forest
	<b>Open habitats</b>
BURN	Dead/burned trees
COLV	Open coniferous forest with low vegetation
LOCO	Low coniferous
LODE	Shrubs
	<b>Low vegetation</b>
LT	Labrador tea
HG	High grass
LG	Low grass (e.g., lawn)
	<b>Mineral substrats</b>
BE	Bare ground
ASPH	asphalt
BUSO	Burned soils
	<b>Wetlands</b>
MARSH	Marsh
BOG	Bog
WATER	Water

## Results and discussion

To assert the accuracy of the final classification map, I used the 909 verification sites as aforementioned. However, these sites were not the most appropriate because most of them were on the border of neighbouring habitats. Have I had the time and resources, it would have been more appropriate to use new verification sites situated at the center of larger stands to avoid border problematics. I nonetheless present here the accuracy of the classification based on these 909 verifications site in order quantify the classification effectiveness even if I hypothesize it to be greater than suggested.

The accuracy of the produced assisted classification can be describe using three indicators and varied greatly among the ground cover classes. The first indicator is sensitivity, which summarizes the proportion of sites of a given class that were correctly classified (i.e., is the classification restrictive enough to distinguish a class from another?). For example, 42% of sites classified as bog were identified correctly through ground-thruthing verification. However, 91% of the sites identified as bog in the field were correctly classified on the map (i.e., is the classification good enough to encompass all of its targeted-class?). This is the positive predictive value (PPV). I also evaluated accuracy of the classification using the post-test probability of true positive (PPTP) which represents the global probability of a site of being correctly classified considering the sensitivity, specificity and the representativeness of each class. In the case of the bog category, the PPTP calculation indicates that this class has a 96% chance of been correctly identified. Sensitivity, PPV and PPTP are summarized for each of my 19 classes in Figure S1.7.



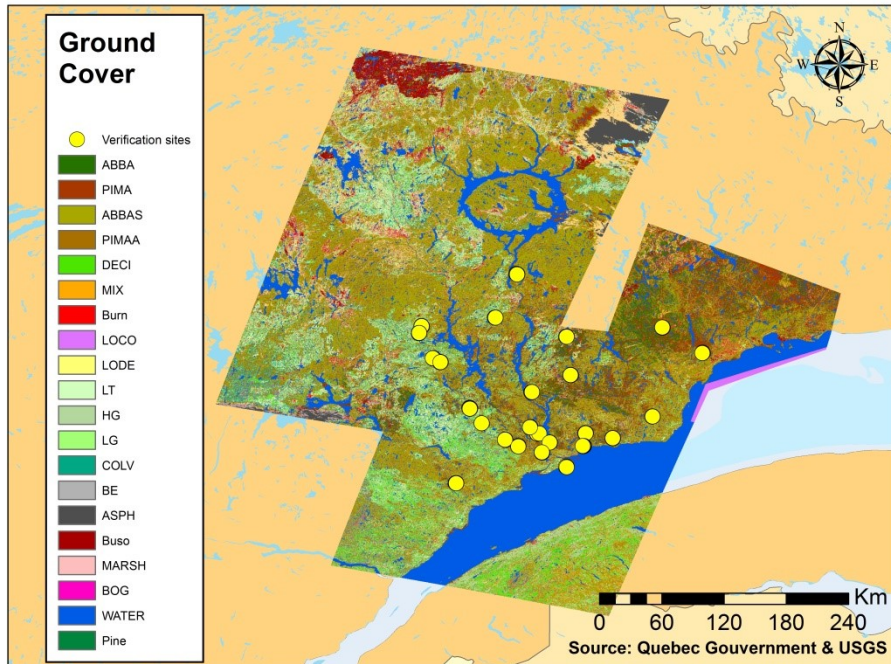
**Figure S1.7:** Results for the final assisted classification. Sensitivity, positive predictive value and post-test probability of true positive are shown by ground cover type.

The first explanation for the PPTP weakness of some classes was the definition of those classes. Indeed, some classes represented a transition between two or more other classes. One example is the mixed forest (MIX) which is a transition between coniferous (ABBA/PISP/ABBA-S/PIMA-B) and deciduous forest (DECI). The same situation was found for the open coniferous forest (COLV) which is a transition between coniferous forest and Labrador tea meadows (LT). On site, it can prove difficult to make the distinction and the boundaries between two habitats are not always clear.

For eight classes (i.e., ABBA/P, PISP/A, DETR, LODE, LT, HG, LG and ASPH), the PPTP is very low (under 10%). One reason for those low probabilities was the low number of verification sites in those classes. Indeed, some classes are poorly represented in the boreal forest such as high grass (HG), low grass (LG), asphalt (ASPH) and even shrubs (LODE). Those classes are also relatively small in area and patches smaller than four pixels had been withdrawn from the map, making it difficult to identify rarer ground cover.

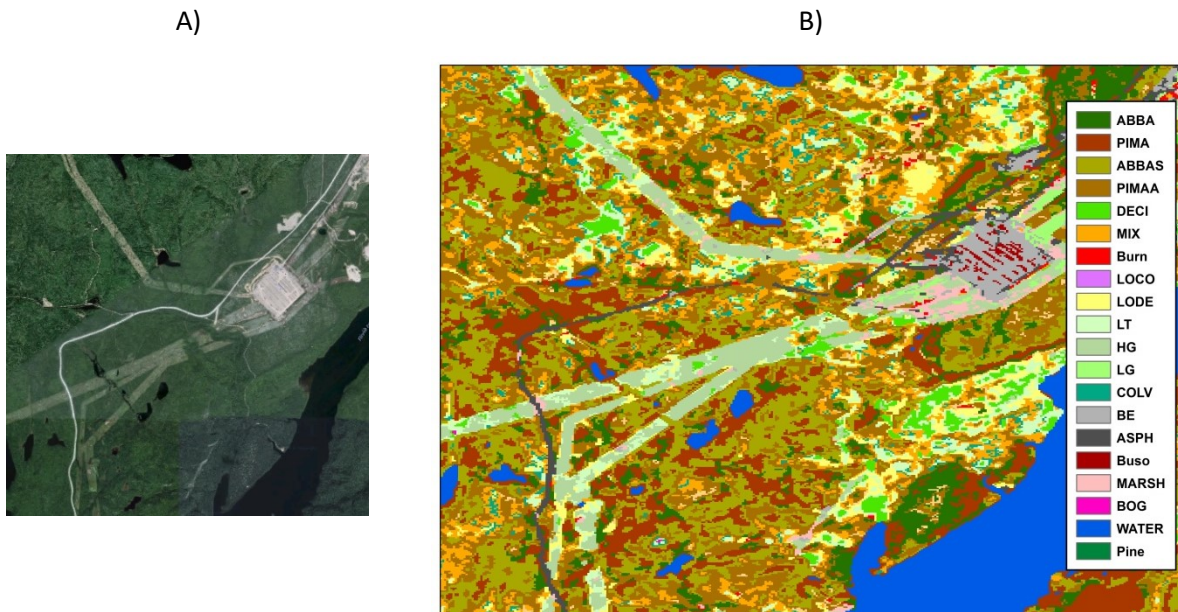
Using the water class, which has a clear multispectral signature, I demonstrated the important influence of having good verification sites by comparing the hydrographic map produced for this project and the one produce at high resolution by the Quebec government. Governmental data were used as “verification sites” (after been corrected for the rise of the water level in the Outardes complex dams and the building of the Toulnoustouc river complex in the past 10 years). The classification sensitivity in an area of 37 494km<sup>2</sup> (32% of the study area, not including the St-Laurent river) was of 92% in comparison to 57% using the verification sites. Thus, with accurate data (i.e., governmental data), it was possible to demonstrate the fitness of my classification beyond what was suggested by the verification sites alone.



