UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

DYNAMIQUE RÉCENTE ET HOLOCÈNE DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE EN FORÊT BORÉALE

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"Dans un oeuf, y'a du blanc et du jaune. Eh bien plus on mélange, plus il n'y a que du jaune !"
Michel Colucci

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et faire un paragraphe d'une seule ligne

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RÉSUMÉ

La tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clemens)) (TBE) est le plus important défoliateur des forêts de l'est de l'Amérique du Nord. Dans un contexte de changements climatiques, la dynamique des perturbations naturelles, et notamment celle des insectes est modifiée, influençant la synchronicité phénologique entre l'insecte et son hôte, mais aussi, tout un essemble d'interactions tri-trophiques entre l'arbre hôte, l'insecte et ses ennemis naturels. En conséquence, la distribution spatiale de la TBE ainsi que la succeptibilité des espèces hôtes, telles que nous les connaissons, pourraient être amenées à changer dans le futur, en fonction de l'augmentation des températures. Afin de mesurer au mieux ce type de changements, il est important de développer de nouvelles méthodes pour étudier la dynamique de la TBE sur de plus vastes échelles temporelles et spatiales.

Dans la première partie de cette thèse, nous nous sommes concentrés sur la vaste échelle temporelle en combinant les macrocharbons et les macrofossiles végétaux avec un nouveau proxy - les écailles de lépidoptères - pour décrire l'écologie Holocène autours d'un lac boréal. Les écailles de lépidoptère se sont avérées être un indicateur plus robuste des épidémies d'insecte que les indicateurs traditionnels tels que les capsules céphaliques et les feces. Nous avons identifié 87 pics d'abondance significatifs au cours des 10 000 dernières années. Ces résultats indiquent que les épidémies de TBE étaient plus fréquentes que ce que suggèrent les études précédentes. Les taux d'accumulation des charbons de bois correspondent à l'historique établie pour les feux de forêt dans l'est du Canada : une fréquence de feux plus élevée au début et à la fin de l'Holocène qu'au milieu. Même si, à certaines occasions, les deux perturbations ont pu aller de pair, nos résultats démontrent plutôt une relation inverse entre la fréquence des feux et les épidémies d'insectes au cours de l'Holocène.

Dans la dernières partie de la thèse, nous avons reconstruit les patrons des épidémies du $20^{\text{ième}}$ siècle à l'échelle du paysage en utilisant des données dendrochronologiques. Pour cela, nous avons compilé une base de données de près de 4 000 arbres au travers d'une aire d'étude de 800 000 km^2. Une interpolation ainsi que des analyses de hotspots ont été effectuées pour déterminer les zones ayant subit des réductions de croissance liées aux épidémies mais aussi pour identifier les patrons spatiotemporels liés à l'activité de la TBE au cours du dernier siècle. Un modèle climatique a été utilisé afin d'estimer les anomalies de températures et de précipitations pour cette période. Nos résultats ont permis d'identifier trois épidémies de TBE avec des patrons spatiotemporels différents au niveau de la durée et de la sévérité des évenements. La première (1905-1930) a affecté près de 40% des arbres étudiés. Elle est le résultat de la synchronisation de plusieurs infestations locales et a atteint les peuplements nordiques en fin de période. La seconde était la plus longue (de 1935 à 1965), mais aussi la moins sévère avec seulement 30% d'arbres affectés. La troisième (1968-1988) aura été la plus courte, mais la plus virulente, affectant près de 50% des arbres étudiés, et la plus extensive pluisqu'elle a touché 70% de l'aire d'étude. Cette épidémie a été identifiée, pour la première fois, au nord de la limite nordique des attributions forestières, étaillant l'hypothèse d'un déplacement vers le nord de la zone de distribution de la TBE au cours du 20^{ième} siècle.

Globalement, cette recherche soutient le fait que les épidémies d'insectes sont un phénomène écologique dynamique et complexe et que la compréhension du cycle des perturbations naturelles à plusieurs échelles est un enjeu important en ce qui concerne la vulnérabilité des forêts dans un contexte de changement climatique.

Mots clés : Tordeuse des bourgeons de l'épinette ; paléoécologie ; écailles ; indicateur ; dynamique spatiale.

ABSTRACT

Spruce budworm (*Choristoneura fumiferana* (Clemens)) (SBW) is the most important defoliator cyclicaly affecting Eastern north america forests. In a context of climate change, insect disturbance dynamics is modified, influencing phenological synchrony between the insect and its host as well as a whole range of tri-trophic interactions among host trees, SBW, and their natural enemies. As a consequence, SBW distribution and host succeptibility, as we know it, could change under expected rise of temperature. In order to better assess these changes, it is important to develop methods to study SBW dynamics at large temporal and spatial scales.

In the first part of this thesis, we focused on long term termporal scales combining macrocharcoal and plant macrofossils with a new proxy— lepidopteran scales—to describe the Holocene ecology around a boreal lake. Lepidopteran scales turned out to be a more robust proxy of insect outbreaks than traditional proxies such as cephalic head capsules and feces. We identified 87 significant peaks in scales abundance over the last 10 000 years. These results indicates that SBW outbreaks were more frequent over the Holocene than suggested by previous studies. Charcoal accumulation rates match the established fire history in eastern Canada : a more fire-prone early and late Holocene and reduced fire frequency during the mid-Holocene. Although, on occasion, both fire and insect outbreaks were coeval, our results show a generally inverse relationship between fire frequency and insect outbreaks over the Holocene.

In the last part of this thesis, we have reconstructed SBW outbreaks patterns during the 20th century at the landscape scale using a dendroecological approach. An important data compilation with almost 4000 trees was conducted around a study area of 800 000 km^2. Interpolation and hot spot analyses were performed to determine the growth reduction related to insect outbreak periods, as well as to identify the spatio-temporal patterns of SBW activity for the last century. Climatic models were used to estimate the temperature and precipitation anomalies for this period. Our results identified three insect outbreaks with different spatio-temporal patterns regarding duration and severity. The first one (1905-1930), affected nearly 40% of the studied trees, first synchronized from local infestation and finally migrated to northern stands. The second outbreak was the longest (from 1935 to 1965), having the lowest level of severity with only 30% of trees affected by SBW activity. The third (1968-1988), was the shortest, the most severe affecting nearly 50% of trees and the more extensive affecting 70% of the study area. This last event was identified for the first time at the limit of the commercial forest revealing evidence of a northward shift on the distribution area of SBW during the 20th century.

Overall, this research support the fact that insect outbreaks are a complex and dynamic ecological phenomenon and that understanding natural disturbance cycles at multiples scales is a major concern facing forest vulnerability under climate change.

Keywords : Spruce budworm ; paleoecology ; scales ; proxy ; spatial dynamics.

INTRODUCTION GÉNÉRALE

LE CONTEXTE BORÉAL

La zone boréale compte parmi les plus grands ensembles de végétation à la surface du globe. Sa superficie s'étend sur près de 1.9 milliards d'hectares à travers le Canada, les États-Unis, la Norvège, la Suède, la Russie et la Chine (Fig 1). Cet écosystème circumpolaire recouvre 14% de la surface terrestre et 33% de ses superficies boisées, mais il renferme également un réseau hydrographique composé de millions de lacs et de rivières. Au Canada, près de 350 millions d'hectares sont occupés par des zones forestières et les trois quarts de ce territoire se situe dans la zone boréale. Ces forêts sont caractérisées par un climat froid et sec en hiver et plutôt frais et humide en été. La végétation est composée d'une vingtaine d'espèces d'arbres, essentiellement des conifères tel que l'épinette, le sapin ou le mélèze, mais aussi de quelques espèces de feuillus à larges feuilles caduques telles que le peuplier ou le bouleau. L'écosystème boréal renferme également une grande diversité d'espèces d'oiseaux, une centaine d'espèces de mammifères et près de 130 espèces de poissons. On estime également à près de 32 000 le nombre d'espèces d'insectes polinisateurs et décomposeurs, bien qu'il s'agisse des organismes les moins bien connus de la forêt boréale.

Un écosystème rentable...

171 municipalités canadiennes basent au moins la moitié de leur économie sur le secteur forestier, 80% des communautés autochtones y habitent et 90% du territoire forestier canadien est géré par le secteur public (Ressources Naturelles Canada, 2016). La forêt boréale représente

Figure 1: La zone boréale (Astrup et al., 2018).

donc un enjeu très important pour les habitants. En effet, le travail de plus de 200 000 personnes dépend directement de l'industrie forestière. Cette dernière a généré 22.1 milliards de dollars en 2015, plaçant ainsi le Canada à la première place des pays exportateurs de bois d'œuvre résineux et de pâtes et papiers au monde (Ressources Naturelles Canada, 2016). La forêt boréale fournit, en plus des ressources ligneuses, de nombreuses autres ressources indispensables telles que l'eau, la nourriture, l'électricité, mais aussi, de nombreux paysages qui constituent un attrait récréotouristique majeur pour le Canada.

... à forte valeure écologique

La forêt boréale constitue également un des plus gros puit de carbone du monde (Tarnocai et al., 2009; Kurz et al., 2013). Elle filtre plus de 60% de l'eau douce (Schindler et Lee, 2010) et participe à la régulation du climat à l'échelle régionale comme à l'échelle mondiale (Schindler et Lee, 2010). La valeur non marchande de ces services écosystémiques est évaluée à 93.2 milliards de dollards soit 2.5 fois la valeur nette du capital qui en est extrait (industrie forestière, mines…) (Anielski et Wilson, 2009).

La dynamique de cet écosystème est assurée par un ensemble de perturbations naturelles telles que les feux de forêt, les chablis ou encore les insectes et maladies des plantes qui permettent l'existence d'une mosaïque forestière constituée de peuplements d'âges et de compositions variées (Gauthier et al., 2001).

LES PERTURBATIONS NATURELLES

LES FEUX DE FORÊT, PRINCIPALE PERTURBATION BORÉALE

Les premières évidences de feux de forêts ont été identifiées dans les enregistrements de fossiles de charbons et remontent à 420 Ma, peu après l'avènement des premières plantes vasculaires (Glasspool et al., 2004; Pausas et Keeley, 2009). Depuis leur apparition, les feux de forêts jouent un rôle très important dans les processus liés à la composition et la distribution des écosystèmes (Uys et al., 2004; Bond et Keeley, 2005). Ils exercent notamment une pression sur ces derniers en réduisant leur biomasse (Bond et Keeley, 2005). Cette pression est considérée, par les études en macroévolution, comme génératrice de biodiversité favorisant des mécanismes d'adaptation particuliers (Pausas, 2015). De nombreuses espèces ont développé des traits adaptatifs tels qu'une écorce plus épaisse, des graines qui germent au contact d'un choc thermique ou de la présence de fumée, ou encore des cônes sérotineux (Pausas et Keeley, 2009; Keeley et al., 2011; Midgley et Bond, 2011; Hernández-Serrano et al., 2013). De plus, les feux de forêt ont également une influence sur les facteurs abiotiques de l'écosystème tels que la chimie de l'atmosphère (Belcher et al., 2013), la streructure du sol ou l'érosion des roches (Shakesby et Doerr, 2006; Doerr et Shakesby, 2013).

Principales caractéristiques des feux de forêt

La source d'un feu de forêt peut être naturelle ou anthropique. Les feux sont allumés de manière naturelle par différents facteurs tels que la combustion spontanée, l'activité volcanique, la chute de roches ou de météorites, ou encore, et surtout, par la foudre (Scott, 2000, 2010). On estime à 1.4 milliard le nombre d'éclairs qui frappent la terre chaque année, soit un taux de 44±5 éclairs par seconde (Christian et al., 2003). Huit milliards de tonnes de végétation à l'échelle mondiale sont brûlées chaque année par des feux d'origine naturelle (Scott, 2001). En plus des facteurs environnementaux, la biomasse brûlée est influencée, depuis la révolution agricole du néolithique, par des facteurs anthropiques (Zong et al., 2007). Le feu a notamment été utilisé par les hommes durant la première partie de l'Holocène pour défricher le territoire et permettre l'agriculture et le pâturage (Marlon et al., 2013). Plus récemment, un certain nombre de pratiques affectent le régime des feux à l'échelle planétaire, tel que les politiques d'extinction ou de prévention des incendies, l'exploitation forestière, la déforestation ou encore les changements dans l'aménagement du territoire (Pausas, 2004; Allen et al., 2002; Mouillot et Field, 2005). L'urbanisation croissante, par exemple, entraîne une augmentation du risque d'allumage des feux par l'Homme. Selon Pausas et Keeley (2009), au cours du 20$^{\text{ième}}$ siècle, on est passé d'un régime de feux caractérisé par une fréquence plus élevée mais des intensités et des surfaces brûlées plus petites, à un régime où les feux sont moins fréquents mais peuvent survenir sur de plus grandes surfaces. Ce changement de régime est influencé par l'action synchrone des facteurs anthropiques, qui favorisent une augmentation de la quantité de combustible et des conditions naturelles favorables telles qu'une année plus sèche ou des vents particulièrement forts (Keeley et al., 1999).

On distingue trois types de feux : les feux souterrains, les feux de surfaces et les feux de couronnes (Scott, 2001). Les feux souterrains, qui brûlent les horizons organiques du sol et produisent beaucoup de charbons, du fait de la température moins élevée et de la limitation en oxygène, constituent une importante source de fossiles (Scott, 1989). Il s'agit également des feux qui ont le plus d'impacts sur les sols au niveau des populations microbiennes, du pH, de la perméabilité, etc. (Doerr et Shakesby, 2013). Les feux de sols sont souvent allumés par des feux de surfaces. Ces derniers sont les feux les plus fréquents, ils brûlent la litière, les souches, les résidus de coupes, la végétation arbustive et la régénération (Albini, 1992). Enfin, les feux de couronnes sont les feux qui correspondent à l'image que l'on se fait généralement d'un feu de forêt, mais sont relativement rare en forêt tempéré (cycle de feu >100ans). Ils brûlent principalement la canopée, ce qui leur permet d'atteindre de très hautes températures ainsi qu'une grande vitesse de propagation. Ils sont plus fréquents dans les forêts boréales et tempérées et sont exclusivement allumés par des feux de surfaces (Albini, 1992).

Différentes méthodes pour reconstituer l'histoire des feux

De nombreuses méthodes existent afin de reconstruire la fréquence, l'intensité ou la distribution des feux du passé. Chacune de ces méthodes présente une résolution spatiale ou temporelle différente et donc, des avantages et des inconvénients en fonction de l'objectif de l'étude. Parmi ces méthodes, la dendrochronologie permet de dater les cicatrices de feu à l'aide des cernes de croissances. Cette méthode présente plusieurs avantages. Elle est relativement rapide, permet une résolution temporelle très fine, à l'année, voir à la saison (Baisan et Swetnam, 1990; Swetnam et al., 1999) et permet, grâce à l'interdatation, de reconstituer l'histoire des feux de forêt à l'échelle régionale ou suprarégionale (Swetnam et al., 1999). Cependant, cette méthode présente plusieurs limites. Par exemple, une cicatrice peut, dans certains cas, abimer ou détruire une cicatrice précédente (Fall, 1998; Swetnam et al., 1999; Conedera et al., 2009). De plus, cette méthode est limitée par l'âge des échantillons et aux individus étudiés qui ont survécu au feu. Ainsi, un feu qui aura détruit tout le peuplement, ne sera identifiable que par l'âge de la nouvelle cohorte et l'enregistrement des feux précédents sera perdu (Niklasson et Granström, 2000; Van Horne et Fulé, 2006; Conedera et al., 2009).

La paléoécologie, quant à elle, permet de remonter plus loin dans le temps en utilisant les charbons fossiles enfouis dans les sols, les lacs ou les tourbières. Les charbons sont des composés inorganiques résultant de la combustion incomplète de matériel végétal en condition anoxique à une température comprise entre 350 et 800°C (Braadbaart et Poole, 2008; Scott et Damblon, 2010). Les charbons, ainsi formés, sont résistants à l'oxydation et à l'activité microbienne et sont persistants dans les sédiments lacustres depuis au minimum la fin du Quaternaire (Herring, 1985). Les charbons fossiles présentent également l'avantage de conserver la structure anatomique du matériel brûlé. Bien que de nombreuses études aient été réalisées dans les lacs et tourbières au travers du Québec (Blarquez et al., 2015; Girardin et al., 2013a), de nombreuses questions restent en suspens notamment en ce qui concerne la variation spatiotemporelle des régimes de feux et ses relations avec la composition végétale et les autres perturbations.

LES ÉPIDÉMIES D'INSECTES ET MALADIES DES PLANTES

Tout comme le feu, les insectes contribuent à la régénération de la mosaïque forestière, mais de manière sélective, en visant par exemple des arbres âgés et vulnérables. Les maladies des arbres contribuent, quant à elles, au cycle des éléments nutritifs dans les forêts et peuvent favoriser la biodiversité en créant des habitats. Cependant, à court terme, les épidémies d'insectes et les maladies des plantes peuvent endommager de grandes surfaces forestières et causer un impact économique significatif. On distingue les insectes et les pathogènes indigènes, dont la présence est le résultat d'un processus naturel sans intervention humaine, des exotiques qui ont été introduits récemment et qui peuvent devenir envahissants en raison de leur présence dans un écosystème dépourvu d'agents limitant leur expansion (prédateurs, parasites, maladies...). À titre d'exemple, la graphiose, mieux connue sous le nom de "maladie hollandaise de l'orme", introduite au Canada en 1940 environ, a décimé les populations d'orme d'Amérique (*Ulmus americana* (Linné)), l'une des essences les plus fréquemment plantées en Amérique du Nord. Parmis les insectes forestiers nuisibles, on compte les xylophages tel que le dendrochtone du pin ponderosa (*Dendroctonus ponderosae* (Hopkins)), qui fore des galeries dans l'écorce de son hôte et y introduit un champignon symbiotique fatal (Fig 2). Ce coléoptère présente

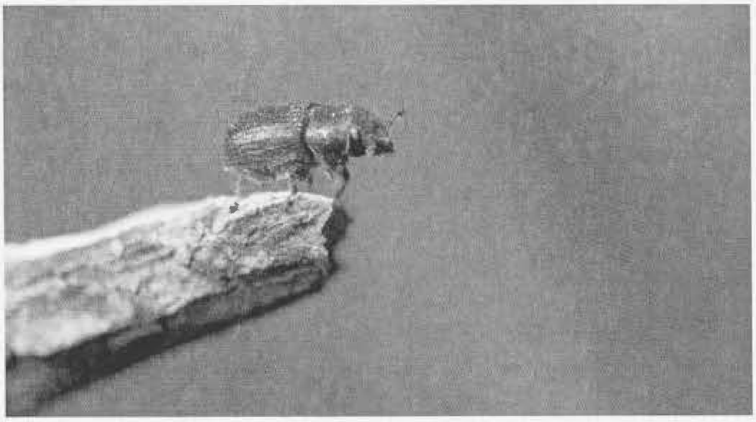

Figure 2: Le dendrochtone du pin ponderosa.

une dynamique de population épidémique, dont la dernière infestation, qui a commencé dans les années 1990 en Colombie-Britannique a causé la mort de près de 50% des pins tordus latifoliés (*Pinus contorta* var. *latifolia* (Dougl. Engelm.)) à valeur commerciale. Parmi les grandes familles d'insectes forestiers, on distingue également les défoliateurs, majoritairement composés de lépidoptères tels que la livrée des forêts (*Malacosoma disstria* (Hübner)) ou l'arpenteuse de la pruche (*Lambdina fiscellaria* (Guénée)). Cependant, la championne toutes catégories des insectes présentant la plus grande distribution et les plus grandes surfaces affectées en Amérique du Nord est sans nul doute la tordeuse des bourgeons de l'épinette (TBE) (*Choristoneura fumiferana* (Clemens)) (Fig 3).

LE CAS PARTICULIER DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE

La TBE est un lépidoptère défoliateur indigène des forêts conifériennes du Canada et du nord-est des États-Unis. Ses hôtes principaux sont le sapin baumier (*Abies balsamea* (L.) Mill.) et l'épinette blanche (*Picea glauca* (Moench) Voss) ainsi ,que dans une moindre mesure, l'épinette rouge (*Picea rubens* Sarg.) et l'épinette noire (*Picea mariana* (Mill.) BSP). Le cycle univoltin de ce papillon de nuit comprend un stade oeuf, une diapause, six stades larvaires, une pupaison ainsi qu'un stade adulte. Ce dernier étant relativement court (deux semaines),

Figure 3: La tordeuse des bourgeons de l'épinette.

l'insecte va passer la totalité de son temps à chercher un hôte pour pondre à nouveau. C'est aux $5^{\text{ième}}$ et $6^{\text{ième}}$ stade larvaire que l'insecte a le plus d'impact sur son hôte. Ainsi, le sapin baumier meurt après trois ou quatre années de défoliation sévère consécutives (MacLean, 1984; Bergeron et al., 1995) alors que les hôtes secondaires subissent des mortalités de têtes et de branches ainsi qu'une réduction de croissance allant jusqu'à 75% (MacLean, 1984; Nealis et Régnière, 2004b).

Dynamique de population

Les facteurs qui influencent le déclenchement d'une épidémie à l'échelle suprarégionale, ou la synchronisation des épidémies à l'échelle locale sont nombreux, et encore relativement méconnus. Il existe cependant deux théories qui sont à la base de notre connaissance actuelle de la dynamique de population de la TBE. La théorie du double équilibre (Fig 4) est d'abord développée en 1963 à partir des données du projet Green River (Morris, 1963). Il s'agit d'un modèle densité-dépendant selon lequel les populations de TBE seraient contrôlées par les ennemis naturels. Dans un contexte de nourriture abondante et un climat favorable, les populations de TBE augmenteraient de plus en plus, échappant au processus de contrôle entretenu par la prédation et le parasitisme. Les populations entrent alors dans une phase

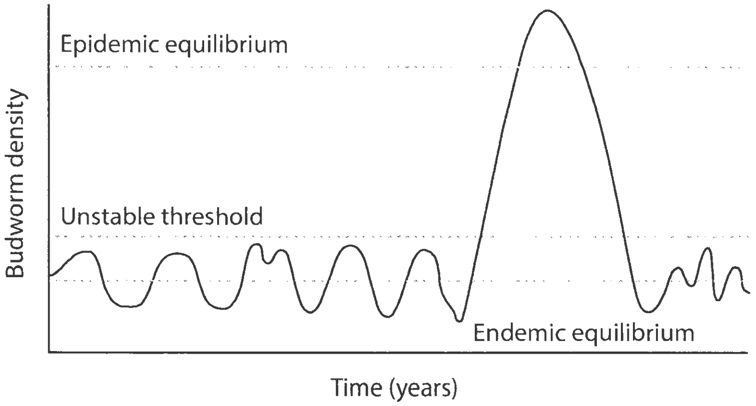

Figure 4: Théorie du double équilibre.

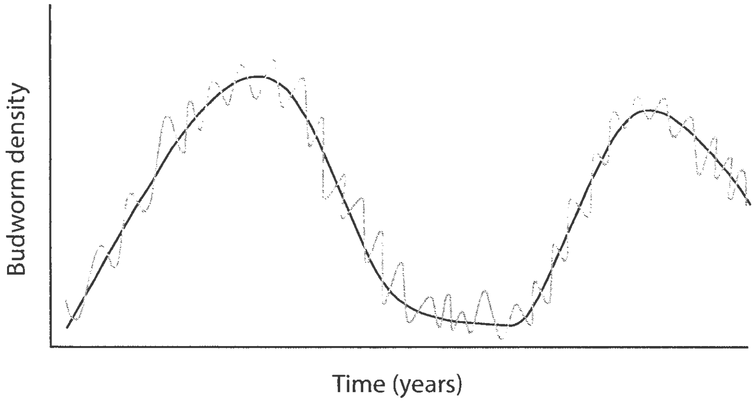

Figure 5: Théorie du mouvement oscillatoire.

épidémique. Finalement, le manque de nourriture fait chuter les populations et les ramènent à un niveau endémique. En 1984, Royama réinterprète les données du projet Green River et propose la théorie des mouvements oscillatoires (Royama 1984) (Fig 5). La densité de populations de TBE suivrait un cycle d'environ 35 ans généré par les facteurs de régulation intrinsèques (densité-dépendants) tels que les parasites, les maladies, ainsi qu'un cinquième agent représentant un complexe de causes inconnues. Un certain nombre de fluctuations secondaires sont enregistrées et reliées à la prédation, le manque de nourriture, le climat ou encore la mort des jeunes larves au printemps et à l'automne. Ainsi, une survie des larves de plus en plus grande, alimentée par un facteur de synchronisation tel que la migration des papillons, serait le moteur de l'oscillation épidémique.

Plus recemment les travaux de Nealis et Régnière (2004a) ont pu démontrer que la fécondité des larves était inversement proportionnelle au taux de défoliation et que les plus gros taux de fécondité étaientt enregistrés au début et à la fin des périodes épidémiques. Les auteurs affirment donc que la dynamique des populations en période épidémique est plutôt liée à la survie des oeufs et des premiers stades larvaires. En effet, la limitation des ressources engendrée par une importante densité d'individus serait à l'origine de périodes de fortes mortalités des jeunes larves ce qui causerait des périodes creuses et des reprises à l'intérieur d'une même épidémie. La population d'insectes retrouverait un niveau endémique lorsque le manque de ressources la ferait chuter suffisament pour que les ennemis naturels puissent la contôler à nouveau (Régnière et Nealis, 2007, 2008).

Pour le moment, la plupart des données disponibles concernant la dynamique de l'insecte proviennent de sapinières ou de forêts mélangées au sud du Québec (Blais, 1965, 1981; Morin et Laprise, 1990; Morin et al., 1993; Krause, 1997; Jardon, 2001; Boulanger et Arseneault, 2004; Boulanger et al., 2012), au Nouveau Brunswick (Morris, 1963; Royama, 1984), en Ontario (Blais, 1954) ou au Maine (Fraver et al., 2007). Cependant, relativement peu d'études s'intéressent à la dynamique des épidémies de TBE dans la zone boréale.

On sait cependant que la TBE est présente au Québec jusqu'au 53$^{\text{ième}}$ parallèle (Levasseur, 2000) et que sa distribution correspondrait à celle du sapin baumier (Harvey, 1985). Elle est présente jusque dans l'Ouest canadien à des latitudes bien supérieures à celles de la distribution du sapin baumier, le long de la rivière McKenzie notamment. Au Québec, le domaine de la pessière à mousses est moins affecté que les sapinières plus au sud (Simard et al., 2011; Tremblay et al., 2011; Navarro, 2013). On y enregistre cependant plusieurs épidémies présentant des dynamiques et des impacts relativement différents (Navarro, 2013).

Le climat dans ce domaine constitue une première contrainte pour l'insecte. En effet, les saisons estivales y sont trop courtes et trop froides pour permettre à l'insecte de compléter son cycle de vie. On remarque ainsi que l'impact et la durée des épidémies diminuent avec la latitude (Gray, 2008). De plus, les peuplements de la pessière à mousses sont majoritairement dominés par l'épinette noire qui n'est pas considérée comme un hôte privilégié de la TBE. En effet, la phénologie de l'insecte ne correspond pas avec celle de son hôte. On note ainsi un décalage de 14 jours entre l'émergence des jeunes larves et le débourrement de l'épinette noire, ce qui favorise la mortalité chez les larves de stade 2 par manque de nourriture (Nealis et Régnière, 2004b). Cependant, l'épinette noire reste un hôte important pour la tordeuse sur le plan nutritif et la dynamique de la TBE dans la pessière à mousses pourrait changer considérablement dans les siècles à venir en fonction des changements climatiques (Pureswaran et al., 2015).

La TBE dans un contexte de changements climatiques

L'écosystème boréal est un des biomes pour lequel les changements climatiques les plus sévères sont prévus (Ruckstuhl et al., 2008). La contribution du premier groupe de travail au cinquième rapport d'évaluation du groupe d'experts intergouvernemental sur l'évolution du climat (IPCC) prévoit une augmentation de température de surface moyenne annuelle de 1 à 4°C ainsi qu'une augmentation des précipitations annuelles de 0 à 20% d'ici la fin du siècle au Québec (IPCC, 2013). Il est probable que ces changements affectent la composition en espèces des forêts boréales ainsi que la répartition géographique des espèces et leur rythme de croissance (Ressources Naturelles Canada, 2016).