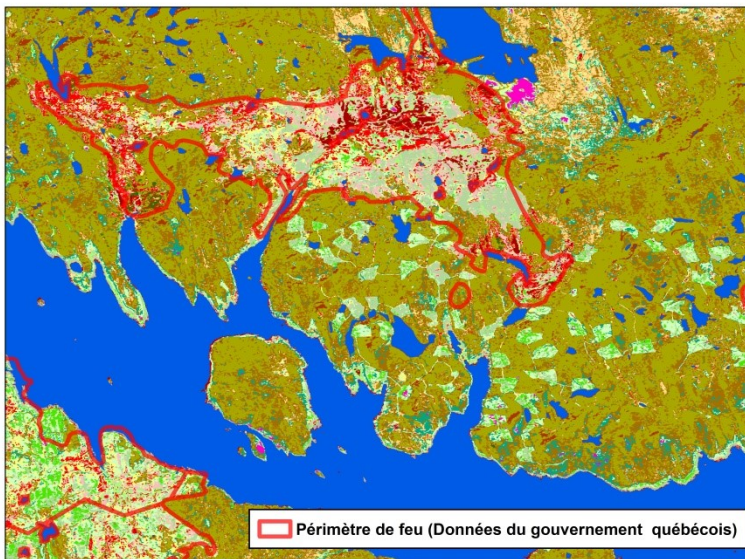


**Figure S1.8:** Final ground cover map with 20 classes and the 24 clusters of verification sites.

Despite these challenges, I remain confident in the final map product for two reasons. The first is that the polygons used to compute the spectral signature of every class were drawn on large and uniform areas whose ground cover class was known (either through verification sites or field experience of sampling sites). Small, neighbouring areas were not used for the classification and could not have biased the spectral signatures. Secondly, visual examination of broad scale patterns on final map suggests its accuracy. As mentioned above, all lakes and rivers are accurately represented and so are the road, the power lines and the infrastructures (Figure S1.9). It is even possible to see the effects of wildfires going back to 1995 along with logging patterns and dirt road (Figure S1.10).



**Figure S1.9:** A) Micoua electric distribution post, Jean-Lesage (Manic 2) dam, Google Earth image. B) Same region from the classification map. In both frames, asphalt roads can be seen along with high grass/Labrador tea under powerlines and bare earth at the distribution post.



**Figure S1.10:** René-Levasseur island (Manicouagan reservoir, southernmost part). In the middle: traces of wildfire in 2005 with partial revegetation. Bottom left corner: Traces of wildfire in 1996 with more advance revegetation. Logging cuts are also visible and are connected by a network of dirt roads.

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## **Chapitre 2: Relationship between morphometric characteristics of parasitoid species and their scale of response to landscape structure**

Olivier Pontbriand-Paré<sup>1</sup>, Véronique Martel<sup>2</sup>, Patrick M. A. James<sup>1\*</sup>

<sup>1</sup>Université de Montréal, Département de sciences biologiques, 90 Vincent-d'Indy, Montréal, Qc, Canada, H2V 2S9

<sup>2</sup>Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Québec, Qc, Canada, G1V 4C7

\*Corresponding author

Patrick M. A. James  
Université de Montréal  
90 rue Vincent d'Indy, room D-221  
H2V 2S9, Montréal, Québec, Canada  
Phone : +1 (514) 343-6864  
Email : [patrick.ma.james@umontreal.ca](mailto:patrick.ma.james@umontreal.ca)

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## **Abstract**

**Dispersal is a critically important ecological process that influences the spatial synchrony of population dynamics in irruptive insect species. It also contributes to determine the spatial scale at which parasitoids respond to landscape structure. However, dispersal is difficult to measure directly in small, elusive species such as flying insects and we therefore have little information on their spatial scale of response to landscape structure. In this study, I use the five most common parasitoids of the eastern spruce budworm (SBW) to examine the relation between dispersal-related morphological traits (i.e. wing load and body size) and the spatial scale of response to landscape. I found that, for a given body size and spatial scale, parasitoids with lighter wing load respond more strongly (i.e., models with higher Adj.  $R^2$ ) to landscape structure (composition and configuration). Additionally, as body size decreases along with wing load, the scale of response increases. As a result, I suggest that wing load is the main driver of dispersal over body size and will determine the spatial scale at which a flying insect will perceive its surroundings. This suggests that the often cited allometric relationship for terrestrial species that says that larger animals have a greater dispersal capacity may be inverted for flying parasitoids because it is less costly to travel for small species with large wings in comparison to their body size (i.e., low wing load).**

**Keywords: body size, dispersal ability, eastern spruce budworm, landscape heterogeneity, parasitoid, wing load**

## Introduction

Dispersal (i.e., the movement through landscape) plays an important role in species biology and population dynamics with impacts on demographic and genetic connectivity (Roff 1974, Roff et al. 2001). Variation in spatial connectivity among populations directly affects population viability (Boyce 1992) and community structure (Liebhold et al. 2004, Tschardt et al. 2004, Baguette et al. 2007). Animal dispersal is a complex behaviour that operates at multiple spatial scales for a given species depending on the biological processes involved (e.g., mate searching, inbreeding avoidance, escaping competition or foraging) (Bowler et al. 2005). However, dispersal ability is unknown for most animal species (Lima et al. 1996). This lack of knowledge regarding dispersal represents a significant obstacle to our understanding of biological systems and our ability to forecast and manage them.

Dispersal ability can be an indication of the spatial scale at which an organism responds to the environment (Tschardt et al. 2004). However, many organisms perceive their environment at multiple spatial and temporal scales through different behaviours such as foraging or migration. The extent of these scales will depend on morphological characteristics such as body size and sensory capacity (Lima et al. 1996), as well as movement behaviour (Cronin et al. 2014). Individuals can perceive what is directly around them but can also perceive a broader portion of landscape by moving through it (Ritchie 1998). In general, the larger the species or the greater its sensory capacity, the broader the perceived scale (Tschardt et al. 2012). For example, in the forest tent caterpillar (*Malacosoma disstria*) system, it has been shown that the scale of response to forest landscape structure was positively correlated with body size for four dipteran parasitoids (Roland et al. 1997).

Movement patterns are often influenced by morphological traits (e.g., wing load, body size). For example, dispersal dimorphism in flying insect (e.g., larger wings) results in highly mobile individuals in a population (Harrison 1980). Movement can also be facilitated or constrained by the landscape heterogeneity (Baguette et al. 2007, Krewenka et al. 2011, Zeller et al. 2012) as it is the case for an alpine butterfly for which meadows facilitate dispersal in a forest landscape (Roland et al. 2000). Developing a robust understanding of dispersal capacity is challenging due to these complex interactions among dispersal behaviour, morphological traits and species-specific responses to landscape heterogeneity.

Understanding how dispersal capacity influences an ecological system at different trophic levels is essential to manage it. Forest ecosystems present the spatial complexity needed to study dispersal along with being of economic importance. Of particular significance to Canada's northern forests is the spruce budworm system (SBW; *Choristoneura fumiferana*). The SBW is a native defoliator of fir (*Abies balsamea*) and spruce trees (*Picea spp.*) whose periodic outbreaks (every ~30-40 years) kill thousands of hectares of coniferous forest (MacLean 1980). SBW associated parasitoids can influence SBW populations, with varying impact, during epidemic periods and in the later years of outbreak but also during SBW endemic periods (Royama 1984). Because parasitoids are influenced by forest structure, it has been hypothesised that altering forest structure could help reduce SBW impacts if done adequately (i.e., silvicultural hypothesis) (Miller et al. 1993). However, the mechanisms that lead to the spatial scale at which parasitoids response to forest landscape structure are unknown as is how this response varies among species with different dispersal-related morphological traits.

Quantifying dispersal for insect species such as those comprising the community of SBW parasitoids presents major challenges due to physical and technical limitations. Individual-based measures of dispersal are challenging with small-bodied flying insects because mark-recapture or direct tracking methods are difficult and time consuming, or even simply impossible (Hassal et al. 2011). Indirect methods (e.g., genetic analyses) (Broquet et al. 2009) can be used to estimate dispersal but cannot necessarily distinguish between the different movement generating mechanisms (e.g., dispersal-based traits or behaviour) (Lima et al. 1996) which would be important to know if you want to extrapolate the results to other systems. Another indirect method that can give us some indications of species dispersal capacity and how it interacts with landscape structure is the scale of response to landscape structure of biological processes such as parasitism (Roland et al. 1997). This method is based on building statistical models at multiple spatial scales and identifying the best scales to explain that biological process without *a priori* assumptions on the mechanisms involved (e.g., the dispersal capacity)(Roland et al. 1997, Roland et al. 2000, Burnett et al. 2003).

Inter- and intra-specific variations in morphological characteristics (i.e., traits) are known to be correlated with dispersal (Tscharntke et al. 2004). Dispersal is not dictated by a single trait, but by an array of related traits (Roff et al. 2001). In flying animals (e.g., insects), the specific trait wing load (i.e., body mass divided by wing area) represents a measure of the physiological costs associated with flying and hence can be used to infer dispersal ability (Danforth 1989). Parasitoid communities, such

as that associated with the SBW system, offer an excellent opportunity to examine the effects of inter- and intra-specific trait variations on dispersal ability because parasitoid communities consist of closely related species whose impact on host populations can be easily assessed through measures of parasitism.

In this chapter, parasitism rates at any location are used as an indication of how well a parasitoid species is thriving at this location. The variation in parasitism rates among sites is explained by a set of spatial variables at multiple spatial scales. Because I hypothesized that dispersal is the main mechanism responsible for the spatial perception of landscape by a given organism, the parasitism events are divided accordingly to species dispersal-related morphological traits (i.e., wing load and body size). In chapter 1, I examined the parasitoid community as a whole to obtain an overall, community-level spatial scale of parasitism. In this chapter, I refined these results and individually examined variation among the five most common species of this community. The morphological-based results from this chapter show that the mechanisms driving the parasitoid spatial scale of response to landscape structure are related to dispersal capacities. These results and the approach used could be applicable to other parasitoid-host systems.

## **Methods**

### Study area

SBW larvae and pupae were collected in the summer of 2014 in the Côte-Nord region of Quebec (Figure 2.1). Forests in this region are dominated by coniferous stands with spruce moss forests in the north and balsam fir-white birch forests in the south (De Grandpré et al. 2008). 18 sites were visited across the region within the area currently undergoing an outbreak (MFFP 2015) (Figure 2.1). Each site was sampled three times throughout the summer at different SBW developmental stages (i.e., L3-L4, L5-L6, and pupae) to capture the known temporal variation in parasitoid species attacking the SBW (Bennett 2008). I aimed to collect 500 individuals per site per sampling period. Individuals were individually hand-picked from the various coniferous species present on site and at various heights within the canopy using telescopic cutter. Timing of sampling was determined using predictions made by the BioSim phenological model (Régnière et al. 2013). This software uses information on local degree days and up to date weather data to predict SBW development stage at a given location and time.

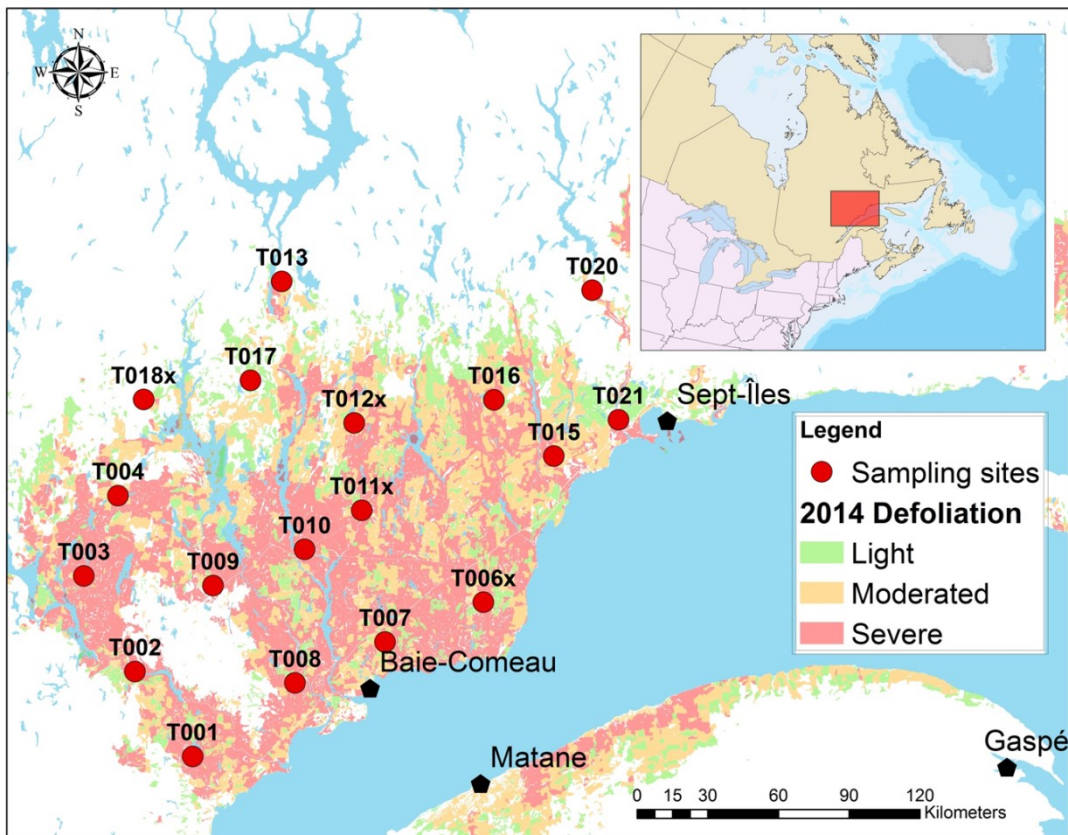


Figure 2.1: Sampling sites within the defoliation area in Côte-Nord region, Qc.

Collected larvae and pupae were reared individually in the laboratory on McMorran synthetic diet (McMorran 1965). Emerged parasitoids were identified to species and sexed using identification keys specific to SBW parasitoids (O'Hara 2005, Bennett 2008, Fernandez-Triana et al. 2010). Only the most common species will be used for this chapter.

### Morphological characteristics

Because sexual dimorphism and sex-related difference in dispersal can be observed in parasitoid wasp species (Ode et al. 1998), I examined males and females of each species separately. Morphological traits were then measured on 10 individuals per species per sex using a stereomicroscope connected through a camera to the Image Pro Plus 7.0 software (MediaCybernetics 2015). As I was unable to differentiate between the sexes in *S. fumiferanae* due to great morphological similarity, 20 grouped un-sexed specimens were used for analysis.

Six morphological traits were measured on all specimens: 1) fore wing area (one wing/individual, left or right depending on specimen condition); 2) hind wing area (one wing/individual, left or right); 3) left hind tibia length; 4) thorax length; 5) abdomen length; and 6) dry weight. Measurements were taken using the Image pro software. For weighing, each specimen was weighed after immersion in 75% ethanol for 20 minutes and allowed to fully air dry. These direct measurements were needed to calculate the wing load and the body size.