Au sein des différents organismes vivants, les insectes comptent parmi les catégories les plus susceptibles aux changements climatiques. En effet, le climat joue un rôle extrêmement important quant à leur développement, leur reproduction ou leur survie (Bale et al., 2002). De plus, en raison de la courte durée de leur cycle vital ainsi que de leur stratégie de reproduction extensive, les insectes sont sujets à des modifications rapides, en terme de phénologie, de

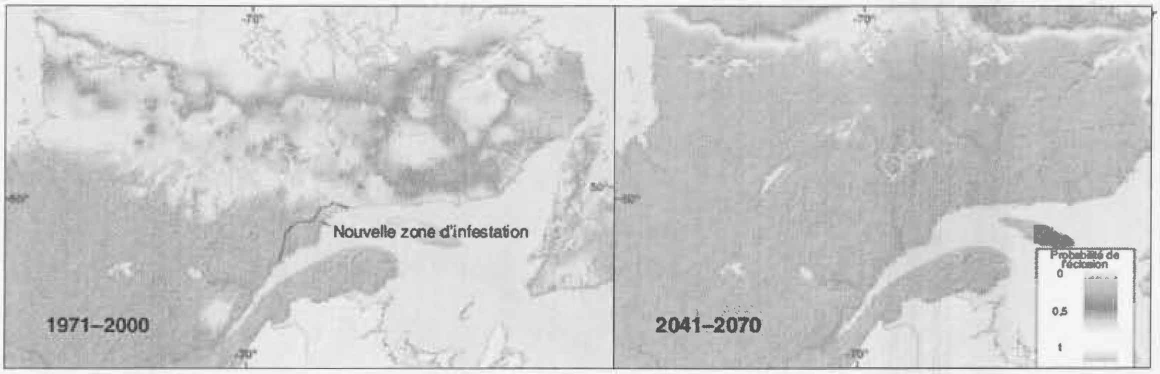

Figure 6: Probabilité de l'éclosion des œufs de la tordeuse des bourgeons de l'épinette avant le début de l'hiver au Québec (Canada), dans les conditions climatiques actuelles et celles prédites (Régnière, 2009).

sélection d'habitats, d'expansion ou de contraction de distribution latitudinale ou altitudinale. Ainsi, selon Menéndez (2007), la hausse de température enregistrée au 20$^{\text{ième}}$ siècle est responsable, chez les insectes, d'un passage plus rapide des stades larvaires, d'une entrée précoce au stade adulte ainsi que d'un allongement de la durée de vol et donc une emprise spatiale plus grande.

En ce qui concerne la TBE, une augmentation de température dans sa zone de confort pourrait avoir un effet sur la survie des populations. Un été plus chaud peut retarder la diapause et donc diminuer les réserves des larves qui ne se nourrissent pas avant l'hibernation et meurent à ce stade (Régnière et al., 2012) (Fig 6). De plus, un printemps hâtif oblige les larves à émerger plus tôt par rapport au débourrement de l'hôte ce qui les oblige à se nourrir sur de vieilles aiguilles, moins nutritives (Régnière et Nealis, 2008), ou à se nourrir jusqu'à la lignification des jeunes pousses, ce qui augmente la mortalité et réduit la fécondité (Lawrence et al., 1997).

Dans la zone nordiques, à la limite de la distribution de l'insecte, on peut s'attendre à ce qu'une plus grande partie de la population puisse compléter son cycle vital, augmenter leur taux de croissance ainsi que leur taux de reproduction du fait des températures moyennes moins froides en été. Les températures plus chaudes en hiver amèneraient quand à elles une meilleurs survie des larves en hibernation (Ayres et Lombardero, 2000). On assisterait ainsi à un déplacement vers le nord de la zone de confort de la TBE (Régnière, 2009; Régnière et al., 2012), ainsi qu'à un allongement de la durée et de la sévérité des épidémies (Gray, 2008). Ce déplacement vers le nord des populations de TBE pose le problème de l'adaptation phénologique entre l'insecte et son hôte. En effet, il a été démontré que l'épinette noire peut avancer sa phénologie de 11 jours en fonction d'un réchauffement de 5°C au sol et de 2°C dans l'air (Bronson et al., 2009). Ainsi, un débourrement hâtif des bourgeons de l'épinette noire pourrait constituer une source plus abondante de nourriture pour la TBE, une compétition moins importante pour les larves qui émergent plus tard et donc une hausse des populations.

On sait par ailleurs que ces changements de phénologie sont plus prononcés dans les latitudes élevées, du fait d'une augmentation plus rapide des températures (Parmesan, 2007) et que la durée de la diapause chez la TBE bénéficie d'une certaine plasticité phénotypique qui peut permettre à l'insecte de s'adapter rapidement aux changements phénologiques de son hôte (Volney et al., 1983). La synchronisation phénologique entre l'insecte et l'épinette noire accompagnée d'une hausse des températures permettrait à la TBE de modifier sa distribution.

De plus, les changements climatiques peuvent avoir un effet sur les niveaux trophiques supérieurs tels que les parasitoïdes ou les prédateurs de l'insecte. On sait par exemple qu'il existe un retard de prédation/parasitisme lié à la plus grande variabilité de la distribution des populations d'insectes induite par l'augmentation de la variabilité climatique (Stireman et al., 2005). La TBE pourrait ainsi se disperser plus vite que ses parasitoïdes dans de nouveaux habitats. De plus, les multivoltins (les insectes qui ont un cycle vital de plusieurs années) doivent changer d'hôte à la fin de l'été et à l'automne quand la TBE est au stade adulte ou en hibernation, ce qui réduit considérablement leur capacité d'adaptation en cas de changement de distribution de la zone de confort de l'insecte (Maltais et al., 1989).

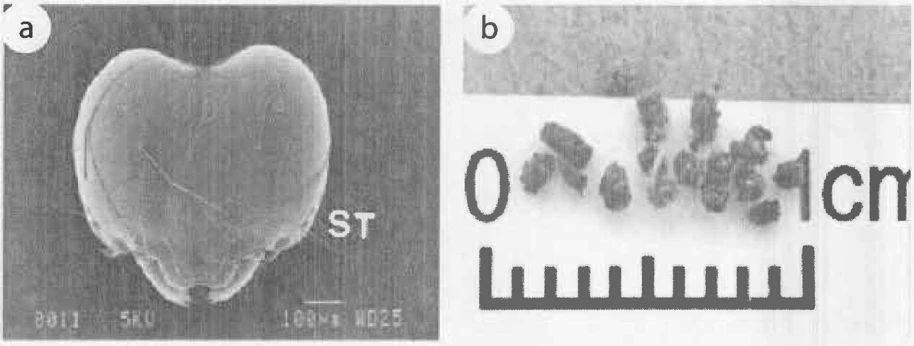

Figure 7: Macrorestes de tordeuse des bourgeons de l'épinette. a) capsule céphalique b) feces.

Tel que décrit par Lyell (1835), et repris par Gould (1965), le principe d'uniformitarisme nous laisse supposer que les processus physiques et biologiques qui gouvernent l'écosystème du présent sont les mêmes que ceux du passé et ont le même type d'action. Ce principe, à la base de sciences telles que la dendrochrologie, stipule donc que le présent est la clé du passé. Par réciprocité, on peut donc poser l'hypothèse que le passé est la clé du futur, c'est-à-dire que la connaissance des conditions environnementales qui révalaient dans le passé peut permettre de prédire ces conditions dans le futur.

La dynamique à long terme, une clé de compréhension de l'écologie de la TBE

La dynamique récente des épidémies de TBE ainsi que les changements observés, ne peuvent donc être compris que comme le résultat d'interactions millénaires entre l'insecte et son environnement. Ainsi, pour bien comprendre cette dynamique, il est important de mieux connaître la fréquence et l'importance relative des épidémies sur la plus longue période possible. Pour cela, on peut par exemple reconstituer l'abondance de l'insecte en identifiant les macrorestes tels que les capsules céphaliques ou les feces (Fig 7) enfouis dans les différentes couches de tourbes. L'utilisation de techniques de datation telle que le radiocarbone permet ensuite la réalisation de diagrammes macrofossiles. En ce qui concerne les épidémies de TBE, quelques études ont été réalisées au Québec et mettent en évidence la présence de plusieurs périodes d'abondance relative de macrofossiles de tordeuse à l'échelle de l'Holocène. Certaines de ces études semblent montrer que la TBE aurait déjà été présente et abondante dans des peuplements desquels le sapin baumier était absent, ce qui suggère une forte activité de l'insecte sur son hôte secondaire, l'épinette noire (Simard et al., 2006). De plus, cette forte abondance de macrorestes a été observée pendant une période relativement chaude de l'Holocène (7000 à 6000 cal. BP) suggérant une synchronisation phénologique entre l'insecte et son hôte. Cependant, ce type d'étude pose le double problème de la quantité de tourbe nécessaire (plus d'échantillons, plus de temps pour l'analyse et plus de coûts), qui varie de 750 à 4500 cm^3 (Elias, 1982b,a; Roper, 1996), et de l'identification des macrorestes qui sont soumis à la décomposition, et donc de la difficulté à répliquer ce genre d'analyse. Cette approche visant l'interprétation de la perturbation et de ses relations avec l'écosystème sur le long terme semble pourtant primordiale dans le contexte d'un aménagement durable des ressources forestières.

AMÉNAGEMENT ÉCOSYSTÉMIQUE, VERS UNE GESTION INTÉGRÉE RESPECTUEUSE DES "FORÊTS NATURELLES"

En vigueur depuis le 1er avril 2013, la loi sur l'aménagement durable du territoire forestier préconise que la planification forestière soit réalisée selon le concept de l'aménagement écosystémique. Ce concept, bien que plus ancien, fait son apparition dans les années 90 aux États-Unis et dans l'ouest du Canada. Son application vise à *"assurer le maintien de la biodiversité et de la viabilité des écosystèmes en diminuant les écarts entre la forêt aménagée et la forêt jugée naturelle"* (Grenon et al., 2010) (Fig 8). L'aménagement écosystémique fait donc suite au concept de gestion intégrée des ressources et du territoire et permet une utilisation rationnelle des ressources forestières avec la nécessité de préserver des écosystèmes fonctionnels à long terme (Gauthier et al., 2008). Toute la complexité de ce type d'aménagement réside donc dans la définition de la variabilité naturelle des écosystèmes et des perturbations qui la

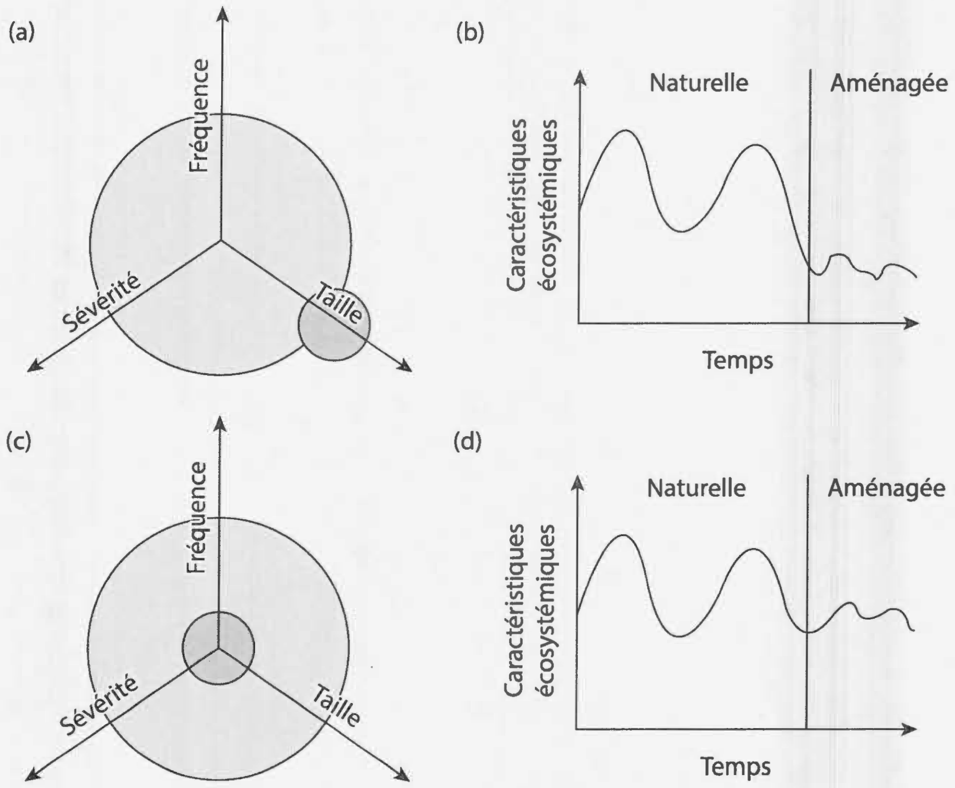

Figure 8: Variabilité des perturbations et des caractéristiques écosystémiques sur les écosystèmes naturels et aménagés : (a) and (c) variabilité de la taille, de la fréquence et de la sévérité des perturbations naturelles dans un écosystème naturel (sphère claire) et aménagé (sphère foncé) ; (b) et (d) représentent les fluctuations des caractéristiques écosystémiques avant et après un aménagement. Dans les diagrammes (a) et (b), l'aménagement a causé la sortie de l'écosystème de sa variabilité naturelle. Dans les diagrammes (c) et (d) l'écosystème est resté dans sa variabilité naturelle, mais l'aménagement a contraint l'amplitude de l'oscillation. Traduit de Haeussler et Kneeshaw (2003).

composent. En effet, le manuel de référence pour l'aménagement écosystémique des forêts au Québec indique que la forêt préindustrielle est utilisée comme état de référence pour la détermination des écarts à éviter (Grenon et al., 2010). Les écarts sont basés sur des attributs écosystèmiques importants tels que la composition végétale, la structure des peuplements, ou encore leur organisation spatiale. Lorsque des écarts significatifs sont détectés, des enjeux écologiques sont identifiés. On évalue ensuite les risques de disparition locale des espèces pour définir des seuils critiques pour chaque enjeux. Finalement, des objectifs spécifiques d'aménagement écosystémique sont fixés en fonction de ces seuils. Cependant, la dynamique épidémique de la TBE est très peu connue pour la période préindustrielle, et certains auteurs soutiennent que la fréquence et l'intensité des épidémies auraient augmentée significativement au 20ième siècle en réponse aux activités sylvicoles (Blais, 1983; Simard et al., 2006). Ainsi, malgré l'importance d'un régime de perturbations tel que celui de la TBE sur la définition d'un modèle de forêt dite "naturelle", son intégration à ce type de modèle semble encore poser problème.

En 1992, le Québec adhère au principe du développement durable lors du Sommet de la Serre de Rio de Janeiro. Dès lors et face à un intérêt croissant de l'industrie pour les matières ligneuses du territoire nordique, un comité est formé en 1998 pour tracer une limite à l'intérieur de laquelle il est possible d'effectuer un aménagement durable des forêts. En 2002, la limite est créée sur les recommandations du rapport de ce comité, publié en 2000 (Ministère des Ressources naturelles, 2000) et se base sur quatre critères d'évaluation :

o Le milieu physique
o La productivité forestière
o Les perturbations naturelles (feux de forêts)
o La biodiversité

Un nouveau comité a été formé en 2005, un rapport a été rendu public en 2014 et un nouveau tracé est entré en vigueur en 2018, se basant sur ces mêmes critères. Là encore, les deux versions de la limite nordique des forêts attribuables ne tiennent pas compte des épidémies de TBE par manque de données concernant sa dynamique en territoire nordique.

PROBLÉMATIQUE ET OBJECTIFS DE LA THÈSE

C'est donc dans le but de combler ces différentes lacunes que nous nous sommes donné comme objectif général de faire ressortir les structures temporelles, spatiales et spatiotemporelles des épidémies à grande échelle. En effet, les analyses actuelles sont bien souvent limitées aux deux derniers siècles ainsi qu'à une dynamique locale, voire régionale. Bien que certaines études repoussent les limites de la dendrochronologie en échantillonnant les arbres subfossils enfouis dans les lacs et les tourbières ainsi que les charpentes des bâtiments ancestraux, il semble important de développer de nouvelles méthodes pour effectuer un suivi plus précis de l'activité de l'insecte sur le long terme.

Nous proposerons donc, dans la première partie de cette thèse, la paléoécologie comme une méthode complémentaire à la dendrochronologie, mais aussi à la palynologie, à l'étude des macrorestes végétaux ainsi qu'à la paléoantracologie afin de reconstruire l'histoire du paysage et des perturbations qui l'ont façonné au cours des siècles. Notre premier objectif spécifique aura donc été de développer un nouveaux proxy paléoécologique capable de mesurer la présence de l'insecte au travers de l'Holocène, présent en grande quantité et facile à identifier. Nous y faisons l'hypothèse que les écailles de lépidoptère pourraient valider ces critères et que leur abondance serait corrélée avec les enregistrements dendrochronologiques des épidémies de TBE dans la région d'étude.

Dans une deuxième partie nous nous sommes concentré sur l'analyse multiproxies d'une carotte sédimentaire au Lac Flévy dans la forêt d'enseignement et de recherche de Simoncouche. Ce lac a été choisi afin de pouvoir interpréter les données liées à la TBE en relation avec une stratigraphie de macrorestes végétaux et de charbons de bois déjà existante. L'objectif spécifique de cette partie a donc été de proposer une analyse des deux principales perturbations en forêt boréale, de leur impacts sur la végétation au fil des siècles et de leurs interactions. Nous amenons ici l'hypothèse que la tordeuse était présente dans la zone depuis la recolonisation forestière qui a suivie la déglaciation (± 8000 cal yr BP) (Simard et al., 2006). Nous faisons également l'hypothèse que les épisodes de forte abondance de fossiles d'écailles ont été relativement rares à l'échelle de l'Holocène et qu'ils correspondent à des périodes où l'activité des feux était relativement faible et où la quantité de macrorestes des espèces hôtes (sapin baumier et épinette) était élevée (Simard et al., 2006). L'abondance de l'insecte serait ainsi soumise à des interactions quadripartites avec l'abondance des feux, de son espèce hôte et avec le climat. On peut ainsi penser qu'un climat plus humide influencerait un cycle de feu plus long et donc une présence plus importante dans le paysage du sapin baumier, ce qui favoriserait l'abondance de l'insecte. Finalement, nous supposons que la fréquence des feux de forêt pourrait augmenter à la suite d'un important épisode de défoliation puisque celui-ci augmenterait significativement l'inflammabilité des peuplements affectés en augmentant la quantité de bois mort sur pied (James et al., 2011). Dans la troisième partie, nous aborderons les problématiques spatiales en nous intéressant notamment à la synchronicité des épidémies, mais aussi à leurs patrons de diffusion, à la distribution nordique des zones défoliées et à son évolution dans le temps. Ce chapitre se veut une méta-analyse de plusieurs bases de données dendrochronologiques accumulées au laboratoire d'écologie végétale et animale de l'UQAC ainsi que de plusieurs bases de données ministérielles. L'objectif spécifique de ce chapitre est d'étendre le travail entrepris par Jardon (2001) au domaine de la pessière à mousses jusqu'à la limite nordique des forêts attribuables, mais aussi d'étendre les connaissance acquises de l'étude des relevés aériens de défoliation (Gray et al., 2000) à l'ensemble du 20^{ième} siècle. Nous posons l'hypothèse que le nombre d'années présentant une réduction de croissance épidémique sera moins important pour les peuplements nordiques d'épinette noire que pour les peuplements de la sapinière. Nous supposons également que l'emprise nordique des épidémies à l'échelle suprarégionnale sera plus importante à la fin du 20^{ième} siècle qu'au début.

STRUCTURE DE LA THÈSE ET CONTRIBUTIONS

La thèse est présentée sous la forme d'un ensemble de quatre articles. Le premier article, intitulé : « A secret hidden in the sediments : lepidopteran scales », constitue une sorte de préface qui met en valeur le potentiel des écailles de papillons en tant que nouvel indicateur paléoécologique. Cette article a été publié dans la revue *Frontier in ecology and evolution* et son format, plutôt court et vulgarisé en fait un bon outil de diffusion scientifique. Cette publication est le fruit d'un travail en collaboration avec Miguel Montoro Girona. Sa passion pour l'écologie forestière, la vulgarisation et la diffusion de nouvelles techniques scientifiques ont été la source et le moteur de ce manuscrit.

Le second chapitre est écrit sous la forme d'une note méthodologique et a été publié dans un numéro spécial du *Canadian Journal of Forest Reasearch* dédié à un atelier de l'IUFRO intitué : *"Effect of climate change on boreal pest range shifts and their ecological consequences"*. Dans ce manuscrit, la méthode d'extraction et d'identification des écailles est décrite en détails et les différentes perspectives de recherche sont discutées. Cet article est le fruit d'une idée originale du professeur Hubert Morin et d'un travail conjoint avec Anne-Élizabeth Harvey, étudiante à la maîtrise en gestion des ressources renouvelables de l'UQAC.

Le troisième chapitre intitulé "A Holocene landscape dynamic multiproxy reconstruction : How do interactions between fire and insect outbreaks shape an ecosystem over long time scales ?" a été publié dans la revue *PLOS ONE*. Ce chapitre présente l'ensemble des résultats obtenus suite à l'analyse d'une carotte sédimentaire de plus de 500 cm de long et qui renferme prés de 10 000 ans d'histoire. Cette publication est l'aboutissement d'un travail d'analyse sédimentaire de plusieurs mois dans lequel j'ai été largement soutenu par les efforts et la patience d'Anne-Élizabeth Harvey, mais aussi de Noémie Blanchette Henry, étudiante au baccalauréat en biologie de l'UQAC. Cet article intègre également les résultats de l'analyse des macrorestes végétaux et des charbons de bois réalisée à l'UQAM par Aurélie Genries et Samira Ouarmim.

Enfin, le quatrième chapitre (qui se trouvait être le coeur de cette thèse avant que les écailles ne pointent le bout de leur pédicelle...) propose de mettre en commun un certain nombre de données dendrochronologiques afin de reconstruire la dynamique spatiotemporelle des épidémies de TBE à l'échelle de l'ensemble de la forêt exploitée du Québec et ce pour l'ensemble du 20$^{\text{ième}}$ siècle. Cette étude est actuellement sous presse dans la revue *Frontiers in Plant Sciences*. Elle se place dans la continuité de la thèse de doctorat de Yves Jardon (2001) et de mon mémoire de maîtrise (Navarro, 2013).

Enfin, l'ensemble de ces recherches n'auraientt pu être réalisées sans les financements obtenus par Yves Bergeron, Adam Ali et Hubert Morin auprès du Fonds de Recherche du Québec - Nature et Technologies (PR-149036) et de la Chaire de Recherche Industrielle du Conseil de Recherches en Sciences Naturelles et en Génie du Canada sur la variabilité des paysages en zone boréale et la croissance de l'épinette noire (IRCPJ 499381-15).

CHAPITRE I

A SECRET HIDDEN IN THE SEDIMENTS : LEPIDOPTERA SCALES

This chapter can be found in the volume 6 of *Frontiers in Ecology and Evolution*

"Montoro Girona, M., Navarro, L., and Morin, H. (2018). A Secret Hidden in the Sediments : Lepidoptera Scales. Front. Ecol. Evol. 6, 1–5. doi :10.3389/fevo.2018.00002."

Forests are complex and dynamic systems, with numerous ecological factors and processes interacting at multiples scales to create landscapes inherited from thousands years of disturbance (Messier et al., 2013; Montoro Girona et al., 2017). Until recently, most paleoecological studies, especially within the boreal biome, have only assessed the influence of wildfire as a disturbance agent (Flannigan et al., 2001; Bergeron et al., 2010). These studies rely on fossil charcoal deposited in lake sediments and peat as a paleoecological proxy of fire events. However, due to the lack of effective proxies for reconstructing insect-related disturbance, the frequency, intensity and impacts of past insect outbreaks on the forest landscape have been neglected or over-simplified. Nonetheless, insect outbreaks are one of the most influential factors that shape forest diversity (McCullough et al., 1998). Spruce budworm [*Choristoneura fumiferana* (Clemens)] (SBW) is the most important defoliator of conifer trees in the North American boreal forest. At the epidemic stage,massive populations of larvae cause widespread damage to tree foliage. The larvae then undergo a metamorphosis to produce enormous flights of moth (Boulanger et al., 2017) (Fig 1.1a). In the province of Quebec (Canada), the forest surface affected by this species of Lepidoptera over the last century is twice the size of the state of California (Morin et al., 2009). SBW epidemics not only have major ecological impacts but also produce important economic consequences due to the loss of forest productivity (Shorohova et al., 2011). Despite the scale and significance of this natural disturbance agent, there is limited knowledge regarding the frequency and severity of SBW outbreaks at a pluri-millennial scale as well as how these outbreaks are related to climate. Given that variations of temperature and precipitation affect organisms' survival, reproduction cycles and spatial dispersion (Dale et al., 2001), it is critical to understand the links between past SBW outbreaks and climate so as to understand the potential of SBW outbreaks under future climate change scenarios (Volney et Fleming, 2000; Klapwijk et al., 2013).

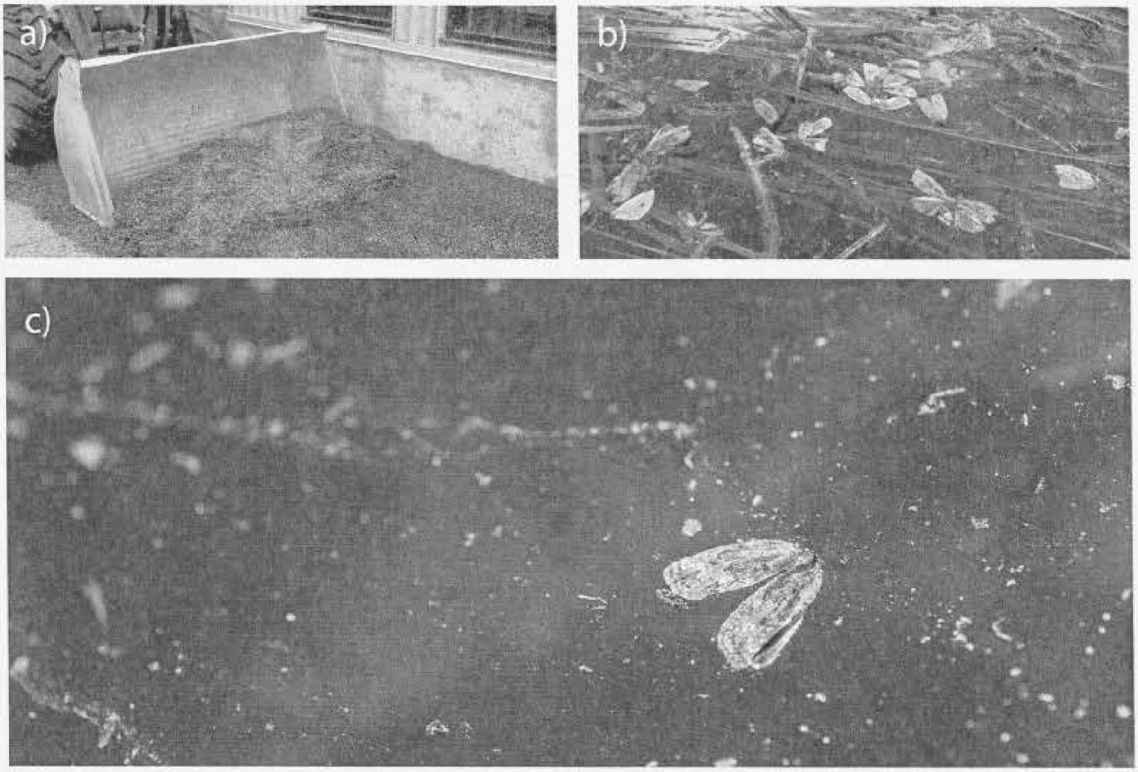

Figure 1.1: Images from spruce budworm (*Choristoneura fumiferana* - SBW) outbreaks. (a) Millions of dead moths in a forest camp after a massive flight of SBW in 2014. (b) Dead moths floating on the surface of a boreal lake north of Lake Saint-Jean, Quebec, in 2017. (c) Scale belts and other components separated from moths lying on the water surface.

Previous studies on long-term SBW dynamics focused on indirect measurements of the insect's activity over the last few centuries (e.g., dendrochronology, aerial surveys, inventories, etc.) (Swetnam et Lynch, 1993; Gray et al., 2000; Boulanger et Arseneault, 2004; Bouchard et al., 2006; Bouchard et Auger, 2014). Lake sediments can be considered as natural "hard drives" recording the environmental conditions and events that affect the surrounding landscape over time (Dodd et Stanton, 1990). The stored information in this ecological hard drive must be interpreted using proxy indicators found within the sediment record (Bigler et Hall, 2002; Mauquoy et Van Geel, 2007). An efficient paleoindicator must be abundant, easy to identify and remain well-preserved over a long period of time. Until recently, the reconstruction of forest insect dynamics was limited to the analysis of fossil insect feces and cephalic head capsules recovered from peat (Simard et al., 2006) ; these proxies do not entirely meet the required criteria. For example, feces are essentially constituted of organic matter and as such are easily degradable, while cephalic head capsules are difficult to identify and are produced in very small quantities.

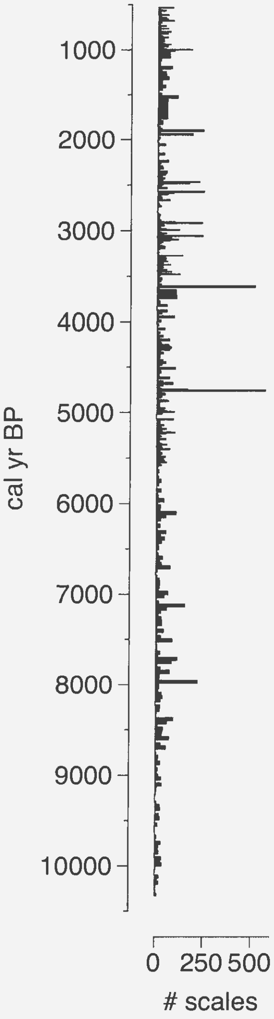

Figure 1.2: Raw number of lepidopteran scales extracted for the last 10,000 years from a sediment core recovered from Lake Flévy, Quebec.

Most SBW studies have focused on the larval stages for which fossilized remains are not preserved in lake sediments. However, working in the Lake Saint-Jean region of Quebec during a recent (2014) SBW infestation, we observed large quantities of adult moth wing scales in the water column, which eventually settle onto the lake bottom. This lead us to believe that due to the chitinous composition of these body parts, the adult SBW stages could be preserved in the sediment record of lakes, and thus serve as a potential paleoindicator of outbreaks. Etymologically, Lepidoptera means "scaled wings", although scales not only cover the wings, but also the thorax, abdomen and genital apparatus of moths. Our observations determined that significant amounts of Lepidoptera scales float on the lake surface to form "scale belts" (Fig 1.1b,c) (Ghiradella, 1998) produced as individual die and the membranes and sockets dry, releasing the scales. In addition to the thousands of scales present on each wing of each individual moth, certain scale shapes can be associated to specific taxa allowing for specific taxonomic identification of moth species. As such, these scales seem to match a priori all criteria for being an effective paleoindicator, although previous studies had never reported them from the sediment record.

Fire reconstruction uses charcoal fragments extracted from sediment by sieving methods, a technique not suitable for recovering lepidopteran scales as the mesh sizes used for charcoal are much too large.

Pollen grains, studied by palynologists, are similar in size to scales, but the extraction of pollen from sediment requires the use of destructive acids that dissolve the more delicate lepidopteran remains. According to Kristensen et Simonsen (2003), the reticulated structure of lepidopteran scales renders them poorly wettable and improves their floatability.We took advantage of these characteristics to propose an efficient and relatively simple extraction protocol (**?**). The procedure involves the sieving of sediment with an appropriate mesh size followed by multiple centrifugations of the rinsed sediment to precipitate the higher density organic matter and to cause lower density particles, such as some pollen and most of the scales, to float to the surface. These insect remains then form a concentrated subsample that can then be mounted onto microscope slides for analysis.

This novel approach allowed us to extract lepidopteran scales from nearly every centimeter of a 500-cm-long sediment core representing 10,000 years of deposition (Fig 1.2). Before attributing any high abundance of fossil scales to past SBW activity, we needed to identify the extracted scales and link them to outbreak species. Given that the shape of wing scales varies between species of Lepidoptera (Anken, 1996) and that this was relatively easy to measure, we evaluated the shape of thousands of scales from the main epidemic species found in Canada. These measurements lead to the development of species-specific morphotypes that we could use as an identification support tool (Fig 1.3). It must be noted that with the scales being very thin and delicate, a significant portion of the extracted scales were broken, folded or covered by other material resulting in a relatively low rate of scale identification. Nonetheless, we could still confirm that peaks of identified fossil scales corresponded to periods of insect outbreak. Thus, considering the wide range of SBW outbreaks on affected areas, and as it is the most damaging defoliator, we confirm that lepidopteran scales are an excellent indicator of SBWabundance.

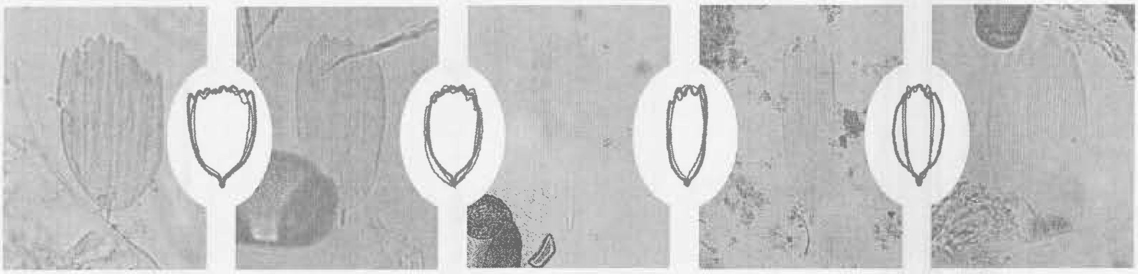

Figure 1.3: Examples of well-preserved scales extracted from a lake sediment core showing the correspondence with spruce budworm (SBW) morphotypes generated from the shape measurements of thousands of SBW specimen scales.

Analysis of the long-term history of insect outbreaks opens the door to an improved understanding of : (1) the interactions between different disturbances at the Holocene scale, (2) the role of insect outbreaks on landscape dynamics and (3) the relationship between climate and insect outbreaks at short-term and pluri-millennial scales. Use of fossil Lepidoptera wing scales also offers numerous potential insights into natural disturbance controls on forest structure with implications for biodiversity conservation and forest management. Insect outbreaks are cyclic phenomena based on the regulation of population density (Royama, 1984). Scales provide a direct measurement of the abundance of Lepidoptera over time, allowing insight into the impact of insect outbreaks on the forest structure and composition in relation to outbreak severity and frequency. Reconstruction of outbreaks would also provide a longer-term vision of insect dynamics and interactions with other natural factors over time (e.g., wildfire versus insect outbreaks versus climate). Furthermore, sustainable forestry management aims to ensure that harvest methods simulate patterns of natural disturbance and thus minimize differences between managed and natural forests (Kuuluvainen, 2002; Gauthier et al., 2009; Montoro

Girona et al., 2016). Understanding the pattern of insect outbreaks will permit mirroring silvicultural practices to the natural severity and frequency of insect outbreaks (Hof et al., 2017). Finally, in the context of climate change that will likely impact the occurrence of insect outbreaks, a longer record of outbreak cycles and consequences would improve forecasts of future ecological scenarios and potential change (Intergovernmental Panel on Climate Change, 2014).

Although we have focused primarily on SBW outbreaks, lepidopteran scales show great potential for other purposes.With more than 160,000 described species, Lepidoptera (moths and butterflies) is the second most diverse faunal order, with the total number of probable species estimated at almost half a million (Kristensen et al., 2007). Lepidoptera are considered to be an effective "umbrella group" for biodiversity conservation, and, globally, there is a high extinction risk for these species (New, 1997; Thomas et al., 2004). Analyses of wing scales could improve our knowledge of the abundance and distribution (e.g., migration, range shifts) of these species, and provide an understanding of how moths reacted to past environmental change, to better discern their future vulnerability to extinction. The use of lepidopteran scales from the past will provide insight into present-day ecosystems and produce amore accurate projection of insect outbreaks that will occur in the future.

CHAPITRE II

LEPIDOPTERA WING SCALES : A NEW PALEOECOLOGICAL INDICATOR FOR RECONSTRUCTING SPRUCE BUDWORM ABUNDANCE

This chapter can be found in the volume 48 of the *Canadian Journal of Forest Research*, dedicated to the IUFRO workshop "Effect of climate change on boreal pest range shifts and their ecological consequences", hosted by the IUFRO Boreal and Alpine Forest Ecosystem Unit Working Group 8.01.06 and co-sponsored by working groups 7.03.07 (Population Dynamics of Forest Insects) and 7.03.05 (Ecology and Management of Bark and Wood Boring Insects), held in Sept-Îles and Baie Comeau, Quebec, on 11–15 July 2016

"Navarro, L., Harvey, A.-É., and Morin, H. (2018). Lepidoptera wing scales : a new paleoecological indicator for reconstructing spruce budworm abundance. Can. J. For. Res. 48, 302–308. doi :10.1139/cjfr-2017-0009."

2.0.1 ABSTRACT

Natural disturbances have a major impact on boreal forest landscape dynamics and, although fire history is well documented at the Holocene scale, spruce budworm (SBW) dynamics are only known for the last three centuries. This is likely due to the difficulty in using and interpreting existing indicators (cephalic head capsules and feces). In this methodological study, we present an original approach using lepidopteran wing scales to reconstruct insect abundance. We analyzed two sediment cores from the boreal forest in central Quebec and extracted wing scales at every stratigraphic level. The required quantity of sediment for paleoecological analysis is relatively small given the large quantity of wing scales produced by Lepidoptera and their small size. Scales are well-preserved due to their chitinous structure and their great variety of shapes offer a high potential for taxonomic identification. A statistical model based on the shape of scales of the three major epidemic lepidopterans in Quebec discriminated 68 % of SBW scales. This indicator allows a more efficient and more precise reconstruction of SBW history with respect to the use of cephalic head capsules or feces.

2.1 INTRODUCTION

Climate change is a major challenge in ecology, greatly affecting forest disturbance dynamics and ecosystem diversity (Gauthier et al., 2015). Boreal forests are the largest terrestrial ecosystems on the planet and produce more than a third of the world's lumber (Gauthier et al., 2015; Montoro Girona et al., 2016). Due to the ecological and economic impacts of insect outbreaks in this ecosystem, it is important to develop a better understanding of how climate change affect these, often devastating, insect events. Forecasts project an increase in the frequency, duration, and timing of insect outbreaks (Nelson et al., 2013). However, there remains a shortage of indicators that permit a more thorough assessment of cycles and impacts of insect outbreaks at the Holocene scale (Simard et al., 2002).

Spruce budworm (*Choritoneura fumiferana*, Clemens) (SBW) is one of the most important agents of natural disturbance in the boreal forests of North America (Shorohova et al., 2011), causing major loss of productivity and death of host species (Hennigar et al., 2013). In the eastern Canadian boreal forest, SBW is, by far, the most damaging defoliator of conifers, reaching cyclically epidemic population densities that allow the insect to affect large forest areas (Pureswaran et al., 2015). During the last outbreak of the 20^{th} century (1974-1988) SBW affected 55 million hectares causing the loss of 139 to 238 million m^3 of fir and spruce (Boulet et al., 1996). This forest pests' short life cycle, mobility, and high reproductive potential allow a rapid response to changes in environmental conditions (Menéndez, 2007). Nevertheless, long-term studies of landscape natural variability focus on the use of charcoal fragments to determine fire activity and often conceal the effect of forest insect outbreaks (Bergeron et al., 1998). However, in eastern Quebec SBW is considered a more important disturbance than fire and the lack of knowledge about its pluri-millennial dynamics is the cause of a serious bias in the understanding of landscape variability. It is therefore important to assess the relative importance of SBW outbreaks and the role played in the entire boreal forest ecosystem at the longest temporal scale possible.

Dendrochronological studies have revealed the epidemic history of SBW over the last three centuries (Boulanger et al., 2012). Tree-ring analysis provides important insights into impact from defoliation as well as the periodicity and synchronism of insect outbreaks across huge areas of forest. Nevertheless, dendrochronology is an indirect measure of SBW impact and its interpretation is limited as multiple factors may influence tree growth (Davis et Hoskins, 1980). In addition, dendrochronology is restricted to the age of survivor trees and reconstruction of long-term chronologies using subfossil trees buried in lakes and ponds is promising but, for the moment, remains challenging.

Paleoecology allows a longer-term reconstruction of SBW activity. Macrofossils such as cephalic head capsules (Lavoie et al., 2009) or feces (Simard et al., 2006) have been used as direct indicators of the occurrence of insect outbreaks. However, the long-term dynamics remain poorly documented as analysis is time-consuming, and temporal resolution is low due to the amount of sediment to be examined. The number of cephalic head capsules extracted from a relatively large amount of sediment or peat material tends to be low and feces become increasingly difficult to identify with depth due to decomposition.

Butterfly and moth wings are covered with thousands of minute overlapping scales of variable shape, forming colour patterns on the wing surface (Dinwiddie et al., 2014). These scales assume many different functions, from attracting and selecting mates (Burghardt et al., 2000) to camouflage (Brakefield et Liebert, 2000), and thermal regulation (Srinivasarao, 1999). SBW scales are partly made of chitin fibrils (Richards, 1947) that are well-preserved in sediments due to increasingly favorable conservation conditions with depth under anaerobic conditions (Sturz et Robinson, 1986). As these scales are produced in a very high quantity, particularly during outbreaks, this should permit many of these microfossils to be retrieved from a very small quantity of sediments. There is also a great potential for taxonomic identification owing to the high diversity of scale shapes. These considerations led us to ask whether lepidopteran scales microfossils are a more suitable paleoindicator of SBW abundance. We hypothesize that this indicator can be extracted in a significant quantity and that its abundance peaks will match known periods of SBW outbreaks.

This methodological investigation proposes a practical technique to collect and extract fossil scales from sediment cores and discusses the potential benefits and difficulties of using scale shape as an indicator of Lepidoptera species. We also present examples from two short sediment cores recovered from a pair of lakes in the central boreal region of Quebec.

2.2 PROPOSED METHODOLOGY FOR SCALE EXTRACTION

2.2.1 SCALE EXTRACTION AND ANALYSIS

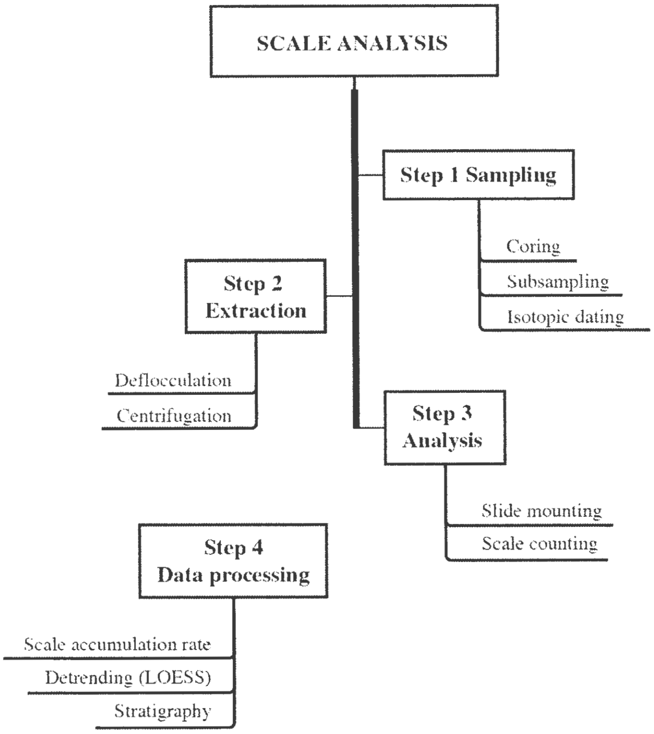

Figure 2.1: Scale analysis protocol.

To set the extraction parameters (sucrose solution density, sieve mesh size, centrifugation speed and duration...), we used a trial and error approach with test samples in which we added a relatively constant quantity of scales (one entire forewing of a SBW per sample). The parameters presented here are those that gave the best results.

We dried samples from a sectioned sediment core at 105°C for 24 h. For each interval of interest, we collected a 0.5 g subsample of dry sediment (± 5 cm^3) and heated it in a 100 mL 10 % potassium hydroxide (KOH) solution at 70 °C for 30 min or until complete deflocculation had occurred (Frey, 1986). The slurry was then sieved through a 53 μm mesh to retain most of the scales. Small particles (mostly fragments of organic matter) were discarded to allow us to analyze a more concentrated sediment subsample. We centrifuged the samples at 500 RCF for 10 min in a 10 mL sucrose solution (relative density = 1.24) to remove higher density particles. This centrifuging was repeated three times. After each run, we recovered the supernatant, refilled the vial with the sucrose solution, and centrifuged again. We combined the three supernatants in a 50 mL plastic vial and, to precipitate scales and any remaining particles, we centrifuged the combined supernatant at 3900 RCF for 20 min. The final pellet was mounted onto microscope slides for microfossil counting. This protocol (Fig 2.1) permitted most of the scales to be easily extracted, at low cost, without using destructive chemicals.

2.2.2 TAXONOMIC IDENTIFICATION OF SCALES AND THE POTENTIAL OF USING SCALE SHAPE

There is very little existing literature about the taxonomic value of lepidopteran scales for paleoecological work. Species of Lepidoptera are usually distinguished by studying wing venation or genitalia, features that are not preserved in the sediment record. Among the other discriminant criteria, the most studied are the iridescent ultrastructure of scales and structural colour production (Dinwiddie et al., 2014). Ultrastructure analysis requires expensive and time-consuming scanning electron microscopy (SEM) that is not easily applicable to paleoecological studies. In the case of moths, colour patterns are dull and extraction techniques, including the use of hot alkali solution, could alter the pigmentation of scales. In some rare cases, when these identification criteria are not sufficient to distinguish two sibling species, scale shape has been used (Anken et Bremen, 1996; Yang et Zhang, 2011).

To test the interspecific variability of shape parameters and their taxonomic potential, we selected three of the major epidemic defoliator lepidopterans in the North American boreal forest : spruce budworm (*Choritoneura fumiferana* Clemens), forest tent caterpillar (*Malacosoma disstria* Hübner) and hemlock looper (*Lambdina fiscellaria* Guénée) (Shorohova et al., 2011). We used eight specimens for each species, half of each sex to take sexual dimorphism into account, and studied scales from the upper and lower surface of each wing. Scales were separated from the wing using a fine brush and mounted on glycerol-coated microscope slides. To ensure random and systematic selection, we used a $10 * 10$ grid beneath the slide and selected the first scale encountered in each cell. We analyzed 2400 scales per species. We used Elliptic Fourier Descriptors (EFDs) and some non-size correlated shape parameters as quantitative measures of scales shape. EFD coefficients were calculated from the chain-coded contours of each scale obtained with SHAPE package v.1.3 (Iwata et Ukai, 2006) using 20 harmonics. These coefficients were normalized to be invariant with respect to the size, rotation, and position. This procedure generated multiple coefficients for each scale. As such, we used principal component analysis (PCA) to summarize the data.

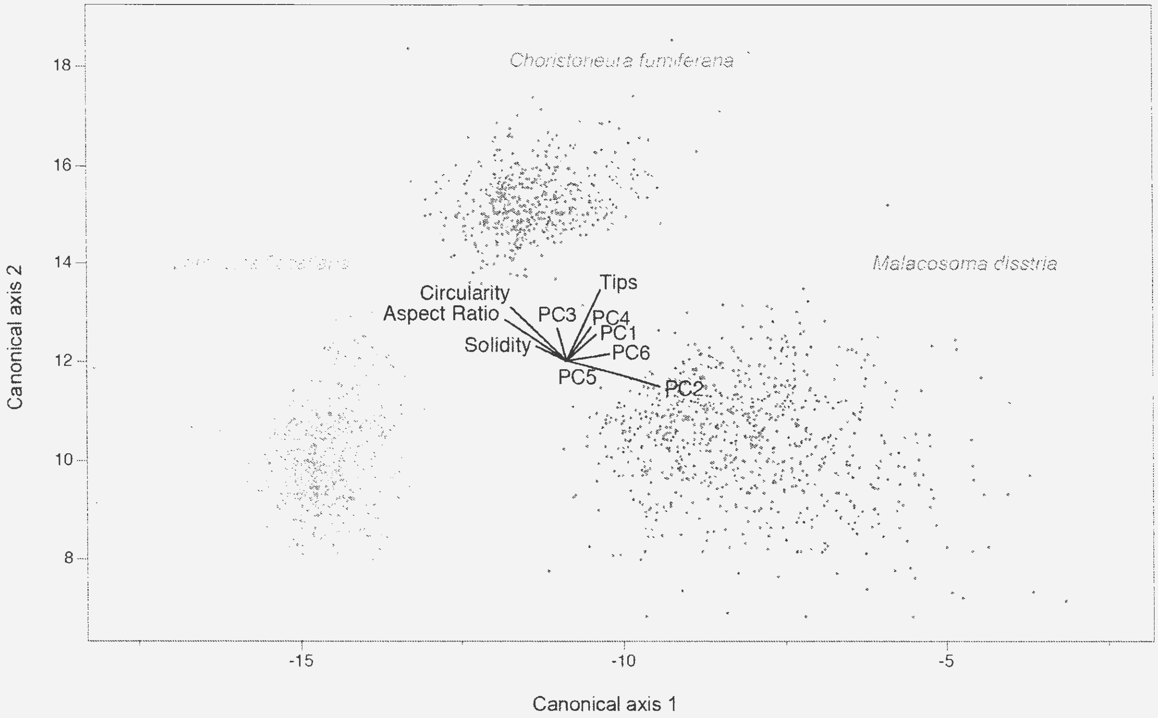

Figure 2.2: Discriminant analysis of the three species of outbreaking lepidopterans based on EFDs principal component scores and four scale shape parameters. Colour points represent highly specific shapes and faded points represent more common shapes.

We used the six principal components scores as shape characteristics. Using image processing software ImageJ v.1.48v (Schneider et al., 2012), we also measured the aspect ratio ($\frac{MinFeret}{MaxFeret}$), circularity ($4\pi * \frac{area}{perimeter^2}$), solidity ($\frac{area}{convexhullarea}$) and the number of apical indentations. We used all these shape parameters to build a discriminating model that correctly classified 68 % of the SBW scales, 79 % of the hemlock looper scales and 62 % of the forest tent caterpillar scales (Fig 2.2). We used well-classified scales having a probability >0.8 to construct ten morphotypes for each species based on a K-mean cluster analysis (Fig 2.3). Each cluster was characterized by the shape of the median scale and of the first two standard deviations. We also reconstructed the ten most common morphotypes (misclassified, probability <0.5). Specific shapes were observed such as the very deep indentations in *Malacosoma disstria* specimens as noted by Grodnitsky et Kozlov (1990) for Lasiocantpidae. *Choritoneura fumiferana* morphotypes showed a higher circularity with a relatively high number of small indentations.

In contrast, most of the *Lambdina fiscellaria* morphotypes have little to no indentation. Moreover, shape analysis revealed a high intra-specific variability for shape variation, confirming a hypothesis of mostly common scale shapes and some specialized ones (Ghiradella, 1994).

These morphotypes based on shape measurement still have limitations as a systematic taxonomic identification tool. Indeed, accurate identification of fossil scales extracted from sediment is not always possible due to the conservation state of scales (broken or folded) (Fig 2.7e) or the soft focus effect. However, it can help differentiate peaks that may be caused by outbreaks of two or more lepidopteran species.

In Canada, 18 species, representing 1 to 2 % of forest lepidopterans, are cyclically outbreaking (Faeth, 1987; Mason, 1987). From long-term abundance reconstruction studies of SBW in Quebec, we can exclude potentially introduced and western species. Moreover, since 1975, 95 % of areas affected by defoliation were caused by SBW. In addition, spatial extension of bioclimatic domains have been quite stable in eastern Canada since 5 ka BP (Dyke, 2005). SBW feces in the sediment record from the northern part of its distribution area attests to its presence since 8 ka BP (Simard et al., 2006). As such, we can assume, with a low risk of misinterpretation, that high variations in fossil scales abundance in Quebec are mainly due to SBW dynamics.

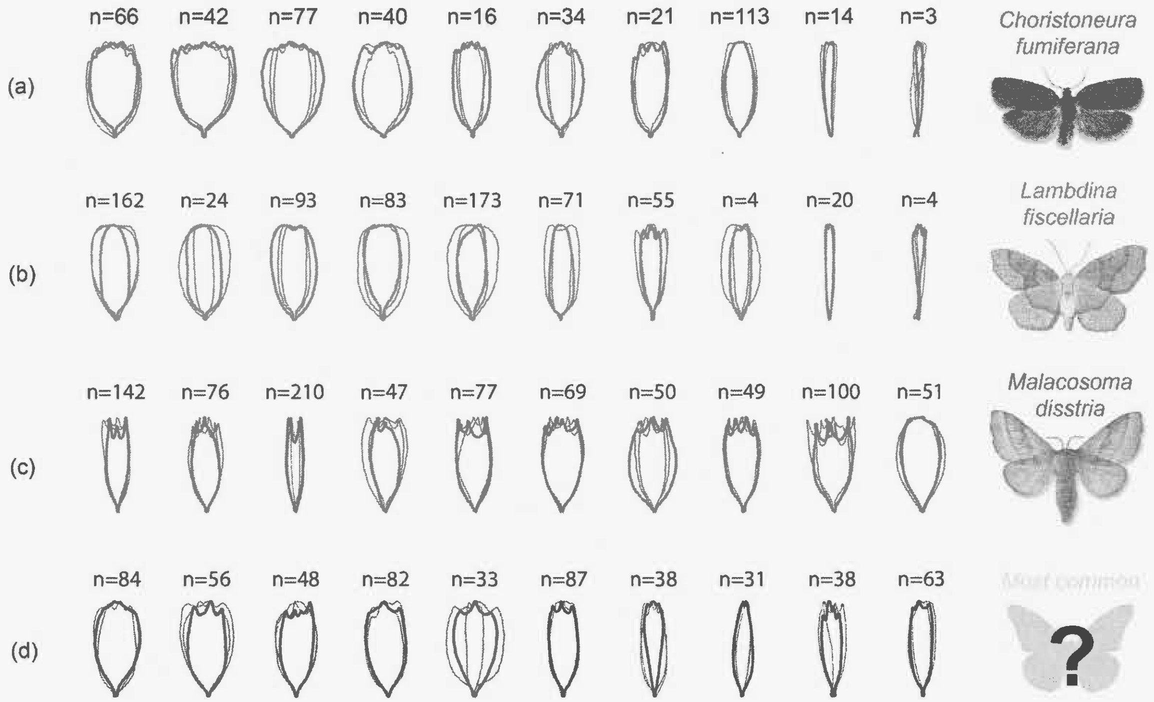

Figure 2.3: Scales morphotypes extract from K-mean cluster analysis of (a) *Choritoneura fumiferana*, (b) *Lambdina fiscellaria*, and (c) *Malacosoma disstria* specific scales and (d) more common scales of the three species . The bold scale represents the median shape for each cluster and light grey scales represent the first standard deviation shape in each cluster.

2.3 CASE STUDY : RESULTS AND INTERPRETATION

2.3.1 STUDY SITES

The paleoecological protocol was tested on surface sediment cores from two lakes located at the Simoncouche Experimental Forest of the Université du Québec à Chicoutimi, Quebec. Lac Flévy (48°13'00.04"N; 71°12'57.21"W) covers an area of 2.33 ha at an altitude of 376 m. Lac Hautbois (48°12'30.65"N; 71°13'22.92"W) covers 3.9 ha and is at an altitude of 398 m (Fig 2.4).We chose small lakes having low outflows, to ensure high sedimentation rates (Millspaugh et Whitlock, 1995; Ali et al., 2009). Both studied sites lie on undifferentiated glacial till and fluvioglacial deposits constituted of loose or compact unsorted deposit (Ministère de l'Énergie des Mines et des Ressources, 1976). Each lake is surrounded by even-aged trembling aspen (*Populus tremuloides*) stands and mixed even-aged stands of black spruce (*Picea mariana*) and poplar. The age structure indicated that these forest stands originated from an intense fire that occurred in 1922 (Gagnon, 1989). SBW has been present in the area for a minimum of 8240 years (Simard et al., 2006) and recurrent outbreaks were reported during the last three centuries, becoming more frequent during the 20th century (Blais 1983). Aerial surveys indicate that defoliation has occurred in the study area since 2012 reaching severe levels after 2015 (Ministère des Ressources Naturelles et de la Faune, 2012a; Ministère des Forêts de la Faune et des Parcs, 2015).