I hypothesize that two traits influence the spatial scale of response of parasitism rates: 1) body size, and 2) wing load. Overall body size was estimated using insect hind tibia length, which is frequently used with insects as a proxy for body size (Sagarra et al. 2001). The relation between tibia length and body size was verified in a linear regression by comparing the measured hind tibia length with a value summing thorax length with abdomen length for all specimens. Wing load was calculated by dividing the total body weight by the total wing area (the sum of one fore wing and hind wing duplicated). Wing load is a proxy for flight ability as the energy required for flight depends on the animal weight and the size of its wings (Berwaerts et al. 2002).

The main question of this chapter was to examine the effect of wing load on the spatial scale of respond to landscape structure. Therefore, parasitoid species/sexes wing load mean was compared using an ANOVA and a subsequent *post-hoc* Tukey's HSD. Categories with the same wing load were then merged together. Based on this grouping, parasitism event were divided in independent matrices of parasitism rates (sites x sampling periods) depending on the parasitoids. Dividing the parasitism events based on the wing load of the parasitoid involved allows building different models that should show different response to landscape structure and at varying spatial scales.

### Landscape metrics

I sought to relate landscape structure at different spatial scales to parasitism rates associated with different trait-based groups of parasitoids. Landscape structure was characterized using a set of landscape pattern metrics calculated using the software Fragstats (McGarigal et al. 1994). Discrete data on landscape composition and configuration was obtained through Landsat8 satellite imagery (USGS 2015) and summarized using 20 ground cover categories, at a 15m resolution, based on their spectral signature (see Chapter 1, supplementary material for details). These 20 cover types were grouped into three categories relevant to the spruce budworm and its parasitoids. The first category

is coniferous forests (i.e., balsam fir, spruce and mixed fir/spruce, without pine). This category is the most common in the study area and represents the main SBW host. Seven other ground cover types (i.e., mixed forest, open coniferous forest, deciduous forest, shrubs, meadows, low grass and high grass) are less common and offer different habitats with feeding sources for adult parasitoids (e.g. wildflowers nectar) or alternate/alternative hosts (Leius 1967, Cappuccino et al. 1998, Cappuccino et al. 1999). Together, these land cover types are referred as the mixed/open habitats. Although the drawbacks related to this category mentioned in the first chapter, I maintained this category because I wanted the explanatory variables to be consistent between chapters to permit comparison. The third category includes non-habitat cover types such as water, lakes, bare ground, and roads that have no biological value for parasitoids.

Landscape metrics were used to quantify landscape structure (i.e., composition and configuration). Landscape diversity was expressed with the Shannon's diversity index (SHDI) computed on the 20 cover types map as it would be meaningless to calculate a diversity index on only three cover types. Moreover, even if ground cover can be misclassified using 20 cover types, it nonetheless captured true variations in habitat diversity (i.e., even if we do not know for sure the identity of a patch, we know that it is different from its neighbours). All subsequent landscape metrics were computed using the mixed/open habitats. Forest composition, which was assumed to reflect parasitoid resource availability, was described using the proportion of mixed/open habitats. Forest configuration, which was thought to influence parasitoid movement, was described using the proximity index (i.e., a measure of the distance between patches of mixed/open habitat of the same type, weighted by the patch size), the mean radius of gyration (i.e., the mean patch extent) and the mean Euclidean nearest neighbor distance. For the forest configuration, the mixed/open habitat was divided into the seven ground cover types constituting it. This approach increases the number of patches in the landscape while capturing more efficiently the patches properties. Coniferous forests habitat was not considered directly for it was correlated with mixed/open habitats metrics and forest configuration metrics (Chapter 1). Non-forest habitats (e.g., water and bare ground) were also not considered because they don't have biological values for parasitoids and are also correlated to the other habitats. Non-forest habitats, as the non-favorable habitat for parasitoids, can have represent physical barriers to parasitoid movements and this will show through the configuration metrics aforementioned. All landscape metrics were computed at 15 scales (circular buffers of 100; 250; 500; 750; 1000; 1250;

1500; 1750; 2000; 2500; 3000; 4000; 5000; 7500; 10 000m radius) around each sampling site (Figure 2.1).

### SBW outbreak status

The SBW outbreak status is divided in two explanatory variables. The first variable consists in the outbreak age measured at multiple spatial scales surrounding each sampling site (same spatial scales as for the landscape metrics). Outbreak age was computed using a cumulative defoliation map assembled from eight annual defoliation maps beginning when the outbreak was first detected in the region (2007) to the year of the study (2014). Data are available on the Quebec governmental website (MFFP 2015) and maps were assembled in ArcGIS (ESRI 2016). The mean age of outbreak was weighted by the surface area of each defoliation patch.

The second variable in the SBW outbreak status is the local SBW density. SBW density for every site was estimated during the first sample collection. The SBW density is a measure of the number of larvae per new year bud on a branch. Ten 45 cm branches collected at mid-crown height using telescopic cutter were used at each site (Sanders 1980).

### Spatial correlation

To capture unmeasured spatial structure, distance-based Moran's eigenvector maps (dbMEM) functions were used. Those eigenvectors express spatial correlation at different spatial scales and can be implemented to a model as explanatory variables (Legendre et al. 2012). The matrix of distances used to compute the dbMEMs represents non-geographic distances based on least cost path distances between sites in a resistance surface in which topography and hydrography act as constraints to parasitoids' movement (Zeller et al. 2012). To construct the resistance map, each cell had a base value of 1 to which was added either the slope declination (i.e. the positive value of slope in degree) or a value of 5 if covered by water. Moreover, sites were connected to each other through a Delaunay's triangulation and thus avoiding connection between distant sites. MEM functions arbitrarily retained for the models were limited to those representing the broadest patterns (the first three) and the smallest patterns (the last three) to avoid excessively high number of explanatory variables in the models.



## Multivariate models

I hypothesized that species with a wing load associated with reduce dispersal (i.e., heavier wing load) should have parasitism rates most strongly correlated at relatively small spatial scales, whereas lighter wing load should be correlated with forest spatial structure at broader spatial scales. To verify this hypothesis, I built independent series of models (one for each of the wing load classes) at varying spatial scales. The models are constrained ordination (i.e., redundancy analysis; RDA; Legendre 2012) and the spatial scales are the same 15 as described in the landscape metrics section. For a given wing load class, the response variable was the corresponding matrix of parasitism rates (sites x sampling periods) and the explanatory variables were local and regional SBW outbreak status variables (i.e., SBW density and age of outbreak), forest structure (i.e., proportion of feeding habitats, SHDI, proximity index, mean radius of gyration, and mean Euclidean nearest neighbour) and a set of variables representing latent spatial structure (i.e., two groups of three MEMs each). Each model was submitted to a two-ways stepwise variable selection based on AIC to obtain the model explaining most variation with as few variables as possible by successively removing or adding variables until it reached the lowest AIC value (Legendre et al. 2012).

Finally, I determined the average spatial scale of response to forest landscape structure for each wing load class. To do so, the models were first ordered in rank from 15 (the best model) to 1 (the worst) accordingly to their respective Adj. R<sup>2</sup>. I then computed the mean scale of response for each series by weighting each scale by their respective rank and Adj. R<sup>2</sup>:

$$Scale\ of\ response = \frac{\sum Rank * Adj.R2 * Scale}{\sum Rank * Adj.R2}$$

Weighting using the rank is a way to enhance the importance of the best models and to reduce the effects linked to the number of models which can blur the results if the series does not show a strong unimodal curve through scales.