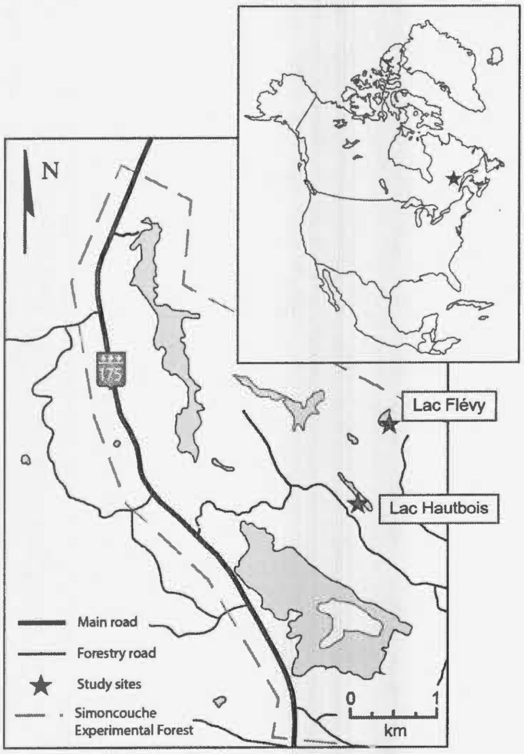

Figure 2.4: Location of the two studied lakes

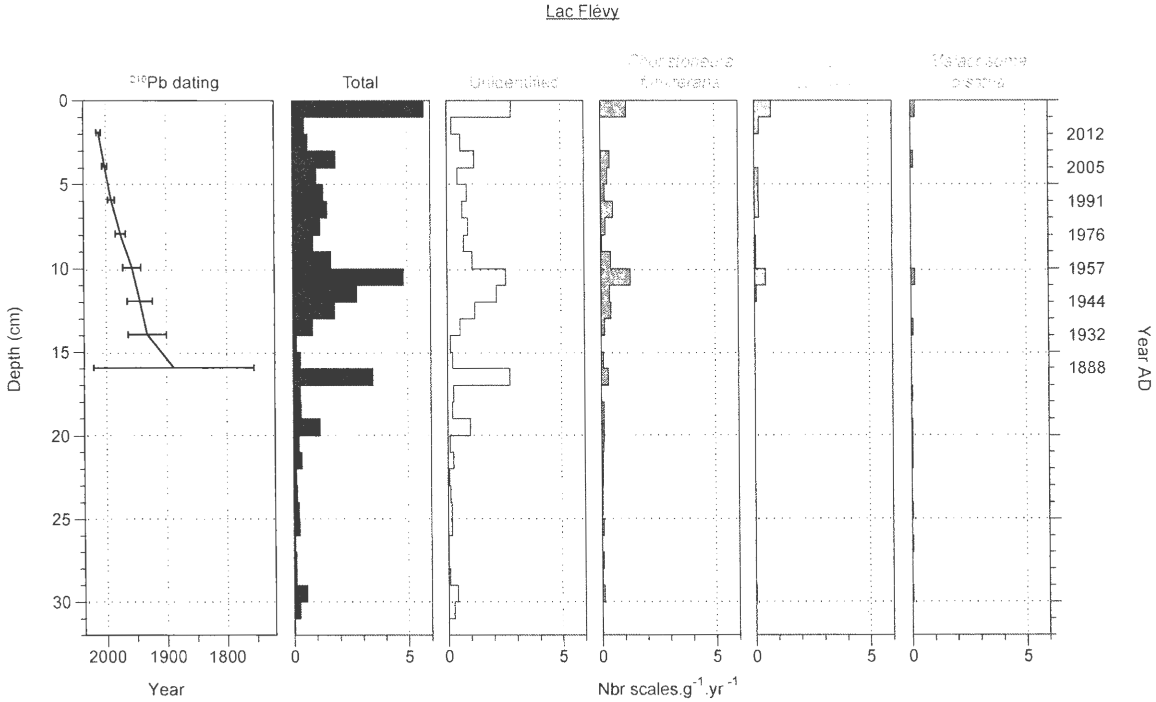

Figure 2.5: Stratigraphy of Lac Flévy. (a) Lead-210 dating based on a constant rate of supply (CRS) model ; (b) Total accumulation rate for the extracted scales ; (c) Accumulation rate of unidentified scales (scales that did not match any morphotypes, common scale morphotypes, damaged scales, etc.) ; (d-f) Scales matching a specific morphotype of one of the three outbreaking species.

2.3.2 *SEDIMENT CORE RECOVERY AND PREPARATION*

We collected two sediment cores from the deepest portion of each lake, one for isotopic dating and the second core for extracting scales. We used a Glew gravity corer for sediment sampling to ensure the sediment/water interface was not disturbed (Glew, 1988). The core lengths for the microfossil cores were 32 cm and 24 cm for Lac Flévy and Lac Hautbois, respectively. The cores collected for the analysis of micro-remains were subsampled in the field at a 1-cm-thick resolution using a vertical extruder (Glew, 1988).

2.3.3 ISOTOPIC DATING

Samples used for dating were dried (105 °C for 24 h) and then sent to the Radiochronology Laboratory at the Centre d'études nordiques, Université Laval for ^{210}Pb and ^{137}Cs analyses by gamma spectrometry (San Miguel et al. 2005). We selected a constant rate of supply (CRS) model for the ^{210}Pb dating of both cores (Turner et Delorme, 1996).

2.3.4 RESULTS FROM SCALE EXTRACTION

Despite the small subsample size (0.5 g dry sediment) and the fact that surface samples are not the most suitable for this kind of analysis (high levels of bioturbation, high water content...), we obtained a substantial quantity of scales from each sampled interval of the sediment cores from both lakes (Fig 2.5 and Fig 2.6). This result is inconsistent with Kristensen et Simonsen (2003) assumption that Lepidoptera fossils are strikingly scarce in lacustrine sediments. All the collected microfossils were well-preserved and the accumulation rate of scales presented a similar order of magnitude in both lakes. Lac Flévy presented two distinctive peaks, the first corresponding to the mid-20th century (±15 years) and the second corresponding to the beginning of the 21st century (Fig 2.5). Both peaks match with known periods of high SBW abundance in the study area. Although the stratigraphy of Lac Hautbois is less clear, it is comparable to that of Lac Flévy : we extracted the most scales from depths corresponding to the early 21st century and the scale accumulation rate decreases slightly prior to the 20th century (Fig 2.6). Due to our conservative identification criteria, our results represent a quite low morphotype identification rate suggesting that this method should be used as a validation tool rather than as a systematic identification method. Nevertheless, in both lakes the species with the highest rate of morphotype match was *choritoneura fumiferana* (Fig 2.5 and Fig 2.6), confirming that SBW is the most common outbreaking Lepidoptera in the area.

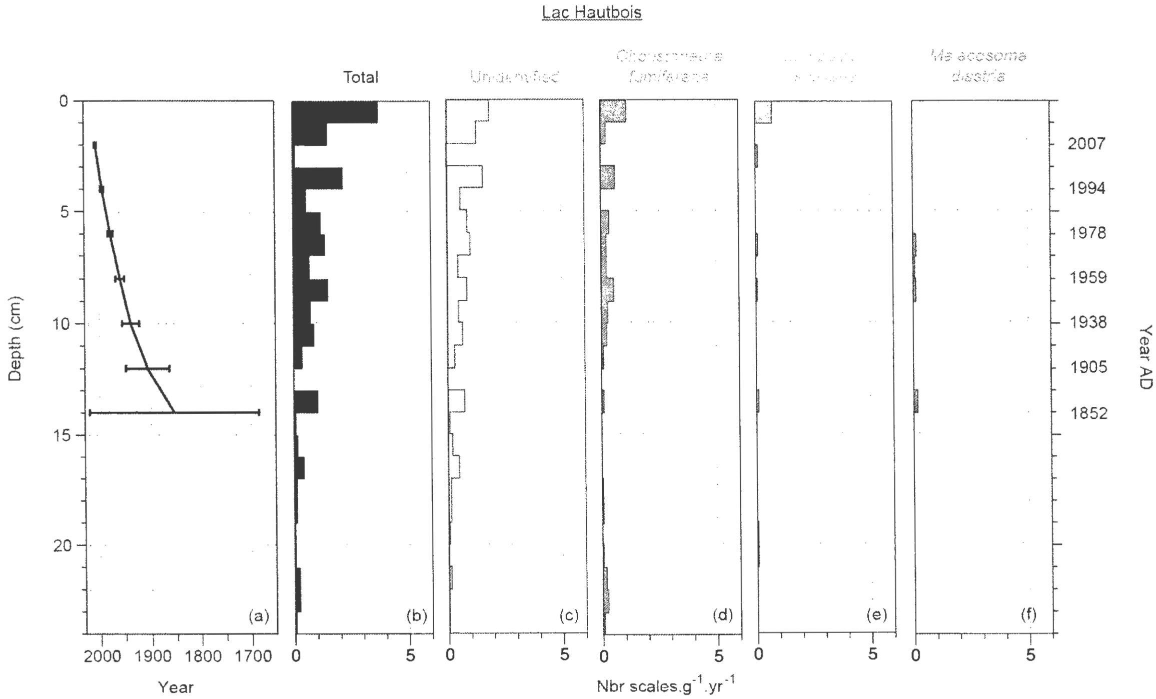

Figure 2.6: Stratigraphy of Lac Hautbois. (a) Lead-210 dating based on constant rate of supply (CRS) model ; (b) Total accumulation rate of extracted scales ; (c) Accumulation rate of unidentified scales (scales that did not match any morphotypes, common scale morphotypes, damaged scales, etc.) ; (d-f) Scales that matched a specific morphotype of one of the three outbreaking species.

Finally, the identified SBW were similar to the unidentified scales suggesting that some SBW scales were unidentified due to a lack in identification criteria or a degraded physical condition. However, surface core scale abundance requires careful interpretation as ^{210}Pb dating precision decreases with depth (Fig 2.5). A lower resolution long-term ^{14}C dated stratigraphy should be undertaken for SBW abundance analysis, which will be the subject of a later study.

2.4 ADVANTAGES AND SHORTCOMINGS

The use of fossil scales of Lepidoptera presents some advantages over other paleoecological proxies. Scales are less degradable than feces and much more abundant than cephalic head capsules. They have been found in nearly every sample analyzed to date, including the examples presented above and within longer sediment cores analyzed for an upcoming publication. Moreover, the use of wing scales requires a relatively small amount of sediment to prepare, simplifying the sampling procedure and allowing wing scales to be analyzed along with additional proxies such as charcoal and pollen from the same core material. Insect infestations should thus be included in any future studies of long-term disturbance dynamics to allow forest management policies to be based on more complete and realistic information. Finally, scale count data can benefit from data processing methods such as the use of a LOESS smoothing to distinguish background variation from locally defined peaks (Higuera et al., 2010). Nevertheless, as all paleoecological studies, this kind of research is time-consuming, restricting the replicability across multiple sites. In addition, the development of other discriminant criteria (texture, pigmentation, ultrastructure characteristic. . .) to improve the relevance of interpretation is pertinent due to the taxonomic potential of scales. This method could be adapted for use in different environments such as bogs, fens, ponds, or peat deposits to be directly comparable with existing proxies (feces and cephalic head capsules). Finally, future studies should explore the taphonomic

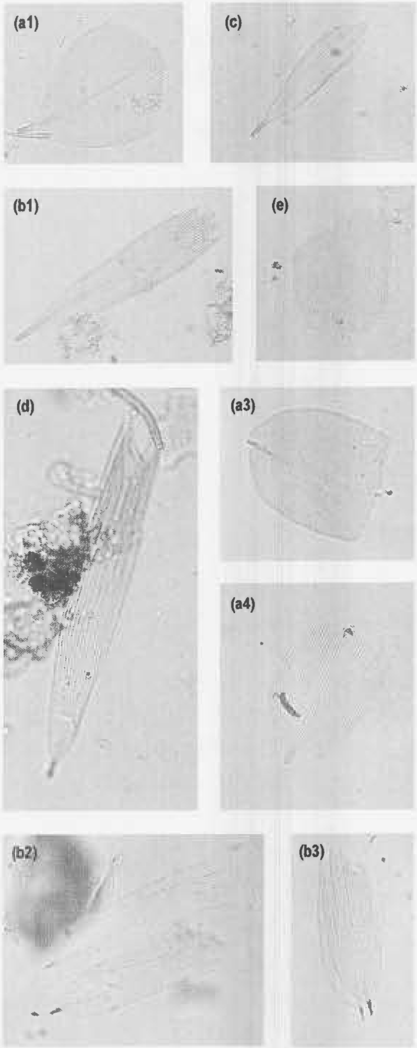

Figure 2.7: Examples of (a) unidentified scales; (b) scales matching a *Choristoneura fumiferana* morphotype; (c) scales matching a *Lambdina fiscellaria* morphotype; (d) scales matching a *Malacosoma disstria* morphotype; (e) a damaged scale.

processes affecting scale deposition, transport and sedimentation, and the magnitude of scale accumulation in endemic areas versus epidemic areas.

This study demonstrates that wing scales can be used as a paleoecological indicator for reconstructing insect outbreak history, being a more effective proxy than feces and cephalic head capsules. Fossil scales have a great potential to improve our understanding of the long-term dynamics of lepidopteran defoliator species that are still poorly known, especially in the boreal forest. This contribution will be essential for improving the accuracy of natural disturbance projections within the context of future climate change.

2.5 ACKNOWLEDGEMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada. We thank Patrick Nadeau for his help in the field and Milla Rautio, Claire Fournier, Marianne Desmeules, and Noémie Blanchette-Henry for their help and advice in the laboratory. We also thank Miguel Montoro, Alison Garside and Murray Hay for their help in reading and improving the quality of this manuscript.

CHAPITRE III

A HOLOCENE LANDSCAPE DYNAMIC MULTIPROXY RECONSTRUCTION : HOW DO INTERACTIONS BETWEEN FIRE AND INSECT OUTBREAKS SHAPE AN ECOSYSTEM OVER LONG TIME SCALES ?

This chapter can be found in the volume 13 of *PLOS ONE*

Navarro, L., Harvey, A. E., Ali, A., Bergeron, Y., and Morin, H. (2018). A Holocene landscape dynamic multiproxy reconstruction : How do interactions between fire and insect outbreaks shape an ecosystem over long time scales ? PLoS One 13, 1–15. doi :10.1371/journal.pone.0204316.

3.0.1 ABSTRACT

At a multi-millennial scale, various disturbances shape boreal forest stand mosaics and the distribution of species. Despite the importance of such disturbances, there is a lack of studies focused on the long-term dynamics of spruce budworm (*Choristoneura fumiferana* (Clem.)) (SBW) outbreaks and the interaction of insect outbreaks and fire. Here, we combine macro-charcoal and plant macrofossils with a new proxy— lepidopteran scales—to describe the Holocene ecology around a boreal lake. Lepidopteran scales turned out to be a more robust proxy of insect outbreaks than the traditional proxies such as cephalic head capsules and feces. We identified 87 significant peaks in scale abundance over the last 10 000 years. These results indicate that SBW outbreaks were more frequent over the Holocene than suggested by previous studies. Charcoal accumulation rates match the established fire history in eastern Canada : a more fire-prone early and late Holocene and reduced fire frequency during the mid-Holocene. Although on occasion, both fire and insect outbreaks were coeval, our results show a generally inverse relationship between fire frequency and insect outbreaks over the Holocene.

3.1 INTRODUCTION

Boreal forests are subjected to various natural disturbances that operate at different spatio-temporal scales (Turner et al., 1993; Turner, 2010) affecting biodiversity and ecosystem dynamics (Cardinale et al., 2005; Arseneault et Sirois, 2004). In Canada, fire and insect outbreaks are the two main disturbances that shape forest stand age and composition (Gauthier et al., 2001; Jardon et al., 2003). Although anthropic disturbances (forest harvesting, hydroelectrical infrastructures, oil and gas extraction, etc.) have had a significant impact on terrestrial ecosystems over the last centuries (Schindler et Lee, 2010), natural disturbances continue to operate at a pluri-millennial scale (Power et al., 2008; Simard et al., 2006). Dendrochronological studies, through use of fire scars and reductions in tree ring growth, provide valuable insight into the history of fire and insect outbreaks. However, although dendrochronology offers a high resolution (yearly) reconstruction of disturbances, it is limited by the length of the assembled time series. The scarcity of long-term dendrochronological records limits the assessment of disturbances over millennial time scales (Davis et Hoskins, 1980). To overcome this limitation, paleoecology, via the analysis of proxies preserved in the sedimentary record, provides an opportunity for reconstructing interactions between organisms and their environment across a longer time scale. Use of micro- and macrocharcoal pieces as proxies of fire frequency and intensity as proven as effective tools for developing a detailed portrait of Holocene fire history in the boreal forest. In contrast, the reconstruction of insect outbreaks remains poorly developed. Spruce budworm (*Choristoneura fumiferana* (Clem.)) (SBW) is the most important defoliator of conifer stands in eastern North America, causing significant growth reductions and mortality in host trees, damaging extensive areas of forest during outbreaks. Despite the scale and impact of SBW outbreaks during the 20th century, the understanding of long-term variability of SBW has been limited due to the lack of indicators. Simard *et al* (Simard et al., 2006; Simard, 2011) reconstructed 8 200 years of insect activity using insect macrofossils, such as feces and cephalic head capsules, as well as transversal sections of spruce needle casts (*Lophodermium piceae* (Fckl.))—a black spruce (*Picea mariana* (Mill.) B.S.P.) needle endophyte (Jasinski et Payette, 2007). At their study site, located in the southeastern portion of the boreal forest in Quebec, they identified two main periods of SBW abundance : ca. 6500 cal yr BP and the 20th century, suggesting that intense SBW outbreaks were relatively rare during the Holocene. The authors also suggested that these two main periods of SBW abundance occurred when fire activity was low, favoring the development of mature host stands, suitable for SBW outbreaks. A 10 000 years fire history from the same region of Quebec showed that in the early Holocene, fire frequency was higher, favoring fire-adapted species, such as jack pine (*Pinus banksiana* Lamb.) (Couillard et al., 2013). As climate conditions became wetter, ca. 4500 cal yr BP, the fire return intervals were longer and species being less adaptated to fire, such as balsam fir (*Abies balsamea* (L.) Mill.), became more predominant. These large-scale patterns of vegetation change and fire frequency match the $\delta^{18}O$ temperature reconstructions for the Holocene (Edwards et al., 1996). From the North American Pollen Database (NAPD), Viau et al. (2006) used over 700 radiocarbon-dated pollen time series to highlight two major periods of warming : the first between 14000 and 8000 cal yr BP and a second from 6000 to 3000 cal yr BP. The cooler periods occurred between 8000 and 6000 cal yr BP and from 3000 cal yr BP to the present. In addition, the authors identified a higher frequency, 1 100-year cycle of ± 0.2 °C during the entire Holocene. The Little Ice Age (1350–1850 AD) and the Medieval Warm Period (1100–1200 AD) (Moberg et al., 2005; El Bilali et al., 2013; Wanner et al., 2008) are the most recent manifestations of this high-frequency variability. Thus, existing boreal landscapes represent a combined inheritance of natural disturbance history and climate conditions occurring over the Holocene Grondin et al. (2014); Asselin et al. (2016). While the interactions between fire activity and climate at different time and space scales are relatively well understood for the boreal forest (Ali et al., 2012; Blarquez et al., 2015; Remy et al., 2017), the interactions between insect outbreaks, fire and climate remain uncertain. In a previous publication (**?**), we presented a new methodology that overcame the shortage of long-term SBW indicators. We showed that fossil lepidopteran wing scales extracted from lake sediments may act as indicators of SBW abundance. This proxy is well-preserved in sediments due to its inert chitinous composition. It also requires a relatively small sample volume (in comparison to using cephalic head capsules and feces). Lepidopteran wing scales can then be combined with other more traditional proxies to reconstruct a landscape dynamic based on insect outbreaks as well as fire history and the resulting vegetation mosaic. This study uses this new approach to reconstruct a multi-millennial history of SBW abundance, analyze interactions between SBW abundance and fire and assess the role of SBW on forest compositions in the context of Holocene climate variation. We use lepidopteran wing scales in combination with charcoal and plant macrofossils (e.g. needles, leaves, seeds) to reconstruct, for the first time, a Holocene-scale history of the boreal landscape that includes changes in vegetation, fire frequency, and insect outbreaks. We hypothesize that lepidopteran scales should be found throughout the entire stratigraphy. Scattered episodes of high scale abundance should correspond to periods of warmer temperatures and lower fire activity which contribute to a good development of the insect populations and a high abundance of mature host trees. Scale abundance should also be correlated with the presence of fir and spruce macrofossils within the sediment record. In a much shorter time scale, higher scale abundance should also increase short-term fire frequency as insect-related defoliation increase the risk of ignition, providing an important quantity of flammable fuel to the forest ground (James et al., 2011).

3.2 MATERIAL AND METHODS

The study was conducted in the university experimental forest and we did not need any permission to sample the sites for this study. The field study did not involve endangered or protected species. This study did not imply vertebrate species.

3.2.1 SITE SELECTION AND SEDIMENT CORING

The study area, Lake Flévy (48°13'00"N; 71°12'57"W), is in southeastern Quebec at the interface between the eastern balsam fir-white birch domain and the western balsam fir-white birch domain (Fig 3.1). The former domain is known to be drier and to has a shorter fire return interval (Bouchard et al., 2008). Lake Flévy is also located in the northern portion of the present-day spruce budworm distribution providing possible insight on the evolution of species distribution under changing climate conditions (Régnière et al., 2012). The surrounding landscape is characterized by highly sloping, forest-covered hills dominated by spruce-fir stands, particularly on well-drained mesic to hydric locations (hill tops and valley bottoms). Lake Flévy is surrounded by even-aged stands of trembling aspen (*Populus tremuloides*

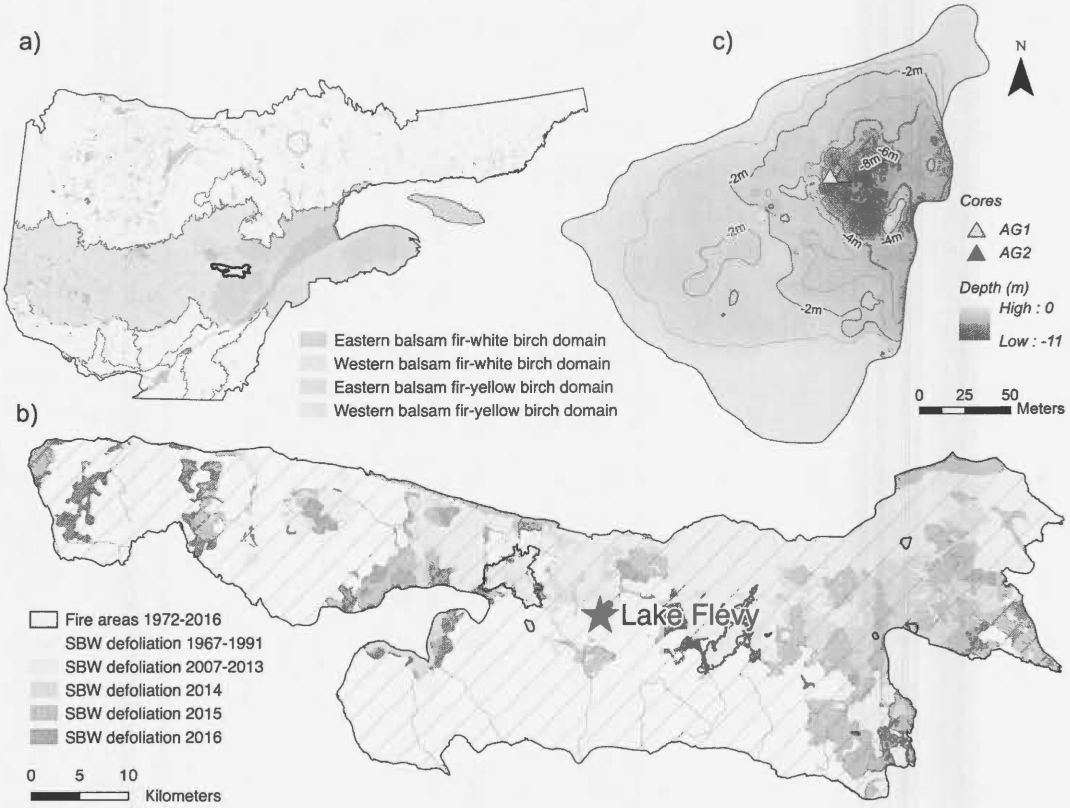

Figure 3.1: Location of the study site : (a) bioclimatic domains in the south-central portion of Quebec, Canada, (b) a map of historical disturbances surrounding Lake Flévy and (c) a bathymetric map of Lake Flévy showing core sites.

(Michx.)) and mixed even-aged stands of black spruce and aspen. These forest stands originated after an intense fire that occurred in 1922 AD (Gagnon, 1989) (Fig 3.1). SBW has been present in the area for a minimum of 8 240 years (Simard et al., 2006) and a number of outbreaks have occurred over the last three centuries, becoming more frequent during the 20^{th} century (Blais, 1983). Aerial surveys indicate that since 2012 AD, SBW-related defoliation has occurred in the resinous stands around the lake reaching severe levels after 2015 AD (Ministère des Ressources Naturelles et de la Faune, 2012b; Ministère des Forêts de la Faune et des Parcs, 2015) (Fig 3.1). Regional climate is continental subpolar with a mean annual temperature of 0 °C, mean annual precipitation of 1 000 mm and an average growing season of 155 days (Blouin et al., 2008). The study lake is located in the university experimental forest of Simoncouche and no permission was required in order to sample this site. The field study did not involve endangered or protected species. The lake was chosen for its small size (2.33 ha) and limited inflow and outflow to the lake, thereby favouring a relatively high sedimentation rate and the retention of a local signal within the sediment record (Fig 3.1). Two cores were extracted from the deepest portion of the lake (4.8 m) using a Livingstone piston corer. The first core (AG1) was analyzed at the Université du Québec à Montréal (UQAM) for plant macrofossils and charcoal. The second core (AG2) was analyzed at Université du Québec à Chicoutimi (UQAC) for SBW microfossils.

3.2.2 SAMPLES PREPARATION

The chronological framework for both cores was determined using AMS radiocarbon dating of organic sediments. Samples from AG1 were analyzed at the Beta Analytic Lab in Miami, Florida. Samples from AG2 were prepared in the radiochronology laboratory of Université Laval's Centre for Northern Studies, then sent to the Keck Carbon Cycle AMS Laboratory, University of California, Irvine. The InCal13 database was used for calibrating ^{14}C dates (Reimer et al., 2013). Sediment accumulation rates were calculated applying a 3^{rd} degree polynomial model using the Clam 2.2 software (Fig 3.2). All dates are expressed as calibrated years BP (cal yr BP) (Table 3.1).

Both cores were subsampled at a centimeter-scale resolution. For charcoal extraction, a ca. 1 cm^3 subsample was collected at each centimeter of AG1. This sediment was deflocculated in a 100 mL, 3 % NaP_2O_4 solution for 3 h. Each sample was then sieved through a 160 μm mesh to collect charcoal derived from local fires (Higuera et al., 2007), then soaked in a 10 % NaOCl solution to bleach the organic matter and help discriminate charcoal fragments. The remaining AG1 sediment was deflocculated and then sieved through a 160 μm mesh. The recovered >160 μm fraction was transferred to petri dishes. Macrofossil remains, such as needles, twig,

Tableau 3.1: Radiocarbon ages obtained from dating of organic sediment from the sediment cores AG1 and AG2. Calibrated ages determined using the IntCal13 calibration curve (Reimer et al., 2013). * Denotes date deemed as an outlier.

Reference	Site and depth (cm)	Dated material	^{14}C age (BP)	±	Calibrated age range 2σ (cal Yr BP)	Median (cal Yr BP)
	AG1					
Beta - 401650	482-487	Organic sediment	930	30	787-922	853
Beta - 401649	533-537.5	Organic sediment	1620	30	1413-1567	1515
Beta - 401648	593-597	Organic sediment	1680	30	1529-1629	1585
Beta - 401647	652.5-658	Organic sediment	2250	30	2157-2265	2299
Beta - 401646	712.5-718	Organic sediment	2950	30	3002-3207	3110
Beta - 401645	774-777.5	Organic sediment	3550	30	3812-3923	3846
Beta - 401644	833-838	Organic sediment	4190	30	4624-4763	4730
Beta - 401643	893.5-896	Organic sediment	4970	30	5611-5747	5693
Beta - 401642	955-956.5	Organic sediment	5510	30	6276-6353	6304
Beta - 401641*	**1002-1002.5**	**Organic sediment**	**19190**	**80**	**22870-23427**	**23122**
	AG2					
ULA-7074	503-504	Organic sediment	725	20	661-688	675
ULA-7075	552-553	Organic sediment	1135	20	969-1081	1024
ULA-7076	576-577	Organic sediment	1810	20	1699-1818	1753
ULA-7077	607-608	Organic sediment	2360	20	2341-2433	2356
ULA-7078	643-644	Organic sediment	2760	15	2791-2882	2851
ULA-7079	684-685	Organic sediment	3030	15	3173-3253	3225
ULA-7080	726-727	Organic sediment	3265	15	3451-3513	3486
ULA-7081	783-784	Organic sediment	4140	15	4581-4725	4683
ULA-7091	871-872	Organic sediment	4850	15	5585-5605	5595
ULA-7092	923-924	Organic sediment	6505	15	7416-7459	7428
ULA-7093	956-957	Organic sediment	7800	15	8547-8600	8579
ULA-7096	999-1000	Organic sediment	8880	20	9981-10156	10037

seeds, and cone scales, were analyzed using a binocular microscope and identified based on comparisons with reference collections (Young et Young, 1992; Crow et Hellquist, 2000b,a).

Samples from AG2 were prepared following ?. Each sample was dried at 105 °C for 24 h to recover a 0.5 g subsample of dry sediment (± 5 cm^3). These samples were then heated in a 100 mL 10 % potassium hydroxide (KOH) solution at 70 °C for 30 min or until complete deflocculation had occurred. The slurry was then sieved through a 53 μm mesh to retain most scales. We centrifuged the samples at 500 rcf for 10 min in a 10 mL sucrose solution (relative density = 1.24) to remove higher density particles. The centrifuging was repeated three times. After each run, we recovered the supernatant, refilled the vial with the sucrose solution, and centrifuged again. We combined the three supernatants in a 50 mL plastic vial and, to precipitate scales and any remaining particles, centrifuged the combined supernatant at 3 900 rcf for 20 min. The final pellet was mounted onto microscope slides for microfossil counting.

3.2.3 DATA HANDLING AND IDENTIFICATION OF PEAKS

Accumulation rates were calculated using CharAnalysis 1.1 (Higuera et al., 2009). In order to balance sedimentation rates variations amoung the two cores, each proxy concentration values and deposition times were interpolated to pseudo-annual intervals. The resulting values were then integrated over 5-year intervals and divided by the average deposition time over those intervals (Long et al., 1998). The influx series so obtained ($C_{i}nt$) allows for core to core comparaision and peak analysis. A stratigraphy was developed using the accumulation rates of each indicator. In Psimpoll 4.27, we used stratigraphically constrained cluster analysis (CONISS) to define three different assemblage zones (Bennett, 2007). Principal component analysis (PCA) was used to identify the main variables that explain the evolution of the ecosystem within these zones. To extract fire events from the charcoal stratigraphy, a background component (C_{back}) was defined using a Lowess smoothing that was robust to outliers and that had a smoothing window of 500 years. C_{back} have been extracted from the interpolated serie of raw data (C_{int}) to define a peak serie (C_{peak}) as a residual of C_{int}-C_{back}. A noise component (C_{noise}) was calculated for the C_{peak} series using a Gaussian mixture model. A threshold for fire detection (C_{fire}) was defined based on the 99^{th} percentile of the Cnoise distribution. Cfire samples and samples preceeding the Cfire sample that have a >5% probability of being from the same Poisson distribution were discarded.. From the fire event dates, we calculated fire frequency over a 500 years bandwidth and smoothed this using a Lowess smoother. This procedure was also used for insect outbreak detection and frequency. In the same way that a charcoal peak is associated with a fire event, a scale peak is associated by charanalysis with a period of high lepidotera abundance. It is important to note, however, that at this temporal scale, a peak could represent multiple outbreaks. All scales from samples that were associated with a peak were identified so as to confirm a correspondence to a known outbreaking lepidopteran morphotype (?). ANOVA was used to determine the mean differences between the relative occurrence of each species morphotype, and a Tukey's range test determined whether the means were significantly different.

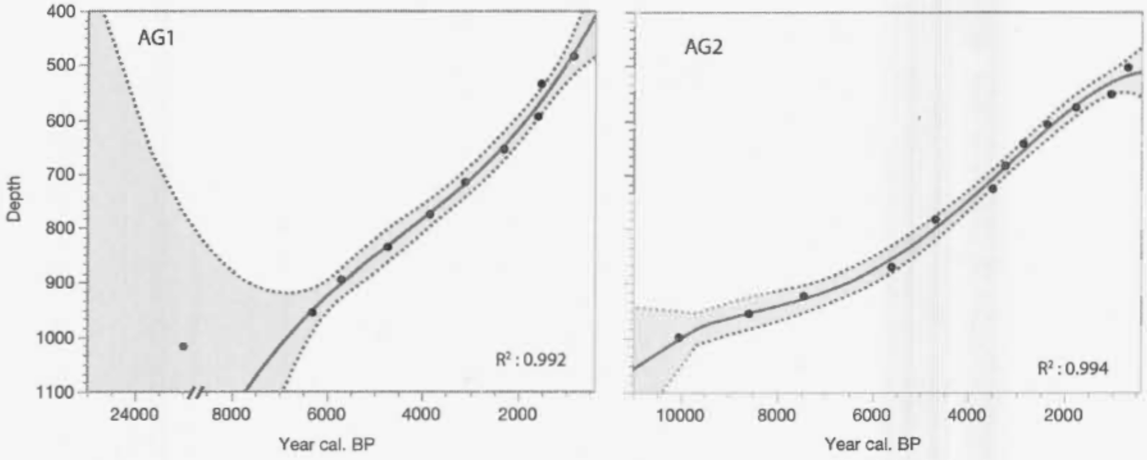

Figure 3.2: Age-depth model of the sedimentary cores collected at Lake Flévy, Quebec. Error bars represent measurement error. Gray shading of age-depth curve reflects calibration curve error. Sedimentation rates represent a linear interpretation between radiocarbon dates.

3.3 RESULTS

Core AG1 was 519 cm long and was dated to more than 6 000 cal yr BP (Fig 3.2). One date was excluded from the age-depth model as it was considered as outlier (Table 3.1). Indeed, the radiocarbon date at the bottom of AG1 (Beta – 401641) was probably influenced by the presence of stromatolites in the sampling lake (B. Lapointe, personal communication), probably originating from the lac Mistassinni (Dionne, 1986) The sediment accumulation rate was relatively stable across the core varying from 6 to 16 $\mathrm{yr{\cdot}cm^{-1}}$. Core AG2 was 511 cm long and represented almost 10 000 yr of deposition. The sediment accumulation rate of AG2 was more than two times slower than that of AG1 from 1 0000 to 6 000 cal yr BP, then was more similar to that of core AG1 over the last 6 000 years (Fig 3.2). The two cores consisted essentially of homogenous organic sediment (gyttja) (Fig 3.3). CONISS identified three distinct assemblage zones along the composite stratigraphy. Zone I (6 700–6 250 cal yr BP) defines the earliest section of AG1. This relatively short time interval had marked presence of larch (*Larix laricina* (Du Roi) K.Koch.), balsam fir and, to a lesser extent, black spruce macrofossils. Some minor charcoal peaks were also identified in this zone. Zone II (6 250–2 700 cal yr BP) covers a major portion of the core. Charcoal was nearly absent from this zone that was characterized by the predominance of eastern white pine (*Pinus strobus* (L.)), a more thermophile and less fire-adapted species. In this zone, black spruce, larch, and balsam fir were less common than in Zone I despite some major peaks ca. 3 600 and 5 800 cal yr BP. Some isolated peaks of jack pine (*Pinus banksiana* (Lamb.)) were also observed during this period. This zone was also marked by a high number of lepidopteran scale peaks around 4 500, 3 600, and 2 900 cal yr BP. Zone III (2 700 cal yr BP to 975 cal yr BP) represents the most recent portion of the lake record. It includes a subzone between 2 700 and 2 050 cal yr BP representing a transition between zones II and III.

In the subzone, every indicator was nearly absent except for lepidopteran scales and some

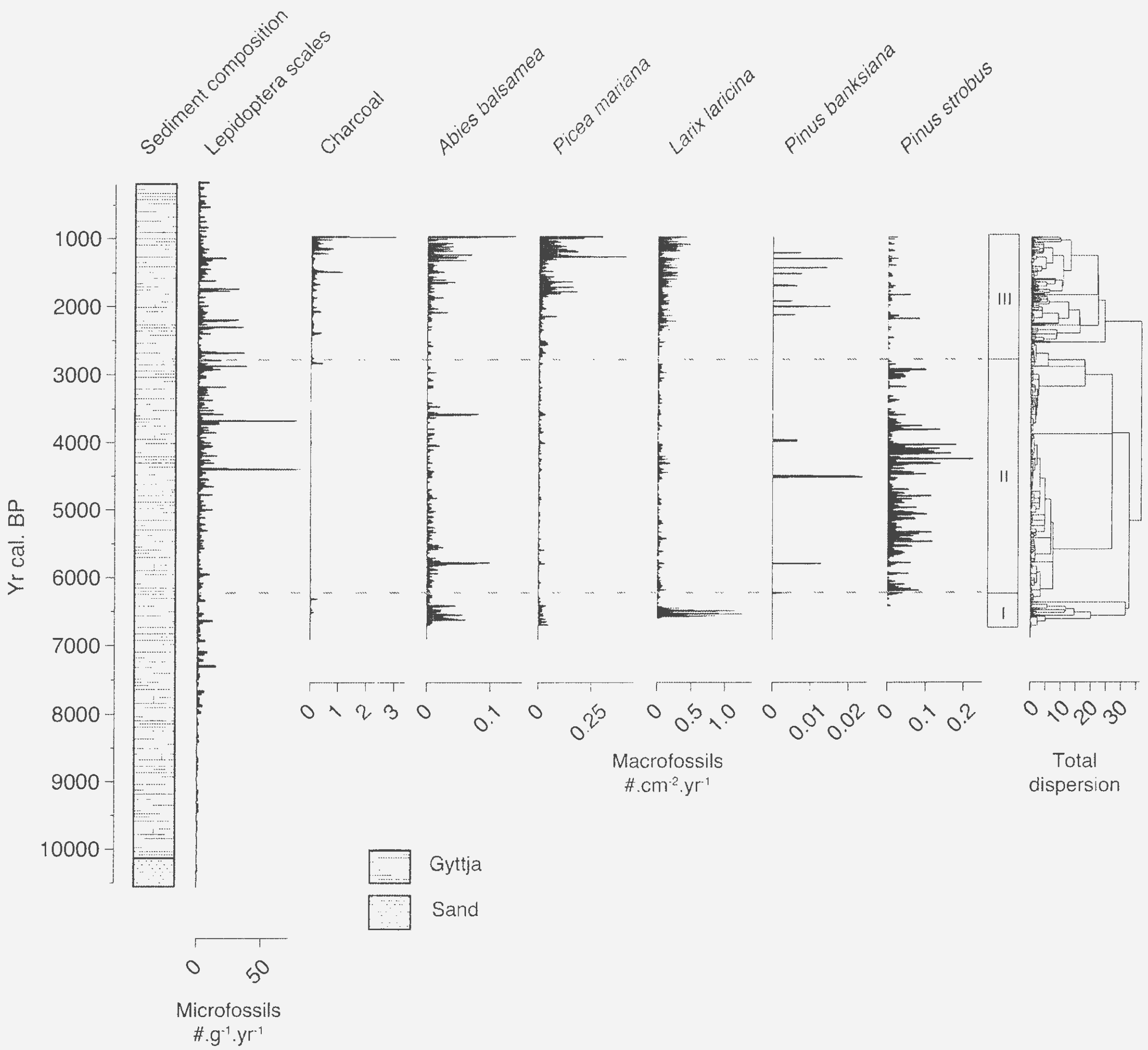

Figure 3.3: Stratigraphy of accumulation rates for lepidopteran scales ($\# \cdot g^{-1} \cdot yr^{-1}$), charcoal and plant macrofossils ($\# \cdot cm^{-2} \cdot yr^{-1}$) from cores recovered from Lake Flévy. Lepidopteran scales were counted from core AG2. Charcoal and plant macrofossils were counted from core AG1

black spruce macrofossils. Between 2 050 and 975 cal yr BP, the landscape returned to an early Holocene similar stage characterized by a higher proportion of boreal taxa such as balsam fir, black spruce and larch. Two high magnitude peaks of lepidopteran scales were observed around 1 300, 1 700 and 2 300 cal yr BP. Charcoal, balsam fir, and black spruce macrofossils showed a delay following those lepidopteran peaks. Some remains of jack pine were also identified between 1 000 and 2 000 cal yr BP, however their abundance was very low relative to the other taxa.

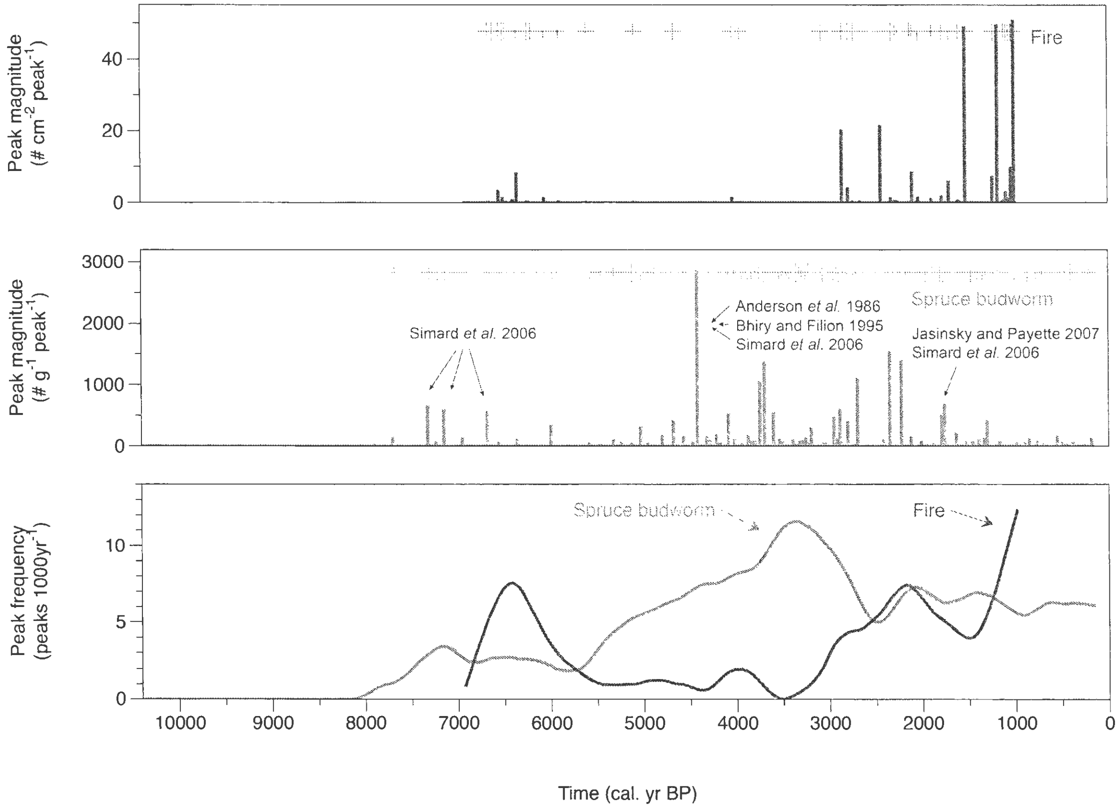

Figure 3.4: Magnitude of fire (a) and Lepidopteran scale (b) peaks ($\# \cdot cm^{-2} \cdot peak^{-1}$). Each peak exceed the 99th percentile threshold of the residual of Cint-Cback (c) The frequency of fire and SBW (peaks·1000yr-1).

A total of 87 lepidopteran scale peaks and 41 charcoal peaks were identified from both cores (Fig 3.4). Although not all scales from these peaks could be identified based on the morphotypes described in Navarro et al. (**?**), 62% of the identified scales corresponded to a SBW morphotype. The ANOVA confirmed that Choristoneura fumiferana was significantly more represented than the other outbreak species ($p < 0.0001$). Morphotypes of the forest tent caterpillar (*Malacosoma disstria* (Hübner)) and hemlock looper (*Lambdina fiscelaria* (Guénée)) were less frequently identified (Fig 3.5) and their relative occurence were not significantly different ($p = 0.28$) from each other. Identification based solely on shape morphotype prevented us from identifying the majority of those scales (77%) extracted from the peaks as many either were broken or folded. The frequency of scale peaks was greater than that of charcoal between 5 500 and 2 500 cal yr BP reaching a frequency of 13 peaks per 1 000 years at ca. 3 200 cal yr BP. Between 1 500 and 1 000 cal yr BP there was a reversal of this trend with a fire event rate reaching a maximum frequency of 13 peaks per 1 000 years. The first two axes of the PCA explained 47.6% of the total variation, 32% represented by Axis 1 and 15.6% represented by Axis 2 (Fig 3.6). The y axis separates Zone 2, mainly influenced by the SBW outbreak frequency and eastern white pine macrofossil abundance, from zones I and III that were more influenced by fire frequency, black spruce and larch macrofossil abundance. Zone I samples were less dispersed than Zone III samples reflecting the higher impact of larch macrofossils. The opposing directions of SBW outbreak frequency and balsam fir macrofossils along with the opposing relationship between fire frequency and eastern white pine macrofossils indicate that these variables varied inversely.

3.4 DISCUSSION

3.4.1 FIRE HISTORY AND CLIMATE

The charcoal accumulation rates from Lake Flévy match the known Holocene fire history in eastern Canada (Power et al., 2008; Ali et al., 2012; Blarquez et al., 2015; Remy et al., 2017) : a more fire-prone early and late Holocene separated by a reduced fire regime—relative to the present—during the mid Holocene. The Holocene fire history recorded in Lake Flévy tracks the $\delta^{18}O$-based, southern Ontario postglacial precipitation reconstruction of Edwards et al. (Edwards et al., 1996) as well as different paleofire regime modelisations from eastern Quebec (Ali et al., 2012; Girardin et al., 2013b; Hély et al., 2010). Post- and neoglacial periods were cold and dry leading to a higher fire frequency and a dominance of more fire-adapted trees, such as Picea mariana, that are resilient to cooler conditions and drought (Belien et al., 2014). Although the mid Holocene was warmer (Viau et al., 2006), fire activity was very low, likely explained by a high relative humidity during this period (Edwards et al., 1996) and the presence of a more stable air mass leading to less frequent drought events (Carcaillet et Richard, 2000).

3.4.2 SBW OUTBREAKS OVER THE HOLOCENE

Based on our dataset, SBW outbreaks are not a rare phenomenon at the Holocene-scale which is in contradiction with our first hypothesis. Multiple peaks of scale abundance were identified downcore. Some have already been previously noted in a mire of the same area (<10km) using faecal macrorests, including outbreaks ca., 1930, 4500, 6650, 7180 and 7560 cal yr BP (Simard et al., 2006; Jasinski et Payette, 2007; Bhiry et Filion, 1996; Anderson et al., 1986). However, the novel use of lepidopteran scales also identified multiple, previously unobserved, periods of high lepidopteran abundance such as events at 2500, 2930, 3110, and 3850 cal yr BP.

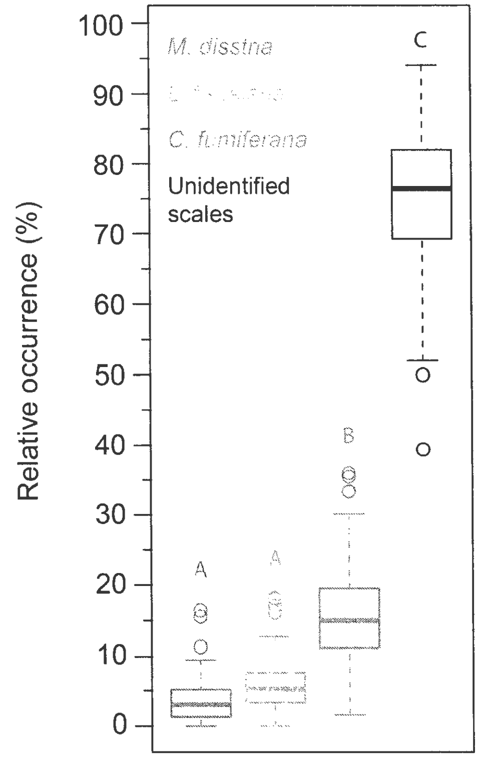

Figure 3.5: Identification of lepidopteran species identified from the 87 scale peaks from AG2. Malacosoma disstria and Lambdina fiscelaria occurrences were not significantly different (p = 0.28) from each other. Choristoneura fumiferana was significantly more represented than the other outbreak species (p < 0.0001) and the relative abundance of unidentified scales was significantly higher than the relative abundance of identified scales (p < 0.0001).

The scale peak at 4500 cal yr BP has been linked to a possible combined action from SBW and hemlock looper across northern Maine and southern Quebec (Simard et al., 2006; Bhiry et Filion, 1996; Anderson et al., 1986). Based on our identification criteria, outbreaks observed in our study site were not associated with hemlock looper. However, given the morphological similarity of the two species' scales, the exceptional quantity of microfossils recovered for this period and the unusual recent hemlock looper activity in the Laurentian Wildlife Reserve (in which Lake Flévy is situated) (Ministère des Ressources Naturelles et de la Faune, 2012a), we cannot completely exclude the possibility of the presence of both defoliators in the area. The

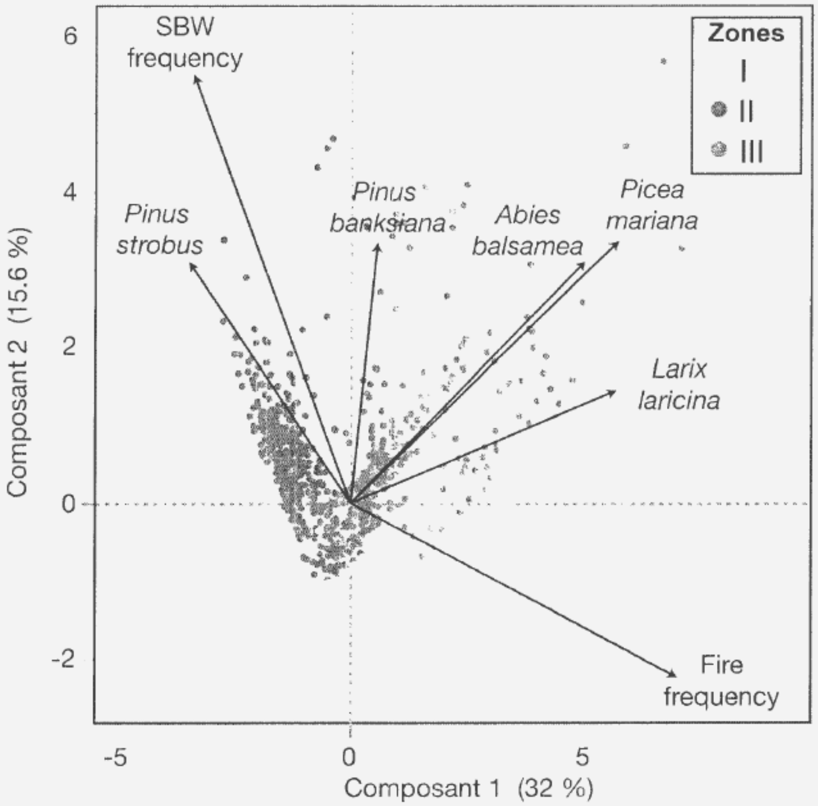

Figure 3.6: Principal component analysis (PCA) biplot of the mean scores along the first two components. The components were calculated using the different proxy indicators recorded from the two sediment cores recovered from Lake Flévy. Colors were assigned to each CONISS-defined zone : Zone I (early Holocene–6250 cal yr BP ; yellow), Zone II (6250–2700 cal yr BP ; red) and Zone III (2700 cal yr BP to the present ; blue).

high number of scale peaks identified in the Lake Flévy sediment record allows us to propose the first detailed Holocene-scale SBW outbreak record. The frequency of outbreaks varies over time with periods having a few outbreaks events (10000–6000 cal yr BP; 2500–1000 cal yr BP) and periods marked by very frequent events (5500–2500 cal yr BP). At a finer temporal scale, some lepidopteran outbreaks (1300, 1800, 4650 cal yr BP) seem to be associated with lagged charcoal, Abies balsamea and Picea mariana macrofossil peaks (Fig 3.3 and 3.5). This suggests a direct (and probably combined) influence of these disturbances affecting the input of plant macrofossils into the sediment record.

3.4.3 FIRE-INSECT INTERACTIONS

Previous studies (Stocks, 1987; Fleming et al., 2002) have shown that SBW outbreaks can enhance fire activity over the short term, providing a 5 to 10 yr window of opportunity during which "ladder fuel" builds up due to crown breakage and windthrow of the killed and damaged trees (Stocks, 1987; Fleming et al., 2002). Following this SBW outbreak-related window, humidity rises and the dead wood generated by the outbreak begins to rot (James et al., 2017). Using a 300 years model of disturbances interactions, James et al. (2011) argue that this ephemeral increase in fire risk due to budworm activity rarely leads to consecutive disturbances at longer timescales (James et al., 2011). SBW is known to be a cyclic, age-dependent, selective disturbance whereas fire ignition requires a more random event such as a lightning stike. Thus, there is less chance of an immediate succession between these two disturbances. In fact, the two disturbances showed an inverse relationship over the long-term (Fig 3.6) suggesting an effect of competition for limited resources (mature trees). When fire frequency is low, trees can grow fully and forests can reach a mature stage that enhances SBW activity. On the other hand, when fire frequency increases, there is less time for mature stands to become established, thereby limiting SBW activity.

3.5 CONCLUSION

Our results constitute an important starting point for combining and understanding the long-term interactions between natural disturbances, such as fire and SBW outbreaks, in the boreal forest. This approach provides valuable insight into long-term forest dynamics and may reveal spatial heterogeneity in disturbances (and their interactions). Recognizing these patterns would favor the development of different types of future sustainable management policies depending on the region. For example, this long-term approach could be applied to reconstructing western spruce budworm (*Choristoneura occidentalis* (Free.)) or mountain pine beetle (*Dendroctonus ponderosae* (Hopk.)) infestations in western Canada and United States and determining the interactions between outbreaks, fire, and climate in these regions. In a context of global change, it is critical to understand the long-term dynamics of the boreal ecosystem and combined role of multiple disturbances.