## Results

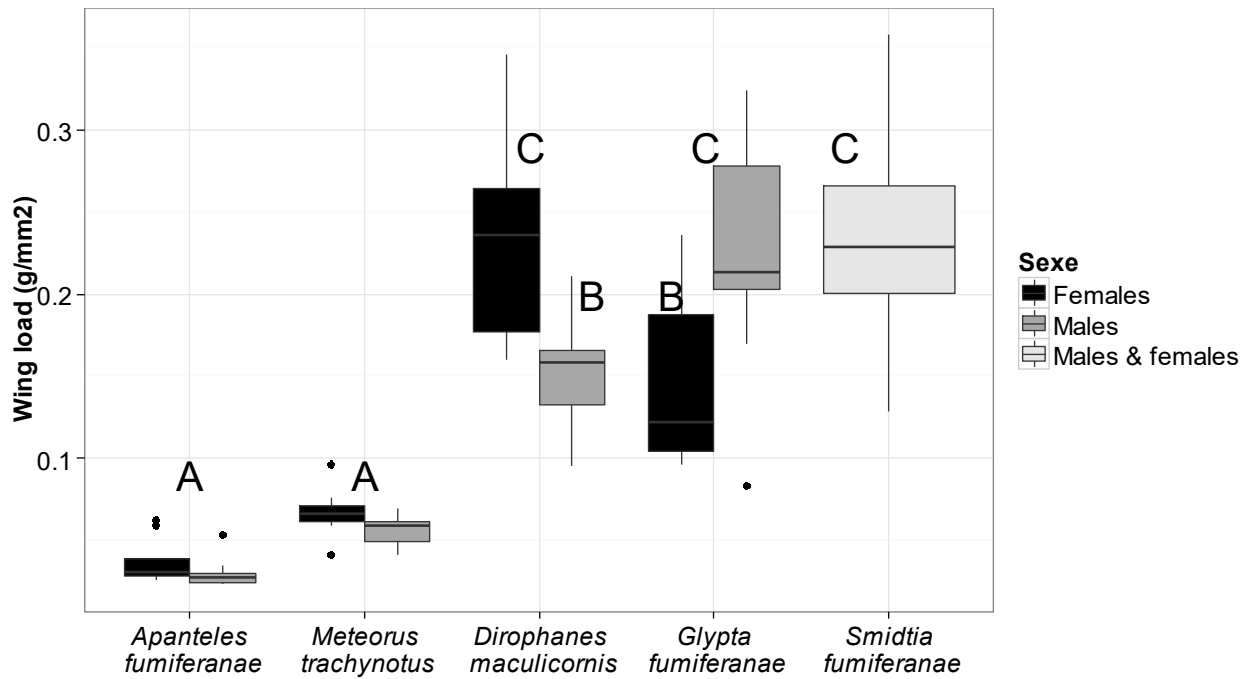
### Study area

3138 SBW parasitoids belonging to 42 species were reared in the laboratory from 20 000 individually collected SBW larvae. Although the SBW food web is extensive (Eveleigh et al. 2007), six species comprised 93.2% of all specimens: *Glypta fumiferanae* [Hymenoptera: Ichneumonidae], 33%; *Smidtia fumiferanae* [Diptera: Tachinidae], 23.8%; *Dirophanes maculicornis* [Hymenoptera: Ichneumonidae], 21.8%; *Apanteles fumiferanae* [Hymenoptera: Braconidae], 9.6%; *Itopectis conquisitor* [Hymenoptera: Ichneumonidae], 1.7% and *Meteorus trachynotus* [Hymenoptera: Braconidae], 1.5%. I therefore focused exclusively on these common species for this analysis.

### Morphological characteristics

#### *Wing load variation*

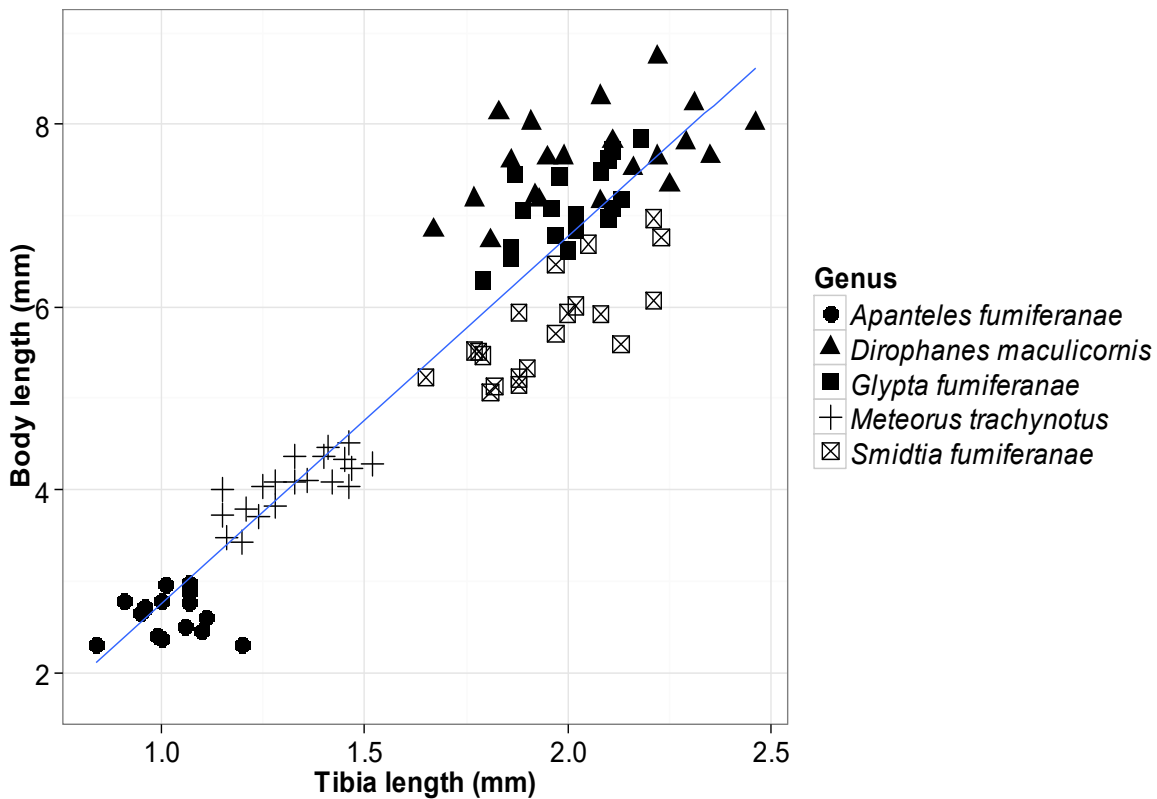
Three classes of wing load were identified in the reared parasitoids: heavy, medium, and light (Figure 2.2). The heavy wing load class included *S. fumiferanae* (male and female indistinctly), *G. fumiferanae* males and *D. maculicornis* females (mean  $\pm$  SD:  $0.231 \pm 0.06$  g/mm<sup>2</sup>). The medium wing load class included *G. fumiferanae* females and *D. maculicornis* males (mean  $\pm$  SD:  $0.148 \pm 0.04$  g/mm<sup>2</sup>). The light wing load class included *A. fumiferanae* and *M. trachynotus*, both males and females (mean  $\pm$  SD:  $0.048 \pm 0.02$  g/mm<sup>2</sup>). Within each class, all individuals were part of the same statistical population according to a Tukey HSD test. *Itopectis conquisitor* (mean  $\pm$  SD:  $0.091 \pm 0.02$  g/mm<sup>2</sup>) was not included in the analysis as it could not be reliably assigned to one of the three other wing load classes according to the Tukey HSD test. Because it only represented 1.7% of total parasitoids, it does not represent enough data to form a class on its own. It was therefore removed from the analysis.



**Figure 2.2:** Wing load grouping. Letters indicate final wing load grouping (excluding *I. conquisitor*) based on results from ANOVA and Tukey's HSD.

### Body size

Tibia length was used as a proxy for body size of SBW associated parasitoids. In examining all samples (n=117), it suggested that tibia length was highly correlated with body length (thorax and abdomen) (Pearson's  $r = 0.86$ ,  $F = 593.6$ ,  $df = 93$ ; Figure 2.3) indicating that tibia length was a reliable proxy for body size. I also found no significant difference between tibia lengths of *G. fumiferanae*, *D. maculicornis*, and *S. fumiferanae* (mean  $\pm$  SD:  $2.00 \pm 0.17$ mm). I also found no significant difference between tibia lengths of *A. fumiferanae* and *M. trachynotus* (mean  $\pm$  SD:  $1.18 \pm 0.19$ mm). I did however identify a significant difference in tibia length between the first class (*G. fumiferanae*, *D. maculicornis* and *S. fumiferanae*) and the second (*A. fumiferanae* and *M. trachynotus*) (Figure 2.3).



**Figure 2.3:** Relation between tibia length and body length (abdomen and thorax) per species.

Scale of response to landscape

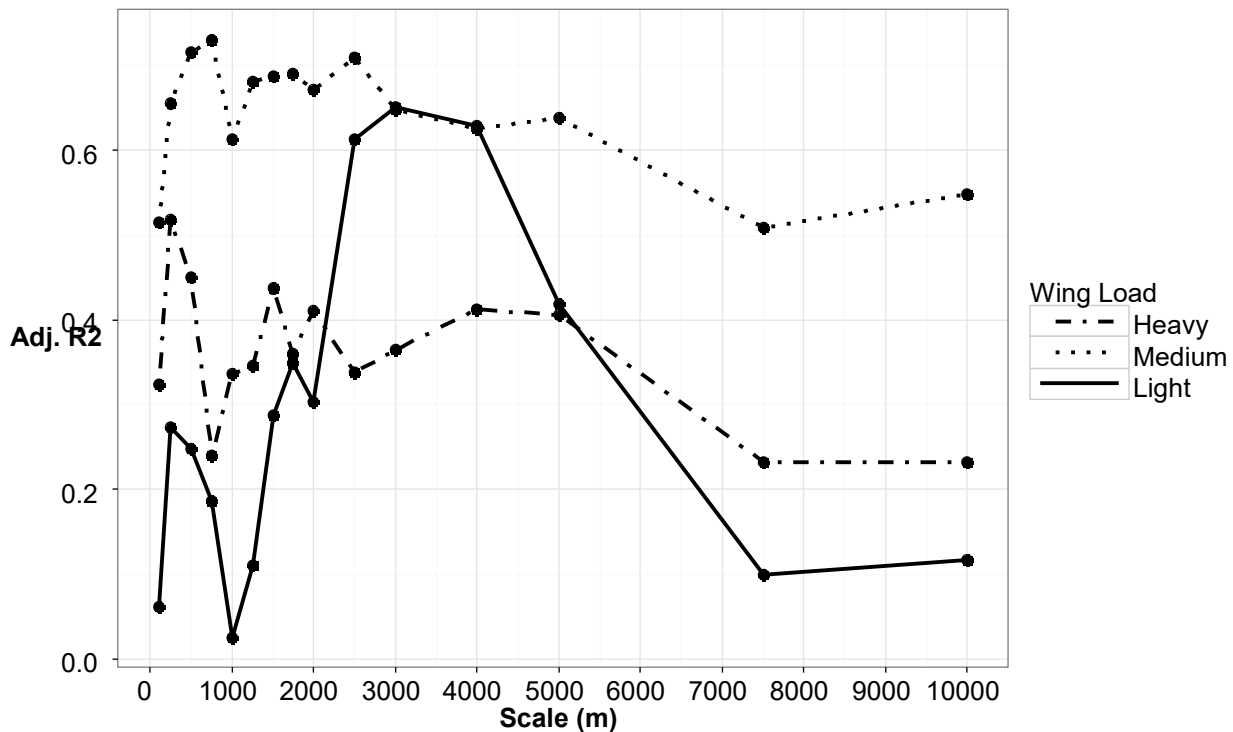
The proportion of variance explained, expressed as an Adj.  $R^2$ , of each model of parasitism rates varied with the scale of landscape structure considered and the wing load class. The heavy and medium wing load model series had similar patterns across all scales examined (Figure 2.4). The adjusted  $R^2$  of each RDA model was highest at small spatial scales between 250 – 2500 m. The heavy wing load class presented greater variations than the medium wing load class and both series had their Adj.  $R^2$  dropped at broader scales (Figure 2.4). The higher Adj.  $R^2$  values in the medium wing load class indicated a stronger response to landscape structure than in the heavy wing load class. Adj.  $R^2$  reached its peak in the medium wing load series at 1000m (Adj.  $R^2 = 0.73$ ) with an average spatial scale of response to landscape at 1871 m. The heavy wing load reached its peak at 250 (Adj.  $R^2 = 0.51$ ) with an average spatial scale of response at 1956 m. Unlike the two first wing load series, the light wing load series presented a strong peak between 2500 and 4000m (average of 2885 m) with an adjusted  $R^2$  peaking at a scale of 3000m (Adj.  $R^2 = 0.65$ ). The scales of response of the three different

wing load classes were similar to the scale identified using all species combined without regard for morphological differences (2000 – 2500 m; Chapter 1). However, models built for each wing load classes separately resulted in a greater explained portion of variation in parasitism rates (Table 2.1).

**Table 2.1: Scale of response to landscape in function of wing load characteristic**

	Wing load			Combined <sup>1</sup>
	Light	Medium	Heavy	
<b>Parasitoids</b>	<i>A. fumiferanae</i> <i>M. trachynotus</i>	<i>G. fumiferanae</i> ♀ <i>D. maculicornis</i> ♂	<i>S. fumiferanae</i> <i>G. fumiferanae</i> ♂ <i>D. maculicornis</i> ♀	(All)
<b>Peak scale</b>	2885	1871 m	1956 m	2000-2500 m
<b>Best model adj. R<sup>2</sup></b>	65%	73%	51%	46%

<sup>1</sup> (Chapter 1)



**Figure 2.4:** Series of models explaining parasitism rates in three wing load classes. Each line is composed of 15 models at different scales where adjusted R squares are used to express the proportion of variance in parasitism rates explained by landscape structure at those scales. Low adjusted R squares indicate scales at which landscape cannot explain parasitism and high adjusted R squares indicate scales at which measured landscape metrics can explain parasitism rates.

The retained scale-specific models for each wing load (Table 2.1) included similar predictor variables (Table 2.2). Landscape composition (SHDI and proportion of mixed/open habitats) and configuration (proximity index, patch gyration and Euclidean nearest neighbour (ENN)) were important in all wing load classes, as were the calculated large and small scale MEMs. The inclusion of these MEMs indicates that some spatially structured processes that were not specifically measured influenced parasitism rates such as latitudinal gradient for large scale MEMs or spatial autocorrelation for small scales MEMs. Indicators of SBW outbreak status however varied among wing load classes. SBW density was less important for parasitoids in the medium and heavy wing load classes and the age of outbreak was not relevant to parasitoids in the light wing load group.