CHAPITRE IV

CHANGES IN SPATIO-TEMPORAL PATTERNS OF SPRUCE BUDWORM OUTBREAKS DURING THE 20TH CENTURY IN EASTERN CANADIAN BOREAL FORESTS

This chapter will be available soon in the journal *Frontiers in plant science*

"Navarro, L. Morin, H., Bergeron, Y., Montoro Girona, M (2018). Changes in spatiotemporal patterns of 20th century spruce budworm outbreaks in eastern Canadian boreal forests. Front. Plant Sci. doi : 10.3389/fpls.2018.01905"

4.0.1 ABSTRACT

In scenarios of future climate change, there is a projected increase in the occurrence and severity of natural disturbances in boreal forests. Spruce budworm (*Choristoneura fumiferana*) (SBW) is the main defoliator of conifer trees in the North American boreal forests affecting large areas and causing marked losses of timber supplies. However, the impact and the spatiotemporal patterns of SBW dynamics at the landscape scale over the last century remain poorly known. This is particularly true for northern regions dominated by spruce species. The main goal of this study is to reconstruct SBW outbreaks during the 20th century at the landscape scale and to evaluate changes in the associated spatiotemporal patterns in terms of distribution area, frequency, and severity. We rely on a dendroecological approach from sites within the eastern Canadian boreal forest and draw from a large dataset of almost 4 000 trees across a study area of nearly 800 000 km^2. Interpolation and analyses of hotspots determined reductions in tree growth related to insect outbreak periods and identified the spatiotemporal patterns of SBW activity over the last century. The use of an Ordinary Least Squares model including regional temperature and precipitation anomalies allows us to assess the impact of climate variables on trees growth reductions and to compensate for the lack of non host trees in northern regions . We identified three insect outbreaks having different spatiotemporal patterns, duration, and severity. The first (1905–1930) affected up to 40% of the studied trees, initially synchronizing from local infestations and then migrating to northern stands. The second outbreak (1935–1965) was the longest and the least severe with only up to 30% of trees affected by SBW activity. The third event (1968–1988) was the shortest, yet it was also the most severe and extensive, affecting nearly up to 50% of trees and 70% of the study area. This most recent event was identified for the first time at the limit of the commercial forest illustrating a northward shift of the SBW distribution area during the 20th century. Overall, this research confirms that insect outbreaks are a complex and dynamic ecological phenomena,

which makes the understanding of natural disturbance cycles at multiple scales a major priority especially in the context of future regional climate change.

4.1 INTRODUCTION

The boreal forest is the second largest terrestrial biome in the world, covering 14 million km^2, and forms a circumpolar forest belt (Burton et al., 2003) that represents about 25% of the world's forests (Dunn et al., 2007). At present, two-thirds of this surface is managed for wood production, and this proportion accounts for 37% of the global wood supply (Gauthier et al., 2015). However, an increasing number of studies predict marked consequences of climate change on boreal ecosystems through modifying the dynamics of natural disturbances at different scales and increasing the frequency and severity of events such as wildfires or insect outbreaks (Overpeck et al., 1990; Dale et al., 2001; Millar et al., 2007; Seidl et al., 2014, 2017; Alifa et al., 2017). Thus, improving our understanding of the variability of natural disturbance cycles at multiple scales will be a major challenge in the mitigation and adaptation of boreal forests and their management to climate change. Natural disturbance regimes determine the dynamics, structure. and composition of forests by altering ecosystem functioning (Anyomi et al., 2016; Montoro Girona et al., 2018b). Insect outbreaks are a key disturbance to consider in any forestry planning due to the important economic and ecological implications from these events Sturtevant et al. (2015). Insect outbreaks affect timber supplies and have a marked impact on overall forest productivity and dynamic. Among all the major insect pests, spruce budworm (*Choristoneura fumiferana* (Clemens)) (SBW) is the most important defoliator of conifer trees in North American boreal forests (Hardy et al., 1983; Morin et Laprise, 1990). In Canada, more than 90% of spruce and fir forests are affected cyclically by SBW outbreaks, and more than 50% of the annual loss of volume caused by insect damage is attributed to SBW-related defoliation (Ressources Naturelles Canada, 1994). While the consequences of defoliation remain relatively moderate in the Western Canadian provinces, in the eastern portions of Canada, SBW is responsible for significant losses for the forest industry, through high tree mortality and a loss of forest productivity (MacLean, 2016). SBW outbreaks are complex phenomena influenced by multiple factors including affected species, ecoregions, and climatic conditions (MacLean, 2016). Although insect outbreaks play an important role in forest dynamics, most studies involving SBW focus on the relationship with its primary host, balsam fir (*Abies balsamea* (L.) Mill.). Mortality occurs in fir stands after four years of severe defoliation and outbreaks affect a very high proportion of trees (MacLean, 1980; Bergeron et al., 1995). For secondary hosts, such as black spruce (*Picea mariana* (Mill.) BSP), the damage (and death) of tree tops and branches are often accompanied by reductions in growth of up to 75% (Nealis et Régnière, 2004b; MacLean, 1984). In black spruce, the resistance to defoliation is the result of a phenological asynchrony between the insect and its host (Volney et Fleming, 2007; Pureswaran et al., 2015). As the buds of black spruce burst 14 days later than those of balsam fir, the former is protected from severe SBW-related damage (Nealis et Régnière, 2004b). Indeed, although SBW is known to reach high latitudes corresponding to the distribution area of balsam fir (Harvey, 1985; Payette, 1993; Levasseur, 2000), its impact on black spruce domain is lower, especially in situations where a cold summer prevents eggs from hatching, disrupting the annual cycle of the insect (Nealis et Régnière, 2009). Thus, it is expected that epidemic cycles should be more difficult to identify in the spruce–moss domain, the ecoregion that supports most of the timber industry in eastern Canada due to its wide range and the excellent wood properties of black spruce (Robitaille et Saucier, 1998; Zhang et Koubaa, 2008). The reconstruction of insect outbreak cycles at the landscape scale is a major challenge as aerial surveys of defoliation—conducted annually since the 1960s—only cover one outbreak in the last century and are concentrated mostly in the balsam fir area. Dendroecological approaches are a reliable alternative for studying natural disturbances in forest ecosystems at a fine resolution (Montoro Girona et al., 2016, 2017). Tree rings provide indirect measurements of insect activity, through the identification of years of growth reduction related to insect outbreaks, thereby allowing the reconstruction of SBW cycles at multiple scales (Morin et Laprise, 1990; Morin, 1994; Krause, 1997; Jardon, 2001; Boulanger et Arseneault, 2004; Boulanger et al., 2012). In regard to the spatial extent of SBW outbreaks, some studies have attempted to produce a portrait of past events via both model from aerial survey datasets (Fleming et Candau, 1998; Gray et Mackinnon, 2006) or tree-ring analysis (Jardon, 2001). However, the spatiotemporal changes of outbreaks dynamics at the landscape scale over the last century in North American boreal forests remains poorly known. The main goal of this study is to reconstruct the SBW outbreaks during the 20th century at the landscape scale and to evaluate changes in the spatiotemporal patterns in terms of distribution area and severity using dendroecological data collected from the eastern-Canadian boreal forest. We hypothesize that the spatial pattern will be similar from one outbreak to another with some variation in terms of intensity and expansion. We expect the last outbreak of the 20th century to have a greater expansion in the spruce domain. This would give credence to the hypothesis of a northward shift of the SBW distribution in Quebec over the last cycles. However, we expect to observe a time lag in the emergence of the epidemic in the north, as well as a lag in growth reductions, both lags due to the lower susceptibility of black spruce stands. To improve the understanding of spatial temporal patterns of SBW activity, historical climatic data were used to examine the influence of precipitation and temperatures anomalies on outbreaks periods.

4.2 MATERIAL AND METHODS

4.2.1 STUDY'S AREA AND DATA HANDLING

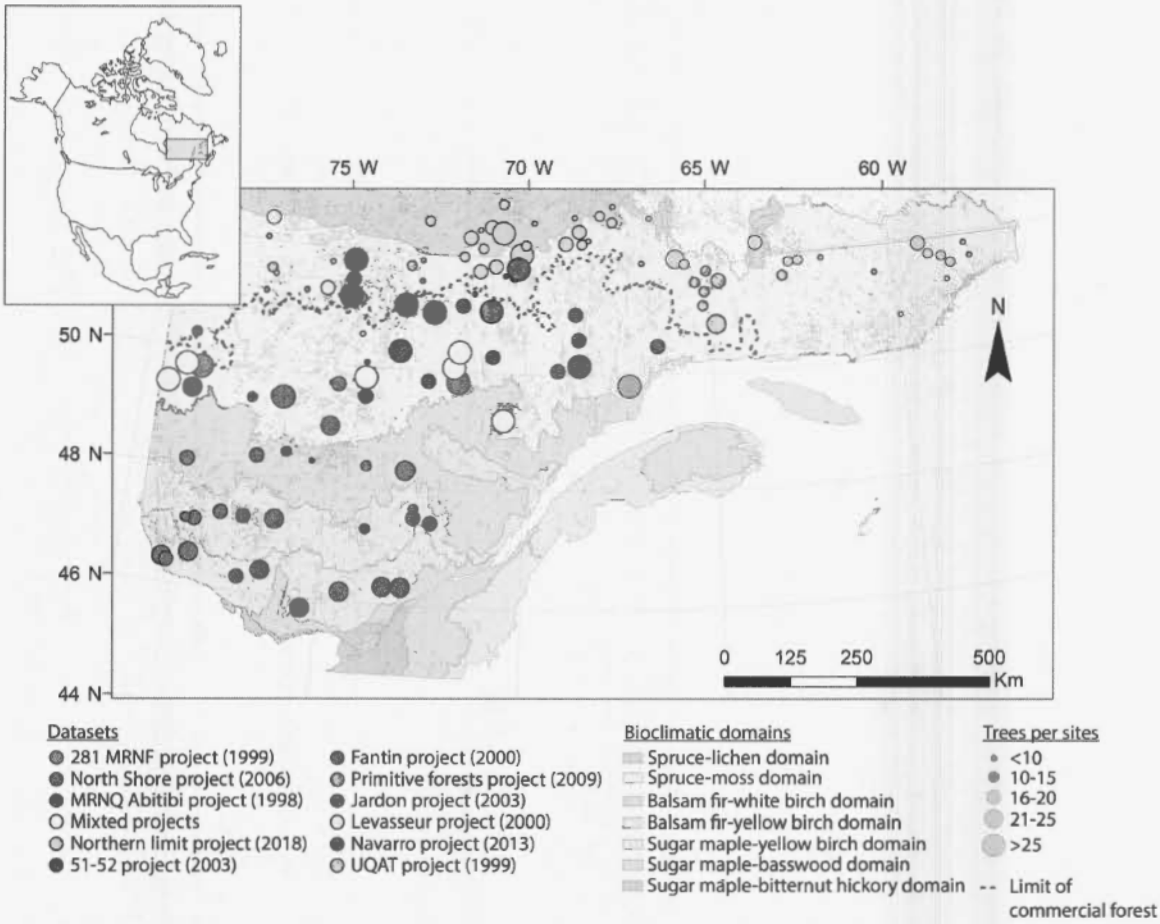

Figure 4.1: Study sites distribution in Quebec (Canada), where different colors correspond to the original dataset.

The study area is located in the boreal zone of Quebec (Canada) covering nearly 800 000 km^2 (45.5–53°N and 58–79°W) (Fig 4.1). This research involves a gradient of stand structures and ecoregions, from closed, dense forests in the fir and spruce–moss domain to the south, to the more open and fragmented forests in the spruce–lichen domain to the north. The study area crosses the northern limit of the commercial forest, separating managed forests to the south from unmanaged ones to the north. The forest landscape is composed of coniferous species, dominated mainly by pure black spruce stands in the north and mixed forests of white spruce, fir, and broadleaved trees in the south. Regional climate is subpolar humid with a medium length of growing season (≥ 170 days) in the fir domain to a cold subpolar sub-humid climate with a much shorter growing season (≤ 100 days) in the spruce domains (Gerardin et McKenney, 2001). The eastern portion of the of the study area has a greater annual precipitation (ranged from 950 to 1350 mm), and the fire return interval is longer ranging from 270 to >500 years (Cyr et al., 2007).

Tableau 4.1: Database compiled in this study

Database	Date	Publication	Species	Trees number	Max age	Site number
281 MRNF	1999	-	*P. mariana*	15	251	1
Project North Shore	2006	-	*P. mariana*	69	234	1
MRNQ Abitibi	1998	-	*P. mariana*	9	205	1
Mixted projects	-	-	*P. mariana*	962	309	6
Project Northern Limit	2018	Present publication	*P. mariana*	738	346	56
Project 51-52	2011	(Tremblay et al., 2011)	*P. mariana*	992	292	13
Project Fantin	2000	-	*P. mariana*	40	179	3
Primitive forests	2009	-	*P. mariana*	50	275	1
Project Jardon	2003	(Jardon et al., 2003)	*P. Glauca*	608	250	32
Project Levasseur	2000	(Levasseur, 2000)	*P. mariana*	203	253	4
Project Navarro	2013	(Navarro, 2013)	*P. mariana*	120	291	4
Project UQAT	1999	-	*P. mariana*	31	176	1
			TOTAL	**3837**		**123**

4.2.2 *DATA COMPILATION AND EXPERIMENTAL DESIGN*

We undertook a data collection strategy to obtain the maximum amount of dendroecological data available for the years 1900–1990 from the study area. This database incorporated sites from eight projects undertaken at the University of Quebec in Chicoutimi over the last 20 years, two datasets from the Canadian Forest Service, and one project from the University of

Quebec in Abitibi-Temiscamingue (Table 4.1). The dataset was complemented by an important field survey by Natural Resources Canada, undertaken between 2005 and 2010 in the northern portion of the study area (northern limit project). In this survey, more than 800 sampling plots (400 m^2 each) were sampled. In each plot, wood disks were collected from seven dominant living trees and the three dominant living saplings. Due to the size of our study area and the diversity of datasets sources, the original dataset was filtered to delete sites having a low number of samples (<8), and to keep only black spruce having an age of >100 years, excluding saplings samples. The age criteria was established to guaranty that tree samples were able to register multiple insect outbreaks during the 20th century providing long chronologies across the study area. Based on the scale of this metanalysis and to maximize the number of trees per location, we aggregated some sites from the same ecoregions if they were close enough ($\leq$20 km). This dataset is original and is quite valuable due to the size of the study area, the high number of trees used in this study, and the inclusion of new chronologies at the limit of the commercial forest in remote areas that are not accessible by road (Table 4.1, Fig 4.1).

4.2.3 DENDROECOLOGICAL DATA

We selected trees based on dominant species criteria to ensure that the samples were representative of the study stands. All sites were composed exclusively of black spruce, with the exception of Jardon et al. (2003) where the samples were composed of white spruce (Table 4.1). For this study, a total of 3837 samples were used. The samples were prepared, measured, and analyzed based on standard dendroecological protocols (Krause et Morin, 1995). Breast height collected wood disks were air-dried and sanded before tree rings were measured with a WinDendro™ system (Guay et al., 1992) or a manual Henson micrometer having an accuracy of 0.01 mm. The tree-ring series measurements covered all the entire life of the sampled tree, and the ring patterns were cross-dated using. COFECHA (Holmes, 1983). We applied a double detrending method having a 50 years window spline and a negative exponential using

ARSTAN (Holmes et al., 1986). Detrending reduced the effects of tree age, genetic growth potential, microsite and stand history, as well as minimizing the effect of climate allowing trees of different growth rates to be compared (Fritts, 1971). Autocorrelation in standardized time series was not removed for the sake of uniformity with similar studies (Krause, 1997; Boulanger et Arseneault, 2004; Tremblay et al., 2011; Boulanger et al., 2012) and because outbreak signal is autocorrelative by nature. The detrended chronologies were averaged to produce a mean standardized chronology for each stand. For the purpose of extracting the climatic signals in host series, most studies use a host–non-host correcting method using the OUTBREAK program (Holmes et Swetnam, 1994). In our case the lack of non-host species in northern latitudes (black spruce domain) make their use at large scales challenging. In order to overcome this issue we used modeled climatic datas (see below). An epidemic period was defined as a growth reduction ($\geq$1.28 SD on the mean standardized chronologies) of at least five consecutive years allowing one year of growth release (Jardon et al., 2003). The severity of insect outbreaks was defined by the proportion of trees at each site that presented such a pattern of growth reduction. This dendroecological approach was used on previous research on black spruce stands (Tremblay et al., 2011; Boulanger et al., 2012).

4.2.4 DATA ANALYSIS

To establish the patterns of SBW activity, spatial data related to insect outbreaks were interpolated based on the percentage of trees affected using an Inverse Distance Weighted (IDW) interpolation (Childs, 2004). Only the epidemic years are shown (Fig 4.4). The complete chronology can be found in the supplementary materials (Sup. 4.7, Sup. 4.8, Sup. 4.9, Sup. 4.10, Sup. 4.11, Sup. 4.12).

4.2.5 CLUSTER AND HOTSPOT ANALYSIS

To evaluate the spatial synchrony of insect outbreaks, hotspot and cold-spot analyses estimated spatial clustering among the study sites affected or not affected by SBW outbreaks in eastern Canada based on the Getis-Ord local statistic using fixed distance band which is estimated as :

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j} x_j - \overline{X} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{n \sum_{j=1}^{n} w_{i,j}^2 - \left(\sum_{j=1}^{n} w_{i,j} \right)}{n-1}}}$$

$$\overline{X} = \frac{\sum_{j=1}^{n} x_j}{n}$$

$$S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\overline{X})^2}$$

where x_j is the percentage of trees affected for site j, $w_{i,j}$ is the spatial weight between i and j and n is equal to the total number of sites.

Hotspot/coldspot fields were recognized based on statistically significant levels (i.e. 0.1, 0.05, or 0.01) ; those are fell into hotspots, where high values intermingled high values (red dots in Fig. 4.4) and coldspots where low values intermingled low values (blue dots in Fig. 4.4). Areas where high values were surrounded by lower values, and where low values were surrounded by higher values were considered as non-significant clusters (tan-colored dots in Fig. 4.4). To summarize the overloading of maps, these outputs were also presented using Hovmöller diagrams (Persson, 2017). This tool is effective for displaying large amounts of data, it is a technique frequently used in atmospheric sciences (Du et Rotunno, 2018). This diagram represents the longitude (or latitude) versus time with the value of the dataset represented through color or shading. RasterVis and LevelPlot R packages were used to plot Gi*Z scores and p-values (Fig 4.3).

4.2.6 CLIMATE DATASET

To improve the interpretation of patterns in the dendrochronological data , we used a climatic dataset provided by the Climatic Research Unit at the University of East Anglia (CRU TS 3.10). This model is based on an updated gridded climate dataset across the global land areas (excluding Antarctica). The data available for our study area was provided by the Canadian Historical Temperature Database (Vincent et Gullett, 1999). The dataset is composed of monthly precipitation and mean temperature observations on a 0.5-degree latitude/longitude grid over the entire 20th century. Anomalies (positive and negative mean deviations) were estimated using the mean values for each cell for the period with best coverage (1961-1990) (Jones et al., 2012). These anomalies were averaged for each season and used as explanatory variables to compute Ordinary Least Squares linear regression in order to model their relationships to the percentage of affected trees (dependant variable). In the absence of non-host chronologies at the landscape scale, this procedure allows us to better assess what proportion of the variability is relative to climatic factors versus the unexplained part (residuals) which can be attributed to SBW outbreak. A Spatial Autocorrelation (Moran's Index) was conducted on standard deviations (SD) of the residual to analyse its clustering level. All the spatial statistics were calculated using the "Spatial Statistic" extension of ArcGIS 10.3 (ESRI Inc, 2017).

4.3 RESULTS

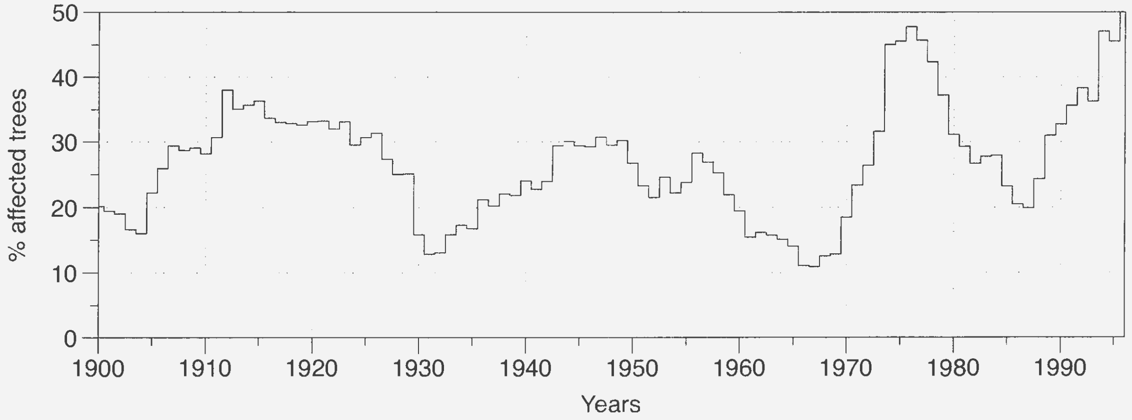

Figure 4.2: Proportion of all trees affected by outbreaking conditions in the study area.

The percentage of affected trees over the entire study area revealed three main SBW outbreak periods in eastern Canadian forests over the last century (Fig. 4.2). Each insect outbreak differed in terms of duration and severity. The first outbreak occurred between 1905 and 1930, and nearly 40% of the studied trees were affected by SBW activity at the epidemic's peak (1914). The second outbreak was the longest infestation, lasting from 1935 to 1965, although it had the lowest severity level with only 30% of trees being affected during the peak (around 1950). The third outbreak from 1968 to 1988, was the shortest, yet it was the most severe affecting nearly 50% of the studied trees in 1977.

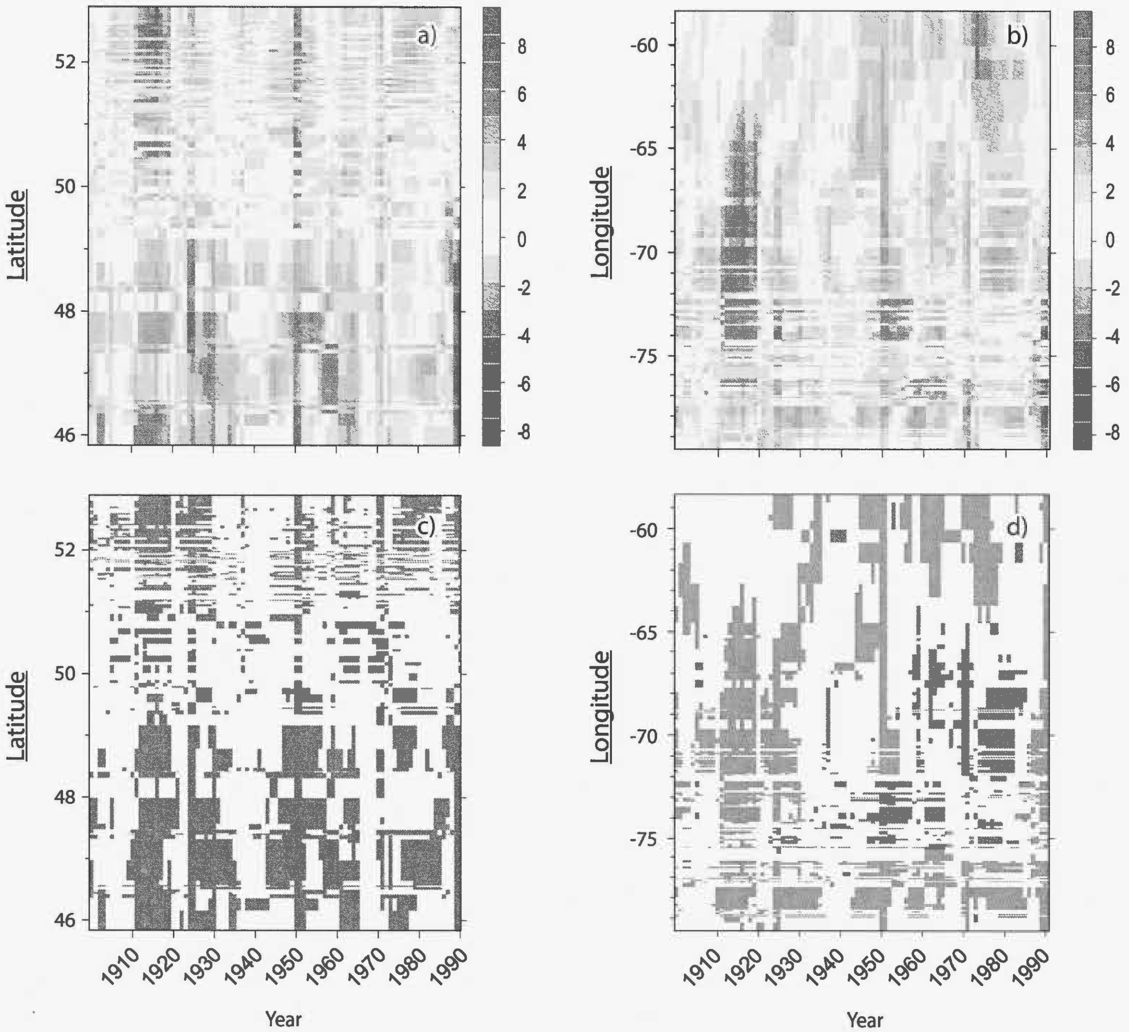

Figure 4.3: Hovmöller diagrams for the spatio–temporal patterns of spruce budworm outbreak impact during the last century in Eastern Canadian boreal forests where a) and b) represents respectively Z-score of Getis Ord Hotspot analysis by latitudes and by longitudes. Red represent hotspot of high percentage of affected trees and blue represent coldspot of low percentage of affected trees. c) and d) present respectively the significativity by latitudes and by longitudes. Red : p-value <0.05 ; white : p-value>0.05

Hotspot and cluster analyses revealed changes in the spatiotemporal patterns of SBW dynamics, as well as the impacts across the eastern Canadian boreal forest during these three periods of budworm outbreak over the last century (Fig. 4.3 and 4.4). From 1905 to 1910, no hotspots were recorded. This pattern indicates no synchronization at the landscape scale, although we detected a pattern of locally affected sites from the southwest to the east with a moderate percentage of affected trees (Fig. 4.4 and 4.7). A significant hotspot, composed of multiple sites was registered in the southwestern portions of the study area in 1911. This infestation reached a maximum affected area of ≈280 000 km2 in 1914, and then fell to a lower impact phase in 1921 (Fig. 4.4 and 4.7). This outbreak affected primarily white spruce sampled within the fir domain (Jardon, 2001). SBW activity demonstrated a temporal delay when the area north of the 50th parallel was affected at a later date (1920–1930), with a lower proportion of affected trees and a lower clustering level compared to previous events to the south of our study area (Fig. 4.3 and 4.4). A similar pattern was observed for the second insect outbreak; various sites recorded moderate to severe outbreaks at the local scale prior to the onset in 1944. Four spots had persistently high percentages of affected trees from the early 1940s (the Abitibi region, southwest of Lake Saint-Jean, the Upper North Shore, and Lake Mistassini). There was a cluster of sites in the southwestern region (1944) that formed a hotspot followed by an eastward expansion of moderate to severe SBW impact until 1957. This outbreak reached an affected area of ≈170 000 km^2 in 1950 (Fig. 4.4). The third outbreak had a widespread impact on stands of the fir domain from west to east across our study area, corresponding to 80% of the forest area (≈550 000 km^2). This insect outbreak period was first recorded in the northern portion of the spruce–moss domain (especially in sites close to the limit of the commercial forest) in 1970. Analysis of the hotspots revealed a significant cluster of high values in the northern forest for a short period (1970–1971). A persistent pattern having a high percentage of affected trees was identified in the southwest in 1973, followed by an increasing eastward distribution until 1978, finally ending in a retraction to its original position from 1978 to 1982 (Fig. 4.3 and 4.4). Based on severity (number of affected trees) and duration (number of years), we determined the differences in SBW outbreak intensity between the northern and southern portions of the eastern Canadian forests over the last century (Fig. 4.5).

In the northern stands, tree-ring chronologies registered a higher number of years of weaker outbreaks than in the southern sites. However, severe SBW outbreaks were rare at the northern limit of the commercial forest during the 20th century (Fig. 4.5). The southern portion of the study area was characterized by shorter, more severe, and more synchronized periods of SBW infestation. Climate regressions presented relatively high R-Squared values for each outbreak period (comprised between 0.56 and 0.7) (Table 4.2), but the significancy of the Koenker and the Jarque-Bera statistics indicates non-stationarity (relationship is spatially inconsistent) and heteroscedasticity (the relashionship changes with explanatory variable magnitudes). Indeed, even if each explanatory variable are significantly correlated to the frequency of affected trees, and even if the Variance Inflation Factors (VIF) indicated no redundancy amoung explanatory variables (<7.5), the model is considered improperly specified. The Moran's Index between 0.36 and 0.47 indicate significative clustering of the regression residuals suggesting that a key variable is missing and that the model is misspecified. As a matter of fact, the spatial pattern of the regression residuals is similar to the one of the measured percentage of trees affected and the higher values are consistently underestimated, in the southwest and southeast portion of the study area for the first and the second outbreak (Fig. 4.6c1 and 4.6c2) and in the southwest and the northeast for the third one (Fig. 4.6c3).

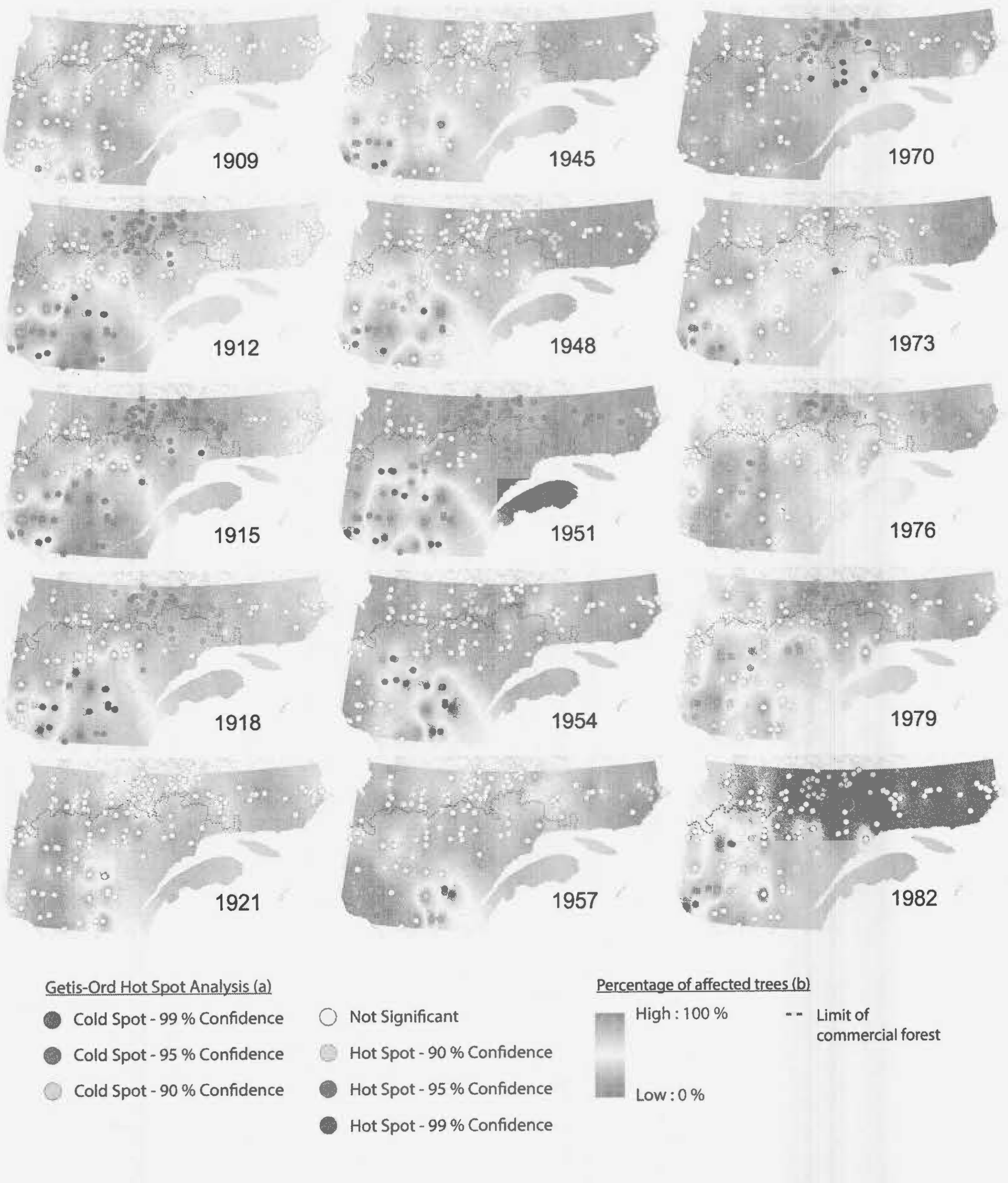

Figure 4.4: Spatio-temporal pattern of spruce budworm impact (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in Eastern Canadian boreal forests for the three most important outbreaks periods over the last century.

4.4 DISCUSSION

Under most climate change scenarios, disturbance regimes are likely to be most pronounced within the boreal biome (Seidl et al., 2017). As a consequence, much research has been aimed on improving our understanding of fire (Cyr et al., 2016; Portier et al., 2016; Drobyshev et al., 2017), insect outbreaks (Boulanger et al., 2016; Montoro Girona et al., 2018b), and windthrow (Anyomi et al., 2017; Saad et al., 2017) in the North American boreal forest. In the recent years, the eastern Canadian boreal forest has been experiencing a SBW outbreak, during which some of the most productive forest areas have been severely damaged (e.g. along the North Shore region), thereby having a strong implication at the ecological (forest dynamics) and economic level (financial losses) due to the large area of affected forest. If the frequency and severity of disturbances are expected to increase under future climate change scenarios, understanding the impact of SBW outbreaks in the past becomes essential for adapting to the uncertainties of climate change. In this study, we provide, for the first time, a landscape reconstruction of the spatiotemporal pattern of SBW dynamics over the last century across a vast study area of almost 1 million km^2 in the eastern Canadian boreal forest, revealing the first evidence of the presence of endemic populations of SBW north of the 50th parallel. This study demonstrated that SBW outbreaks have a major impact on forest ecosystems in terms of growth reduction, influencing tree survival, regeneration, and succession (MacLean, 2016). Dendroecological series across the entire study area identified three main periods of elevated SBW activity (Boulanger et al., 2012; Morin et Laprise, 1990; Jardon et al., 2003). Contrarily to our preliminary expectation, the first hypotheses was rejected, because each insect outbreak was manifested by a different spatiotemporal pattern, severity, and duration, thereby demonstrating the complexity of this ecological phenomenon.

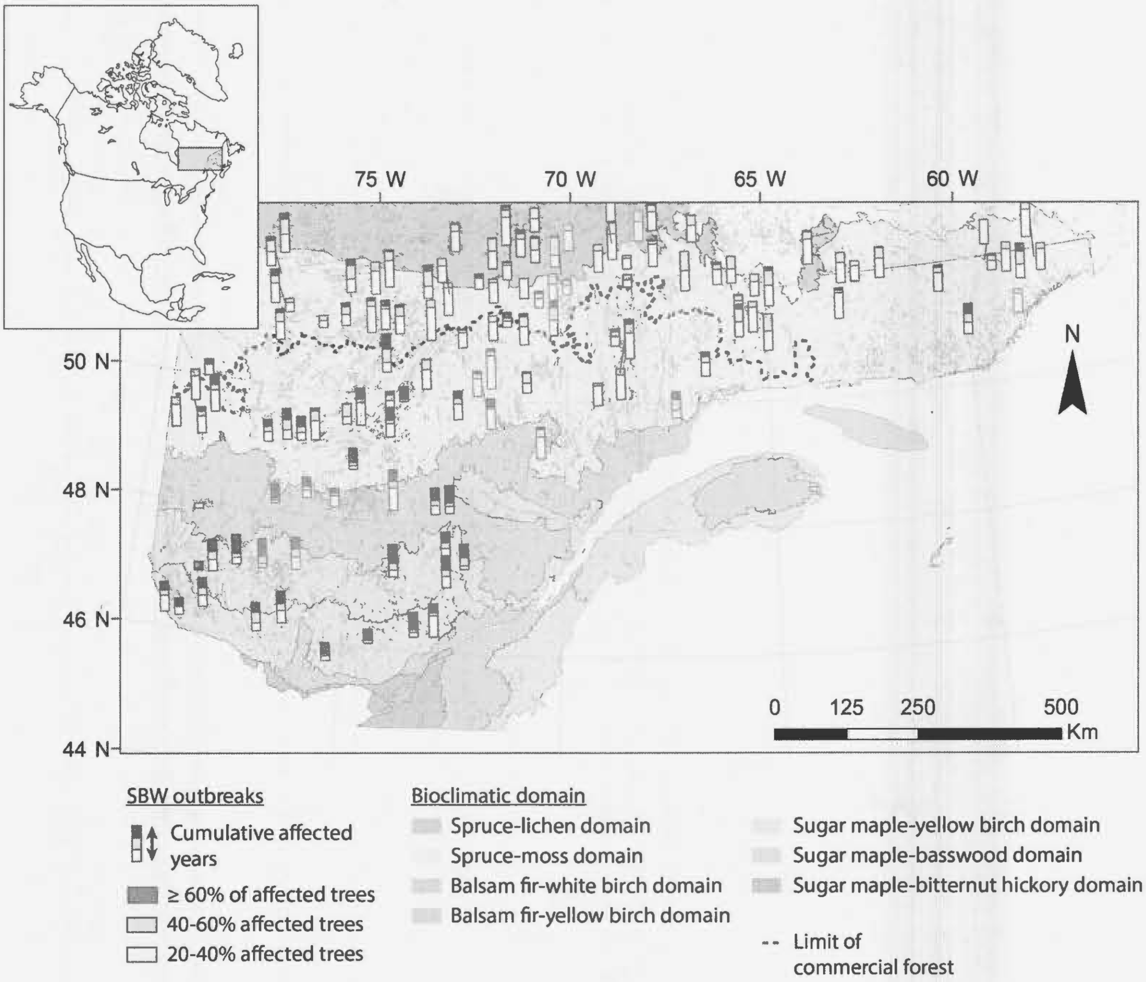

Figure 4.5: Cumulative years of infestation over the study area by category of severity

4.4.1 SPATIO TEMPORAL PATTERNS AT THE LANDSCAPE SCALE

These different patterns manifest themselves by an expansion of the spatial extent of the affected area over the 20th century. According to Jardon et al. (2003), this dynamic is confirmed at a wider temporal scale as outbreaks in the 19th century were less synchronous and presented a lower diffusion rate. This could be the result of a long-term forest transformation process. Baskerville (1975) described SBW as a super silviculturist, killing overstory trees and promoting the development of shade tolerant species such as balsam fir (Morin, 1994; Morin et Laprise, 1997). Even if the anthropogenic influences on SBW dynamics remain a matter of debate (MacLean, 2016), we know that fire suppression, clear cutting, and insecticide spraying also tend to favor the development of fir (Blais, 1983), SBW's most vulnerable host (MacLean, 1980). This forest transformation process, enhanced by the diminution of fire frequency since end of the Little Ice Age (Drobyshev et al., 2017), could be mainly responsible for the onset of the first SBW outbreak in the early 20th century (Bergeron et al., 1998; Jardon et al., 2003). Furthermore, this outbreak occurred during the driest decades of the last century (1910-1920) (Girardin et al., 2009), recuding host trees vigour and favoring its suceptibility to subsequent stress (Berdanier et Clark, 2016; Flower et al., 2014) such as fire or SBW outbreak. The full spatial extent of this outbreak is described here for the first time at the landscape level using dendrochronological data and including sites from both fir and spruce domain. From 1909 to 1921, this outbreak affected mainly the fir domain south of the 50th parallel. Several local infestations were recorded in the years 1905–1909, prior to the synchronized outbreak in the southwestern portion in 1910. This synchronization at a regional and supra-regional scale could stem from favorable weather conditions (Moran effect) (Myers, 1998; Royama et al., 2005) combined with the exchange of eggs by moth dispersion (Williams et Liebhold, 2000). The northern part of the study area was affected moderately and synchronously later during the 1920s. A second infestation (1935–1965) was smaller in extent, had a milder impact in more northern latitudes. However, this event does present the same pattern of the first outbreak with local infestations occurring during a few years prior to a synchronized outbreak at a wider scale. Our data tend to confirm the theory of Blais (1981), suggesting that an outbreak following a stand replacing epidemic event will have a lower impact due to the establishment of less vulnerable younger stands. Finally, the 1968–1988 epidemic was the largest, most synchronous, and best documented SBW outbreak in Eastern Canada (Morin et Laprise, 1990; Morin et al., 2008). Its dynamics in the spruce domain presented a very different pattern from the earlier outbreaks, and it appears to have reached almost all study sites. Furthermore, although spruce are less vulnerable to SBW than fir stands (MacLean, 1980), many spruce stands recorded a significant impact from this outbreak.

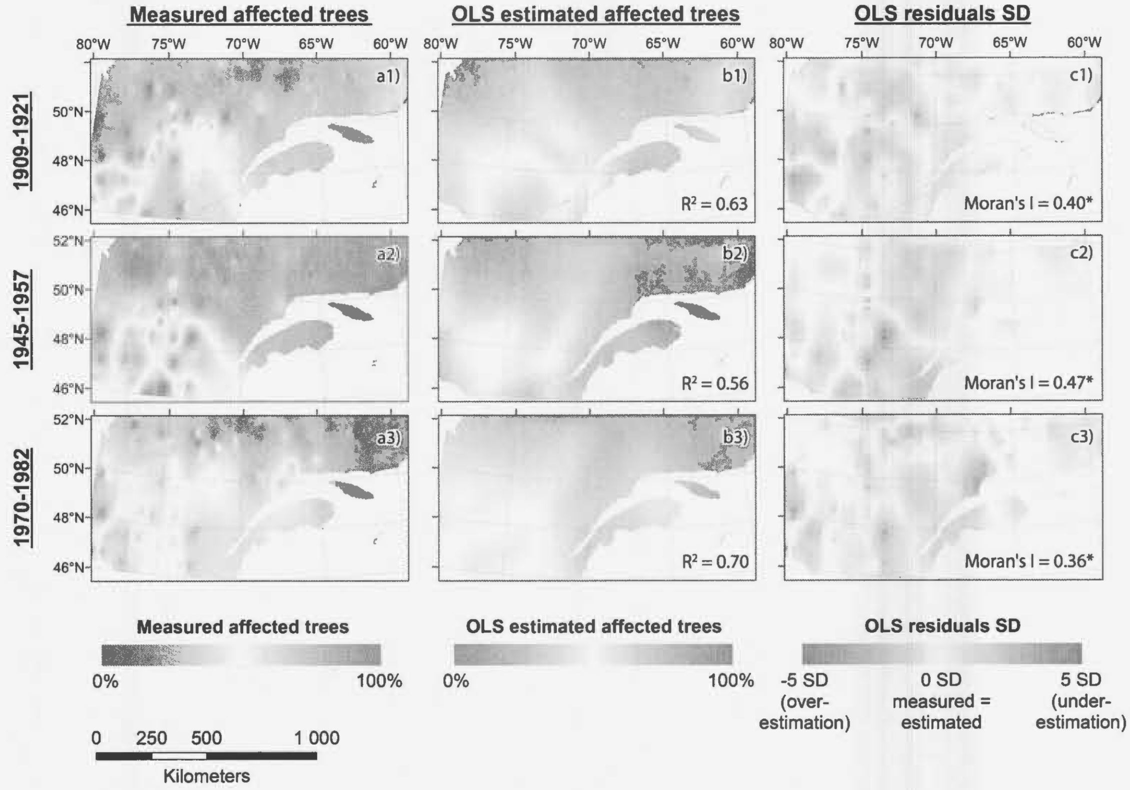

Figure 4.6: Ordinary Least Squares (OLS) model for each outbreak period. a) Average measured percentage of affected trees over an outbreak period. b) OLS estimated percentage of affected trees over an outbreak period using sessional precipitation and temperature as explanatory variables according to the Table 2. c) Residuals of the OLS model.

Tableau 4.2: Ordinary Least Squares model for each outbreak period. The variables included were selected among spring, summer, fall and winter precipitation and temperature in order to best fit the model (Variance Inflation Factor -VIF<7.5 and significant coefficient). Values in bold correspond to significant results ($P < 0.05$), SE correspond to standard error.

	First outbreak : 1909-1921				
R^2	F-value	Koenker	Jarque-Bera	Moran's I	
0.63	**261.81**	**89.63**	**29.67**	**0.4**	
Variable	Coefficient	SE	t-Statistic	P	VIF
Intercept	-3.07	2.54	-1.21	0.227	—
Summer Temperature	45.36	2.3	19.73	**<0.0001**	2.93
Fall Temperature	-64.86	3.57	-18.12	**<0.0001**	3.21
Winter Temperature	-12.39	2.32	-5.34	**<0.0001**	1.57
Spring Precipitation	-1.09	0.1	-10.73	**<0.0001**	1.31
	Second outbreak : 1945-1957				
R^2	F-value	Koenker	Jarque-Bera	Moran's I	
0.56	**132.65**	**93.6**	**26.95**	**0.47**	
Variable	Coefficient	SE	t-Statistic	P	VIF
Intercept	-3.73	2.17	-1.72	0.0864	—
Winter Temperature	-35.62	2.16	-16.46	**<0.0001**	1.14
Fall Temperature	39.73	2.28	17.46	**<0.0001**	1.48
Spring Temperature	22.67	3.86	5.87	**<0.0001**	1.18
Winter Precipitation	0.71	0.1	7.34	**<0.0001**	1.44
Summer Precipitation	-1.44	0.08	-17.52	**<0.0001**	1.25
Spring Precipitation	0.35	0.1	3.5	**0.0005**	1.11
	Third outbreak : 1970-1982				
R^2	F-value	Koenker	Jarque-Bera	Moran's I	
0.7	**247.79**	**34.84**	**33.4**	**0.36**	
Variable	Coefficient	SE	t-Statistic	P	VIF
Intercept	37.59	1.32	28.4	**<0.0001**	—
Winter Precipitation	-1.18	0.16	-7.4	**<0.0001**	3.6
Fall Precipitation	-0.89	0.17	-5.12	**<0.0001**	1.6
Spring Precipitation	1.4	0.14	9.8	**<0.0001**	2.66
Winter Temperature	-50.27	2.94	-17.09	**<0.0001**	2.11
Fall Temperature	42	5.47	7.68	**<0.0001**	2.96
Spring Temperature	39.67	8.13	4.88	**<0.0001**	2.13

4.4.2 FACTORS INVOLVED IN SPATIO-TEMPORAL PATTERNS AT MULTIPLES SCALES

These differences in spatiotemporal patterns could be explained by many factors, one of the most important being climate. In fact, as climate influence SBW population dynamics, it also cause stress to host stands yielding them to be more vulnerable to subsequent biotically-induced disturbances (De Grandpré et al., 2018a). Greenbank (1956) demonstrated that hot and dry summers influenced the onset of the 1912 and 1949 SBW outbreaks in New Brunswick. Hot summer temperatures are required for the insect to complete its life cycle (Pureswaran et al., 2015). Drought can also increase host vulnerability by enhancing the carbohydrate content of leaves (Mattson et Haack, 1987). The northern portion of our study area is characterized by cold and short summers that, at present, prevent the establishment of endemic populations. Early frosts in the northern stands prevent eggs from hatching (Blais, 1958; Pureswaran et al., 2015). Thus, the outbreak impacts observed on trees from the more northern sites during the 1920s could be evidence for the arrival of immigrant populations from southwestern Quebec. Recently, the use of weather radar has allowed the identification of such mass exodus events (Boulanger et al., 2016). However, the 1968–1988 outbreak provides a different picture as severe and synchronous local epidemics were recorded in the early phases (1970–1971) of the outbreak within the North Shore region before any growth reduction was recorded in the fir domain (1972) (Fig 4.4 and Sup 4.7e). This phenomenon matches with the distribution of our regression analysis residuals, discarding the hypothesis of a climatic event influence as a unique factor of growth reduction (Figure 6). This could therefore be the first evidence of the presence of endemic populations of SBW north of the 50th parallel. In addition, as black spruce phenology and overall shoot length increase in response to experimental warming (Bronson et al., 2009), this could have reduced the phenological asynchrony between the insect and host making northern sites more suitable for infestation. These argument give weight to the hypothesis of a northward shift in the extent of SBW outbreaks during the 20th century (Pureswaran et al., 2015; Régnière et al., 2012). Gray (2013) identified the North Shore region and Gaspé Peninsula as the areas having the highest increases in outbreak severity and duration ; this agrees with our dataset from the North Shore and with the onset area of the current infestation. Unfortunately, our dataset did not contain sites from the Gaspé Peninsula.

SBW dynamics recorded at the regional scale differ between the northern and southern portions of the study area. In the spruce domain, we observed more cumulative years of growth reduction than what was observed in the southern regions (Fig. 4.5). However, we have found only a few occurrences of severe SBW impacts on black spruce in comparison to the fir domain where white spruce were periodically severely affected. First, as black spruce is less vulnerable to SBW than white spruce or balsam fir. This is due to an asynchrony of approximately 14 days in budburst phenology causing high rates of mortality for second instar larvae trying to feed on this host (Nealis et Régnière, 2004b). Despite the fact that white spruce buds burst in a time frame more similar to balsam fir than black spruce, white spruce also produces more buds that develop and lignify faster (Nealis et Régnière, 2004b). According to MacLean (2016), balsam fir and white spruce, being less resistant species, are more prone to secondary mortality agents, such as shoe-string root rot, *Armillaria mellea* (Vahl ex Fries), which occurs in most defoliated trees. In addition, southern mixed forest beneficit from a greater diversity of SBW natural annemies, which could also explain the lower frequency and shorter duration of outbreaks in this zone (Campbell et al., 2008; Cappuccino et al., 1998).

4.4.3 METHODOLOGICAL AND FOREST MANAGEMENT IMPLICATIONS

Similarities were observed between our spatiotemporal patterns and the aerial surveys of defoliation in the area (Gray et al., 2000; Gray et Mackinnon, 2006). Although these surveys were not conducted specifically to measure SBW impacts on black spruce at these latitudes, they still show an important spread of the epidemic in 1974, especially in the spruce–moss domain. It is possible that dendrochronology detects epidemic thresholds earlier as it is more sensitive, and the technique is better suited to black spruce. Indeed, growth reductions can be observed for defoliation levels that are not detectable with aerial surveys, which are categorial (none, light, moderate, severe).

The dendroecological approach has shown its effectiveness in the study of past insect outbreak dynamics (Boulanger et al., 2012; Jardon et al., 2003; Morin et al., 2007). Given the large amount of dendrochronological data that has been published during the last decades, large-scale meta-analyses are increasingly important and can provide a complete portrait of historical SBW outbreaks, placing recent events into a larger spatiotemporal context, and completing the existing monitoring proxies. Therefore, to provide a more relevant understanding of the SBW dynamics, future sampling efforts should be more homogeneous with sampling sites evenly distributed and with uniform sampling methods. Furthermore, the inclusion of northern latitude sites demonstrated its potential for improving our understanding of past outbreak patterns, but also the methodological difficulties associated with the inclusion of a secondary host in the analysis. The inclusion of such chronologies will be challenging, nonetheless, given the difficulties in accessing sampling sites, finding old trees able to provide long chronologies, and, moreover, the difficulty of finding non-host trees to refine the epidemic signal. We recommend continuing the collection of more samples from northern latitude sites, considering new areas (e.g. Ontario and Gaspe peninsula), as well as adding other species affected by SBW (e.g. balsam fire). Getting more details across the historical distribution area of SBW will improve the resolution of the existing dendroecological database. Based on our results concerning the potential links between climate and SBW activity (Fig. 4.6), we suggest that future research should be developed to better discriminate the interactions connecting climate anomalies, as a triggering or interrupting factor of growth reduction, to SBW and its hosts dynamics. Natural disturbance regimes are an integral part of boreal forest ecosystems, and silvicultural methods are now attempting to emulate their impacts by adapting more appropriate harvesting treatments (Kuuluvainen et Grenfell, 2012; Montoro Girona et al., 2018a). Many studies have focused on the role, impact, and frequency of fire cycles on the management of boreal ecosystems (Bergeron et al., 2002; Kuuluvainen et Grenfell, 2012); however, the understanding of the role and impacts of insect outbreaks remains incomplete, in particular at a larger scale (De Grandpré et al., 2018b; Robert et al., 2018). Understanding SBW disturbance regimes at the landscape-scale and implementing effective management strategies requires to define outbreak dynamics in both time and space (Bouchard et Pothier, 2010). Currently, sylvicultural practices aim to imitate fire disturbances promoting large clearcuts (Hunter, 1993). In order to reduce boreal forest vulnerability to SBW outbreaks some authors proposed to adapt sylvicultural treatments and forest management promoting the harvesting of the most susceptible stands such as mature fir stands (MacLean, 1996, 1980; Sainte-Marie et al., 2015) and promote enven-aged spruce and mixed stands through silvicultural practices such as partial cuttings (Bergeron et al., 2017). Integrative multiple-disturbance research is needed to better understand the climatic and ecological context of insect outbreaks and to identify the type of interactions that occur during these events; as such, adequate management strategies can be developed in accordance with the forest structure at regional and local scales.

4.5 CONCLUSION

Natural disturbance regimes define forest ecosystems by influencing their structure, species composition, and functional processes. The evaluation of outbreak periods during the last century demonstrated that SBW is a major disturbance event in eastern Canada, affecting large surfaces and having an impact on forest ecosystem dynamics. Landscape-scale reconstruction of the spatiotemporal patterns of SBW outbreaks in eastern Canadian forests highlighted three outbreaks during the 20th century, each having different spatiotemporal patterns, duration, and severity. This study revealed the diversity and complexity of outbreak dynamics over time as well as the importance of meta-analyses for better understanding the SBW patterns at the landscape scale and evaluating the impacts on forest ecosystems. Furthermore, this study represents a major contribution to forest ecology providing valuable data from remote sites located at the limit of commercial forests. Under climate change, natural disturbances regimes and species' distributions are expected to be altered. Based on dendroecological approaches, we demonstrated evidence of SBW activity north of the 50th parallel, adding weight to the hypothesis of a northward shift in the extent to the outbreaks during the 20th century (Pureswaran et al., 2015; Régnière et al., 2012). Finally, improving our understanding of natural disturbance cycles at multiple scales should be a priority for assessing boreal forest adaptation and modification to future climate change.

4.6 ACKNOWLEDGEMENTS

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4.7 SUPLEMENTARY MATERIALS

Figure 4.7: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1900–1914.