**Table 2.2: For all models within the scale of response range (i.e., “best” models) per wing load class, proportion of times a variable is retained after a stepwise analysis. Values range from 0 (never retained) to 1 (always retained).**

Wing load	Number of models	SBW Density	Open/mixed habitats	Large MEM	Small MEM	Age of outbreak	SHDI	Proximity index	Gyration index	ENN
light	3	1	1	1	1	0	1	1	0.33	1
medium	7	0.43	0.71	1	1	1	1	0.29	1	0.86
heavy	7	0.14	0.57	1	1	1	0.43	1	1	1

## Discussion

In chapter 1 of this thesis, I showed that the spatial scale of response to landscape structure in the SBW parasitoid community ranged from 2000 to 2500m and that the variables at these scales explained 46% of parasitism rates. In this chapter, I separated this community in functional groups based on their wing load and divided this previous range in three ranges (i.e., 1871m; 1956m and 2885m) explaining respectively 73%, 51% and 65% of parasitism rates. Because those three trait-based groups capture more variation in parasitism rates, one can conclude that wing load is an important trait that is associated with the species scale of response to landscape and may indicate important trait-driven differences in parasitoid dispersal capacity among species within a single landscape.

### Landscape structure

Models series for medium and heavy wing load classes are similar in shape (i.e., higher proportion of variation explained in smaller scales with noise than lower proportion explained in broad scales) but also in the variables selected within each model (Figure 2.4). My results suggest that forest configuration is important to parasitism rates as either proximity index, gyration index or ENN were retained in every reduced model for all wing load classes. Forest configuration variables (i.e., proximity index, gyration index and ENN) were selected in greater proportion in the two groups with heavier wing load (Table 2.2). This greater sensitivity to spatial configuration could be due to smaller dispersal capacity in these classes which makes it more difficult for parasitoids to travel through the landscape and inhospitable patches.

The selection of forest composition variables, especially in the light wing load class, in the reduced models once again underlines the importance of spatial heterogeneity in parasitoid-host systems in both agricultural (Gagic et al. 2011, Krewenka et al. 2011, Zihua et al. 2012) and in forest habitats (Eveleigh et al. 2007, Charbonneau et al. 2012) as heterogeneity in the landscape offers a variety of habitat to sustain different biological needs. Landscape structure can also affect dispersal (Roland et al. 2000, Baguette et al. 2007, Cronin et al. 2014). Open vegetation such as meadows in the open/mixed habitats can facilitate parasitoid dispersal (as it does for another flying insect) (Roland et al. 2000).

### Scale of response to landscape

How broadly a parasitoid perceives its surroundings will determine if two patches should be considered functionally connected (Baguette et al. 2012). The range of perception is influenced by dispersal capacity (wing load) and body size (tibia length) and both characteristics are likely correlated (Holling 1992). Having the same body size for both heavy and medium wing load allowed me to control for variation in scale of response due to body size and to look at the influence of wing load alone. If both heavy and medium wing load groups have mostly the same scale of response (i.e. 1871 - 1956m), the class with greater mobility (i.e., medium wing load) is more strongly correlated (28% higher in average) with forest composition and configuration (Figure 2.4). For specimens in the medium wing load group, movement is likely less energetically costly (due to a lower wing load)

which makes it more likely for them to exploit the landscape thoroughly and to cross inhospitable areas such as water bodies and bare ground.

The light wing load class strongly differs from the other two as it does not share any common species (it is composed of the species *A. fumiferanae* and *M. trachynotus* of both sexes). These species are twice as small as the medium and heavy wing load groups and have 3 to 5 time lighter wing loadings. This is an interesting unexpected result as a smaller body was expected to lead to smaller foraging scale whereas smaller wing load should lead to broader foraging scale (Tscharrntke et al. 2004). My results indicate that wing load has a greater effect on the spatial scale of response than body size (Table 2.1). The reason for this result is likely that the most limiting factor in movement is the energetic cost required to travel and it is therefore less costly for parasitoids with light wing load to travel. Indeed, individuals labelled as “migrants” in flying insect populations of a same species tends to have lighter wing loading (Harrison 1980). If energetic cost is the limiting factor, the difference in body size would not be great enough to counterbalance costs associated to the flight. It is also possible that even though the body sizes of the three wing load classes were statistically different, the difference is not biologically meaningful. That is, the different body sizes should be considered similar with regards to its effect on the scale of response to landscape structure.

The results presented in this research do not support the importance of the body size for the spatial scale of response to landscape as it does in another research on forest pest parasitoids (Roland et al. 1997). This previous research was however done on Diptera only whereas the community of parasitoids in this thesis is mainly composed of Hymenoptera. This could suggest that the morphological characteristics in both orders do not influence dispersal in the same way.

## **Conclusion**

This chapter (along with the first) offer an answer to the fundamental question: If parasitoids are influenced by landscape structure, what spatial scale should be considered relevant? Knowing the scale at which parasitoids (through parasitism) respond to landscape can help to build more realistic models and deepen our understanding of the SBW system. The spatial scale of response can also be used to create integrated forest management plans that aim to favour parasitism and therefore reduce SBW impact on coniferous forests. My results help understanding fundamental questions of movement probability and patch connectivity in real large scale landscape (Cronin et al. 2005) by



giving and approximation of the spatial scales at which parasitoids can respond depending on functional traits.

Taking a functional trait-based approach to evaluate the landscape scale of response resulted in models that explained a greater portion of variance in parasitism than model based on the whole community. SBW-parasitoid species that differ in flight-related morphological traits of the SBW did not respond to landscape structure at the same scale. As hypothesized, a lighter wing load is correlated with a broader spatial response to landscape. Because I assumed that wing load was related to dispersal capacity, this suggests that wing load is an important morphological trait to estimate the scale of response to landscape and more appropriated than body size for flying insects.

The multiple spatial scales of response to landscape have implication in forest management. Management approaches that aim to increase the efficacy of natural enemy populations through manipulations of forest landscape structure (i.e., silvicultural hypothesis) may be unsuccessful if implemented at a single scale. Because the parasitoid community is diverse, and response to forest landscape structure at a diversity of scales, management approaches that aim for spatial and temporal complexity (Puettmann et al. 2009) may be more successful at facilitating natural biological control in the SBW system.

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## Conclusion

La question de l'échelle de perception est centrale en écologie du paysage. Pourtant, il est difficile d'identifier cette échelle puisqu'elle ne peut pas être mesurée directement sur le terrain. De plus, un même système peut être influencé à de multiples échelles spatiales selon les espèces qui le composent (Tscharntke et al. 2004). C'est le cas pour le système de la tordeuse des bourgeons de l'épinette où les dynamiques du défoliateur, de l'arbre hôte et des parasitoïdes ne sont pas structurées à la même échelle spatiale.

Pour ce mémoire, je me suis attardé à l'échelle de réponse de la communauté de parasitoïdes de la TBE. Les parasitoïdes jouent un rôle important dans la dynamique de la TBE et de ses épidémies (Miller 1963). Plusieurs informations sont toutefois manquantes pour arriver à bien comprendre les mécanismes qui relient les parasitoïdes à la structure de la forêt. Une de ces informations manquantes concerne l'échelle spatiale à laquelle les parasitoïdes vont percevoir le paysage et y répondent.