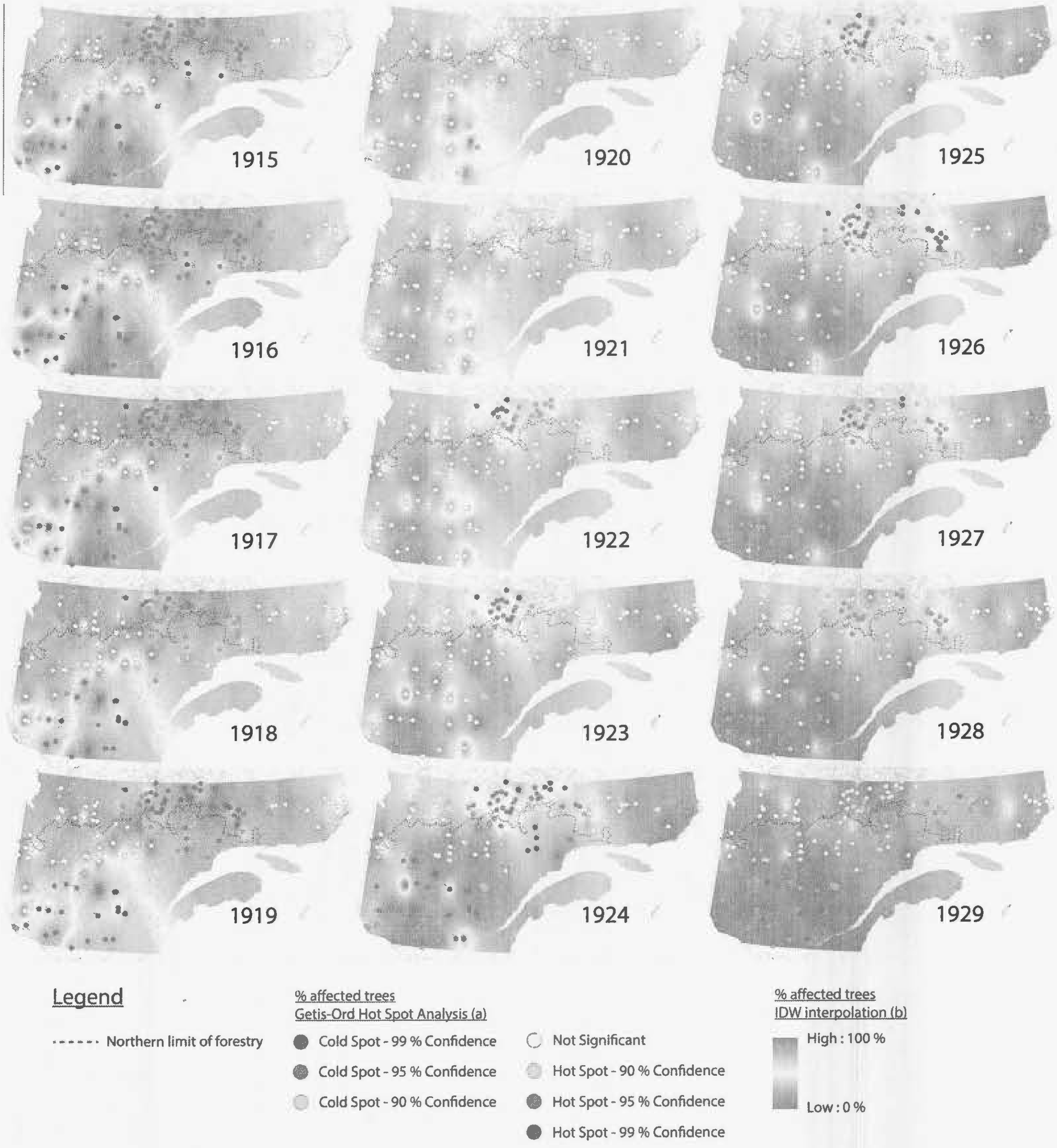

Figure 4.8: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1915–1929.

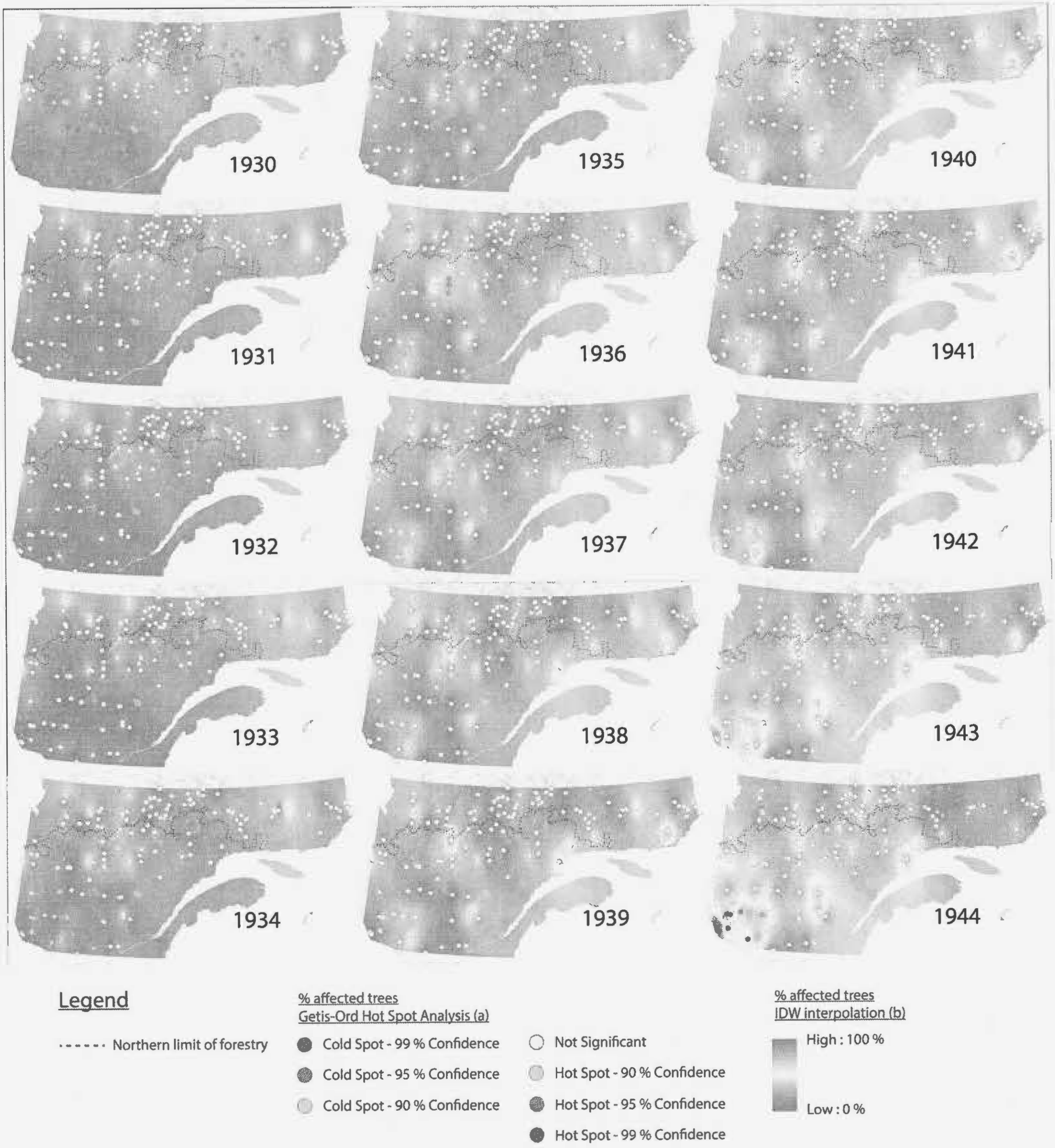

Figure 4.9: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1930–1944.

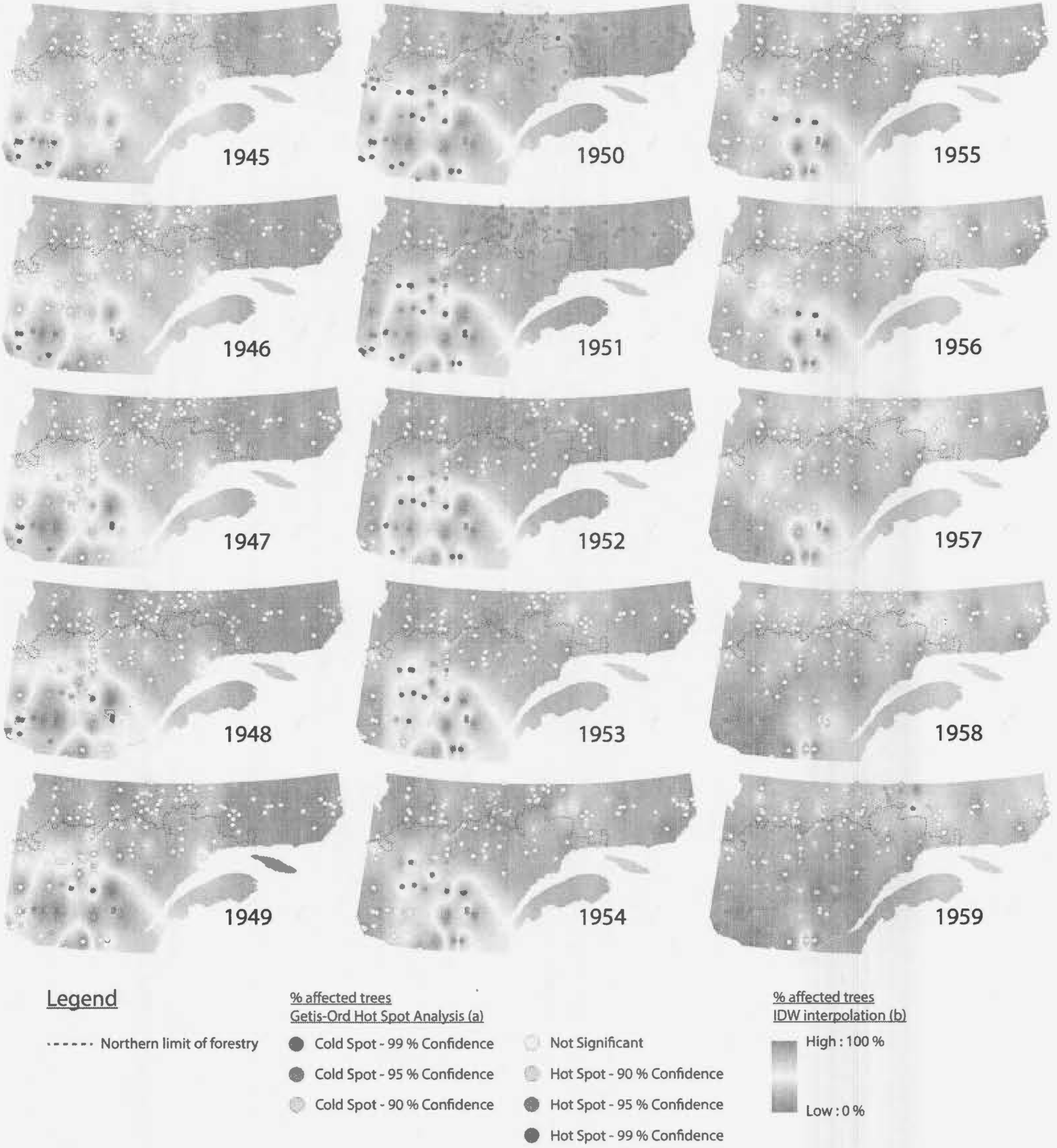

Figure 4.10: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1945–1959.

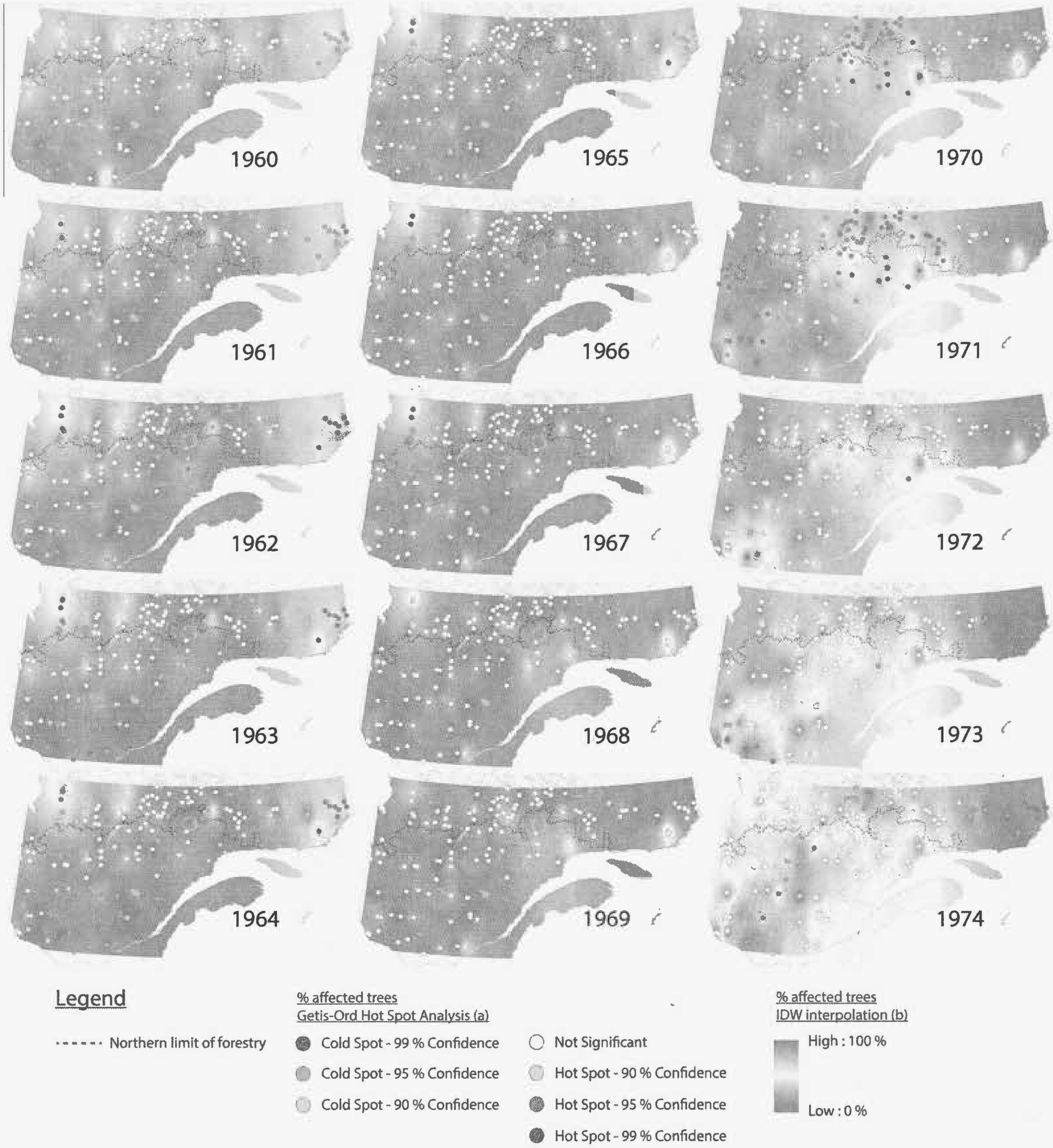

Figure 4.11: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1960–1974.

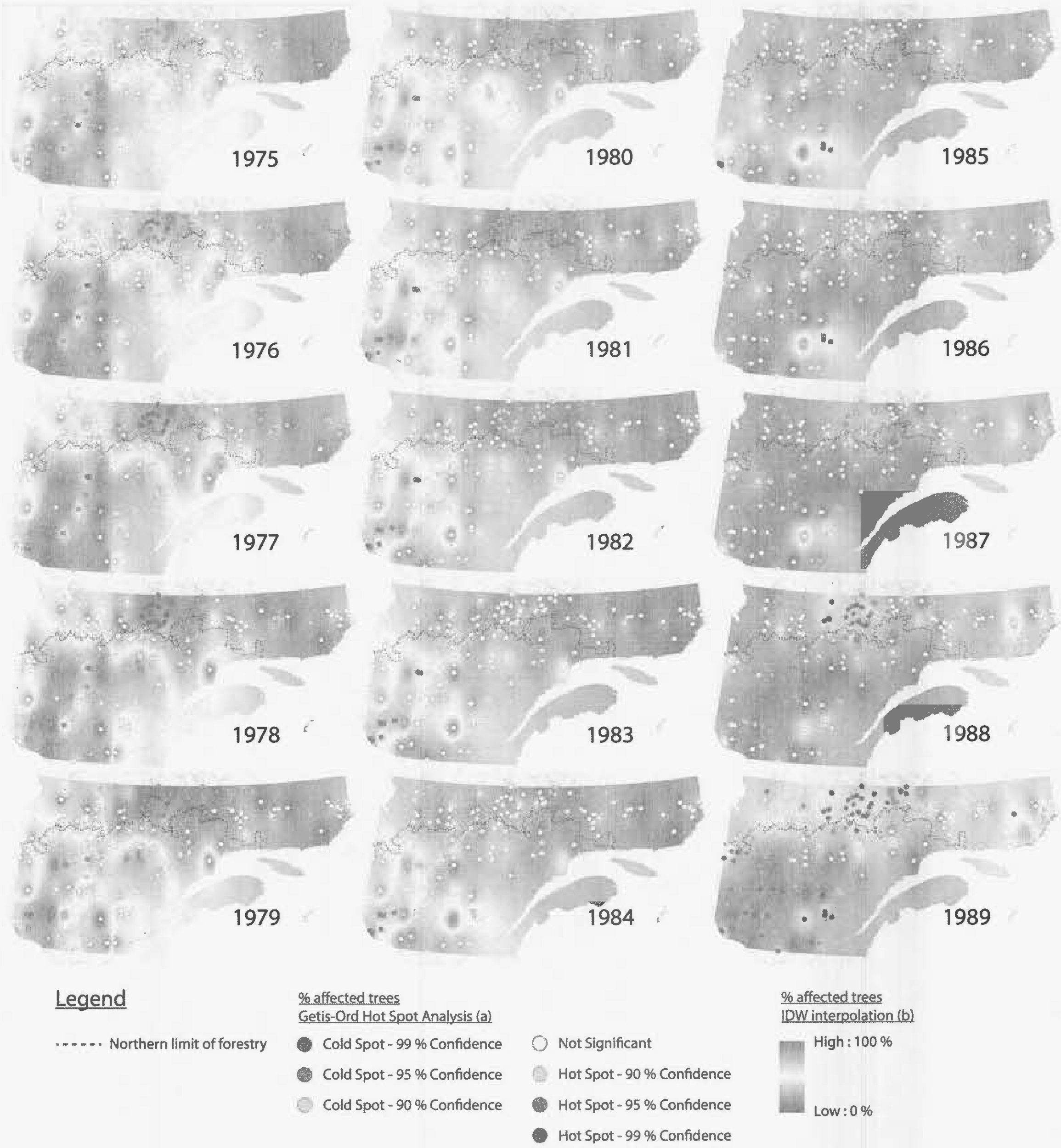

Figure 4.12: Spatiotemporal pattern of spruce budworm impacts (percentage of affected trees) and synchrony (Getis-Ord hotspot analysis) in eastern Canadian boreal forests for the period 1975–1989.

CONCLUSION GÉNÉRALE

L'objectif général de cette thèse était d'étudier les structures temporelles, spatiales et spatio-temporelles des épidémies de TBE à grande échelle. Cet objectif a été atteint en utilisant une approche multidisciplinaire qui combine à la fois les méthodes de la paléoécologie, de la dendrochronologie et de l'analyse spatiale. Cette contribution se veut innovante puisqu'elle a permis d'élargir à la fois la zone d'étude de la TBE aux latitudes nordiques de la pessière à mousses, mais aussi de reconstruire la dynamique de l'insecte à l'échelle Holocène.

À cet égard, les écailles de papillons se sont avérées être un indicateur très efficace du fait de leur grande abondance et de leur très bonne capacité à se conserver dans les sédiments lacustres pendant des milliers d'années. En effet, des écailles en parfaite condition ont été extraites de sédiments datant de plus de 10 000 ans. De plus, la diversité des formes d'écailles observées sur les trois principaux lépidoptères épidémiques au Québec a présenté un bon potentiel d'identification, renforcant ainsi l'intérêt de l'utilisation de ce proxy pour la reconstruction paléoécologique de la dynamique de la TBE. Finalement, des points communs ont pu être mis en évidence entre les stratigraphies de deux carottes de surfaces et les enregistrements dendrochronologiques de la région et ce, malgré la différence de résolution entre les deux méthodes et les contraintes liées à l'utilisation de carottes de surface (bioturbation, pécision de la datation...).

L'utilisation d'un proxy tel que les écailles de lépidoptères sur une carotte vieille de plus de 10 000 ans nous a permis d'enrichir les connaissances parcellaires déjà disponibles sur la dynamique plurimillénaire de la TBE. En effet, nos résultats confirment l'hypothèse que la TBE est présente au Québec depuis le retrait des glaciers et l'extension septentrionale des forêts (Simard et al., 2006). Sa dynamique est fortement corrélée à celle de ses hôtes pricipaux, elle-même influencée par les variations climatiques et par le régime des feux. Nos résultats suggèrent par exemple d'importantes augmentations de la quantité de macrorestes de sapins et d'épinettes extraite du sédiment à la suite d'épisodes épidémiques majeurs. Nos résultats démontrent également une importante opposition entre la fréquence des feux de forêt et celle des épidémies de TBE. Ainsi, le début et la fin de l'Holocène sont marqués par une fréquence des feux relativement importante qui pourrait avoir restreint le développement d'épidémies fréquentes en réduisant la quantité d'hôtes matures dans le paysage. Nos résultats suggèrent également que les épidémies auraient été beaucoup plus fréquentes et possiblement plus sévères au milieu de l'Holocène alors que les feux avaient une emprise moins importante (ou plus locale) sur le paysage.

À l'échelle plus récente du 20ième siècle, l'analyse spatiale des données dendrochronologiques a révélé, sans grande surprise, trois périodes épidémiques majeures. Cette représentation de l'étendue et de la diffusion des épidémies de TBE à partir de la réduction de croissance enregistrée dans des cernes d'arbres a permis de compléter les données d'inventaires aériens accumulées par le Ministère des Forêts, de la Faune et des Parcs et disponibles uniquement depuis 1967 et d'en extendre la portée dans la pessière à mousses. Nous avons ainsi proposé la première représentation cartographique des épidémies de 1905-1930 et 1935-1965 à l'échelle du Québec. Les patrons spatiotemporels observés soutiennent l'hypothèse d'un mouvement oscillatoire de l'abondance de l'insecte à l'échelle du paysage qui serait le résultat de la synchronisation de populations locales, favorisée par des facteurs tels que le climat et/ou la migration des papillons. Nos résultats démontrent également une emprise nordique plus importante de l'épidémie de 1968-1988, ce qui va dans le sens de l'hypothèse d'un déplacement vers de nord de la zone de distribution de l'insecte en réponse au changements climatiques. De plus, la présence d'une zone d'infestation précoce dans les régions de la Haute-Côte-Nord et de Manicouagan de 1970 à 1972 suggère la possibilité de l'établissement de populations endémiques dans la pessière à mousses depuis la fin du 20$^{\text{ième}}$ siècle.

LIMITATIONS DE L'ÉTUDE

Concernant l'analyse paléoécologique des écailles de lépidoptère, l'identification des écailles fossiles, bien que prometteuse reste une limitation importante dans la mesure où seulement 25% des écailles ont été identifiées en fonction des morphotypes décrits dans le chapitre II. Plusieurs pistes ont été suggérées pour améliorer la caractérisation des écailles de TBE, en utilisant par exemple des critères nécessitant l'analyse de l'ultrastructure de l'écaille ou encore, l'utilisation de marqueurs génétiques, mais ces méthodes ne pourront être mises au point que par la réplication d'analyses spécifiques et l'accumulation de spécimens.

L'extraction et l'analyse des écailles reste à ce jour une tâche laborieuse qui nécessite beaucoup de temps, ce qui réduit grandement les possibilités d'effectuer des réplications ou de multiplier les sites analysés. Il est ainsi difficile d'évaluer la significativité des résultats ou d'extrapoler l'interprétation au-delà des peuplements voisins du lac échantillonné.

Bien que la méthode d'extraction des écailles soit relativement simple et peu coûteuse, les échantillons observés contiennent encore trop de "bruit", entre autres des débris végétaux, des cladocères et des pollens. Ces derniers allongent la durée de l'analyse d'un échantillon, réduisant ainsi le volume de sédiments analysés et rendant les écailles difficiles à identifier.

Enfin, la stratigraphie présentée au chapitre III (Fig 3.3) reste à ce jour le seul exemple publié d'épidémies de TBE reconstituées à partir d'écailles fossiles. Le manque d'éléments de comparaison aussi bien récents qu'Holocènes complique l'interprétation des résultats.

En ce qui concerne la méta-analyse présentée au chapitre IV, l'une des principales limitations concerne l'homogénéité des sites étudiés. En effet, certaines zones présentent une densité de sites ainsi qu'un nombre d'arbres par site plus élevé que d'autres (Fig 4.1). Certaines zones telles que la péninsule Gaspésienne ainsi que la portion du territoire au sud du St-Laurent sont exclues de l'analyse.

De plus, le fait que les sites de la sapinière soient constitués de séries d'épinettes blanches alors que les sites de la pessière à mousses soient constitués de séries d'épinettes noires peut être jugé comme un biais considérant la réponse différente que présentent ces deux espèces aux infestations de TBE (Hennigar et MacLean, 2008). Le choix délibéré de ne pas utiliser de chronologies d'arbres non-hôtes pour corriger les séries étudiées afin de préserver une uniformité à l'échelle suprarégionnale compléxifie également l'interprétation des réductions de croissance légères, locales ou asynchrones.

Enfin, l'ensemble de ces limitations sont héritées de la réalité du terrain, de la distribution des espèces, de la difficulté d'accessibilité du territoire ou des données et illustrent bien le défi que représente la réalisation d'analyses à grande échelle sur des données non modélisées.

PERSPECTIVES DE RECHERCHE

Cette étude propose l'utilisation d'un nouveau proxy pour la reconstruction des épidémies de la TBE à l'échelle plurimillénaire. Bien que prometteuse, cette technique ouvre la porte à un certain nombre de perspectives de recherches afin de renforcer la puissance d'un tel indicateur et de promouvoir son utilisation pour mieux comprendre la dynamique de l'insecte sur le long terme.

Concernant l'identification au genre, ou à l'espèce des écailles fossiles de papillons, plusieurs avenues sont à explorer. Étant donnée la grande diversité de formes observées, aussi bien au niveau intraspécifique qu'interspécifique, la construction et l'amélioration de morphotypes caractéristiques semble la solution la plus simple et la moins coûteuse. Cette méthode nécessite cependant que des études entomologiques soient menées afin de comparer les écailles spécimens et d'identifier des caractéristiques discriminantes. À ce titre, la forme du contour de l'écaille serait un critère simple à mesurer et certaines techniques, relevant des domaines de la statistique, ou de l'intelligence artificielle, telles que la reconnaissance d'image ou l'apprentissage automatique supervisé pourraient s'avérer être des outils très efficaces.

Des études pourraient également être menées afin de comparer des stratigraphies d'écailles de papillons et des données dendrochronologiques issues d'arbres vivants ou de bâtiments patrimoniaux (Boulanger et al., 2012; Boulanger et Arseneault, 2004) mais aussi d'arbres subfossiles (Simard et al., 2011) extraient du même lac que la carotte sédimentaire. Les processus taphonomiques qui interviennent entre la mort de l'insecte et la sédimentation des écailles restent à explorer afin de caractériser le décalage temporel qui peut exister entre une épidémie et son enregistrement dans la stratigraphie. Des recherches impliquant l'utilisation de trappes à sédiments sont actuellement en cours dans plusieurs lacs bordés de peuplements plus ou moins défoliés au nord du Lac Saint-Jean.

Le protocole d'extraction des écailles de papillon pourrait également être modifié pour être intégré à d'autres routines plus fréquemment entreprises telles que l'étude des pollens afin de permettre de multiplier le nombre de stratigraphies incluant la reconstruction des épidémies de TBE. Des recherches allant dans ce sens sont en cours au lac des Pères, dans le parc national des Monts-Valins.

Les interactions entre les feux de forêts et les épidémies d'insectes à l'échelle Holocène, mal comprises à ce jour, semblent pourtant primordiales pour la compréhension de la dynamique des perturbations naturelles dans un contexte de changements climatiques et d'aménagement écosystémique. Selon MacLean (2016) on peut s'attendre à une vulnérabilité accrue de la forêt si les infestations d'insectes coïncident avec des événements de sécheresse, de feux... La multiplication d'études paléoécologiques intégrant ces perturbations au travers du territoire semble donc être un enjeu important.

L'utilisation d'écailles fossiles en paléoécologie pourrait également être adaptée à l'étude d'autres espèces épidémiques boréales telles que la Livrée des forêts ou l'Arpenteuse de la Pruche, mais aussi à l'étude des migrations d'espèces exotiques telles que le Monarque (*Danaus plexippus* (Linnaeus)) ou la Belle-Dame (*Vanessa cardui* (Linnaeus)).

Finalement, la compilation de données dendrochronologiques provenant de différentes sources au travers du Québec s'est avérée un bon moyen de reconstruire le patron de chacune des épidémies du 20ième siècle. La mise en place d'une base de données libre d'accès et dédiée à l'analyse des épidémies d'insectes permettrait d'augmenter le potentiel de ce type d'analyse en y incluant de nouvelles zones, des chronologies plus longues ou encore de comparer la réponse de différentes espèces. Enfin, l'ensemble des données récoltées pourrait permettre de construire des projections à l'échelle du paysage qui serviraient de support décisionnel aux planifications forestières et à l'aménagement écosystémique.

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