Ma première approche (Chapitre 1) fut de considérer la guildes de parasitoïdes dans son ensemble et d'examiner comment les taux de parasitisme infligés par celle-ci à différents stades de développement de la TBE variaient en fonction du paysage et d'autres variables liées à la TBE (densité et âge de l'épidémie). L'objectif était d'obtenir une vue globale de l'effet du paysage sur l'impact des parasitoïdes. Cette approche a permis d'identifier l'échelle de perception du paysage au niveau de la communauté de parasitoïdes. Les résultats suggèrent que cette communauté répond au paysage à une échelle spatiale oscillant couvrant une région circulaire de 2000 - 2500 mètres de rayon. Cette échelle spatiale est étonnamment grande pour des insectes qui mesurent entre 2 (*A. fumiferanae*) et 13 mm (*I. conquisitor*) de long. C'est probablement en raison de leur petite taille que plusieurs études sur les parasitoïdes de la TBE (et d'autres défoliateurs) présentées au chapitre 1 ont été menées à des échelles spatiales beaucoup plus petites. Pourtant, à la lumière de ce mémoire, ces échelles plus petites ne sont pas suffisantes pour intégrer toute l'information contenue dans la structure du paysage. À l'avenir, il faudrait envisager d'étendre la couverture spatiale des études sur les parasitoïdes de la TBE pour s'assurer que l'aire d'étude soit plus grande que l'échelle à laquelle les processus biologiques sont structurés.

La grandeur de l'échelle spatiale de réponse à la structure du paysage peut tout de même présenter un avantage pratique dans le domaine de l'aménagement forestier. En effet, il serait plus facile pour l'industrie forestière d'altérer la structure spatiale de la forêt à une grande échelle (i.e., larges zones de coupes) qu'il ne le serait à une échelle plus petite (i.e., petites zones de coupes). Présentement sur la Côte-Nord, 60% des coupes sont des agglomérations de coupes avec bordures (Bertrand et al. 2010). Ce système de coupes, en plus de permettre la régénération naturelle, se prête bien à l'aménagement forestier puisqu'il crée des parcelles de différents habitats (i.e., parcelles de forêt à différents stades de régénération). Cette propriété est essentielle si l'objectif est de maximiser l'hétérogénéité du paysage forestier pour favoriser des taux de parasitisme élevé chez la TBE (Chapitre 1 et 2) et diminuer les impacts des épidémies.

Le premier chapitre propose une idée de l'échelle spatiale à laquelle on devrait approcher le système de la TBE et de ses parasitoïdes en plus de donner des pistes d'actions pour la gestion durable des forêts. Ce chapitre ne donne toutefois pas d'indications sur les mécanismes responsables de cette échelle spatiale de réponse à la structure du paysage. Ma seconde approche fut donc de me pencher sur ces mécanismes que je suggère dans mon second chapitre être liés à la capacité de dispersion des espèces composant la communauté de parasitoïdes. Une plus grande capacité de dispersion (c.-à-d. une faible charge alaire) augmenterait l'échelle spatiale de réponse tandis qu'une faible capacité de dispersion (c.-à-d. une grande charge alaire) la diminuerait.

En utilisant les cinq espèces les plus communes de la communauté de parasitoïdes, j'ai séparé les taux de parasitisme selon trois classes de parasitoïdes; ceux avec une charge alaire légère, intermédiaire et lourde (de la plus grande à la plus petite capacité de dispersion). Cette méthode a permis d'obtenir l'échelle spatiale de réponse pour chacune des charges alaires (2885, 1871 et 1956 mètres respectivement). Ces échelles sont similaires à celle obtenue dans le chapitre 1 (2000 – 2500 m). Non seulement la classe avec la capacité de dispersion présumée la plus élevée (c.-à-d. la charge alaire légère) présente la plus grande échelle de réponse (2885m), mais les modèles dans les trois groupes sont plus efficace pour décrire les taux de parasitisme que l'était celui regroupant tous les parasitoïdes (65%, 73% et 51% versus 46%).

Ce chapitre a démontré qu'à l'intérieur d'un même système, on retrouve plusieurs échelles spatiales différentes selon les caractéristiques des organismes (c.-à-d. l'espèce, le sexe et la charge alaire). Cet ensemble d'échelles spatiales complexifie encore plus l'organisation du système de la tordeuse et,



ultimement, sa gestion. Ainsi, il n'existerait pas d'échelle unique structurant la communauté de parasitoïdes, mais plutôt un ensemble d'échelles spatiales. La charge alaire a été suggérée dans cette recherche comme étant responsable de l'échelle spatiale de réponse avec la prémisse qu'il s'agissait d'une bonne approximation de la capacité de dispersion. Les résultats semblent indiquer que c'est effectivement le cas. Toutefois, d'autres traits pourraient aussi jouer un rôle dans la manière dont les parasitoïdes se dispersent dans le paysage comme par exemple le comportement dispersion (est-ce une espèce qui a tendance à migrer?) ou l'espérance de vie sous forme adulte (de combien de temps dispose le parasitoïde pour se déplacer?). Ces traits sont autant de pistes à suivre pour approfondir notre compréhension de la relation qui lie les parasitoïdes à la structure du paysage forestier. L'ensemble de cette étude porte sur une seule saison en supposant qu'elle est représentative d'une épidémie. Le fait d'avoir un période de défoliation différente selon le site permet de collecter des communautés de parasitoïdes à différentes phases durant une épidémie. Toutefois, il serait intéressant de refaire cette dans le futur pour voir si les communautés de parasitoïdes correspondent selon l'âge de l'épidémie et si les résultats sont consistants d'une année à l'autre.

Les deux chapitres présentés dans ce mémoire ont des implications à différents niveaux. Le premier chapitre, en regardant la communauté de parasitoïdes dans son ensemble, présente des implications pratiques. En effet, il suggère une échelle spatiale à laquelle la forêt devrait être modifiée à travers les différentes pratiques d'exploitation forestière pour favoriser les parasitoïdes et peut-être ainsi diminuer les impacts des épidémies. Le second chapitre, en se penchant sur les traits morphologiques liés à la capacité de dispersion relève plus du domaine fondamental. Il suggère qu'il est possible de relier la capacité de dispersion des espèces à l'échelle spatiale de réponse au paysage.

Bien que ce mémoire apporte de nouvelles connaissances pour améliorer notre compréhension du système de la tordeuse des bourgeons de l'épinette, certaines pistes restent encore à explorer. Du côté des parasitoïdes, un volet important à investiguer serait la communauté d'hyperparasitoïdes qui s'attaque aux parasitoïdes primaires et qui peut affecter le pouvoir répressif de ceux-ci sur la TBE. Les hyperparasitoïdes sont eux aussi affectés par la structure de la forêt (Eveleigh et al. 2007) et il serait intéressant de vérifier si les observations faites sur les parasitoïdes primaires peuvent être en partie expliquées par leurs interactions avec les hyperparasitoïdes. L'étude d'un système multi-trophique composé d'espèces réagissant à différentes échelles spatiales présente un haut niveau de complexité

et il reste encore beaucoup de chose à apprendre pour bien comprendre les dynamiques du système de la tordeuse des bourgeons de l'épinette.

Un autre volet qui n'a pas été investigué à l'intérieur de ce mémoire est lié à la compétition entre les parasitoïdes pour l'hôte. En effet, seul le parasitisme effectif a pu être observé pour cette recherche ce qui ne permet pas d'évaluer l'importance de la compétition pour la ressource dans le système. Il est probable que certaines espèces de parasitoïdes, bien que présentes sur les sites, ne soit pas d'efficace compétiteur et qu'elles soient sous-représentées dans le jeu de données. Cette compétition a pu créer un biais dans les données en favorisant les espèces étant les meilleures compétitrices. Une façon de contourner ce problème serait d'utiliser des méthodes de *bar coding* qui permettent d'identifier toutes les espèces présentes dans l'hôte sans devoir attendre l'émergence d'un parasitoïdes.

Je crois que ce mémoire, sans donner une réponse complète à toutes les questions relatives aux parasitoïdes de la TBE, offre des pistes de réponse concernant le lien entre la structure de la forêt et l'impact de ceux-ci sur la TBE. Plus encore, il propose une méthode pour approcher la question de la réponse à la structure du paysage à différentes échelles spatiales et il souligne l'importance de cette échelle en écologie du paysage de manière générale.

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