



DYNAMIQUE SPATIO-TEMPORELLE DES ÉPIDÉMIES DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE DU 20^{ÈME} SIÈCLE AU QUÉBEC

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RÉSUMÉ

Les épidémies de la tordeuse des bourgeons de l'épinette (TBE) constituent une perturbation majeure des forêts nord-américaines. Au Québec, Canada, l'histoire récente des épidémies de la TBE à l'échelle locale est bien connue. Les études à l'échelle du Québec demeurent toutefois rares malgré la nécessité de mieux comprendre la dynamique des épidémies de la TBE à plus grande échelle. Cette étude visait à reconstituer la dynamique spatio-temporelle des épidémies de la TBE au cours du 20^{ème} siècle dans l'ensemble de l'aire de répartition de l'insecte au Québec méridional. Pour ce faire, nous avons échantillonné 83 peuplements répartis sur l'ensemble du territoire d'étude. Ces peuplements ont été sélectionnés en fonction de leur âge et de la présence d'épinettes noires, blanches et rouges. En effet, le genre *Picea*, contrairement au sapin baumier, survit aux épidémies de la TBE et peut les enregistrer dans ces cernes de croissance. Dans chaque peuplement, des carottes ont été prélevées sur 20 épinettes. Les séries dendrochronologiques de plus de 1600 arbres ont été analysées et nous avons identifié, grâce au regroupement des peuplements par k-moyennes, trois patrons de croissance des arbres dans lesquels les trois épidémies de la TBE du 20^{ème} siècle précédemment documentées ont été mise en évidence. Les épidémies n'étaient pas homogènes dans l'aire de répartition de l'insecte. Deux groupes de peuplements ont présenté des épidémies de forte intensité au début (1905-1930) et à la fin du siècle (1968-1988) et une épidémie de moyenne intensité au milieu du siècle (1935-1965). Ce schéma s'explique principalement par la présence de l'insecte dans les domaines bioclimatiques de la sapinière à bouleau jaune et de la sapinière à bouleau blanc, zones où les épidémies tendent à être les plus sévères en raison de l'abondance du sapin baumier, la principale espèce hôte de la TBE. Cependant, ces deux modèles diffèrent en termes de durée des épidémies. Un troisième groupe de peuplements, plus septentrional, a connu des épidémies moins sévères au cours du 20^{ème} siècle, ce qui tend à s'expliquer par un climat plus froid et une plus faible proportion de sapins baumiers dans le paysage du fait de la proximité avec le domaine bioclimatique de la pessière à mousse. Notre étude montre que, d'une part, ces trois groupes de peuplements sont définis par des épidémies de durée et de gravité spécifiques, et que, d'autre part, ils sont spatialement distincts et soumis à des conditions climatiques différentes.

MOTS-CLÉS : Épidémies d'insectes, dynamique spatio-temporelle, sévérité des perturbations, dendrochronologie, interactions multi-échelles, conditions climatiques, *Choristoneura fumiferana* (Clem.)

ABSTRACT

Spruce budworm (SBW) outbreaks are a major disturbance in North American forests. In Quebec, Canada, the recent history of SBW outbreaks at the local scale is well-known. Studies at the Québec scale nonetheless remain rare despite the need to better understand the dynamics of SBW outbreaks at a larger scale. This study aimed to reconstruct the spatiotemporal dynamics of SBW outbreaks during the 20th century across the insect's range in southern Quebec. To this end, we sampled 83 stands throughout southern Quebec. These stands were selected according to their age and the presence of black, white, and red spruce. In fact, spruce, unlike balsam fir, survives the SBW outbreaks and can record them in these growth rings. In each stand, cores were taken from 20 spruce trees. The dendrochronological series of more than 1,600 trees were analyzed, and we identified, through the k-means grouping of stands, the spatial patterns of tree growth for the three previously documented 20th century SBW outbreaks. The outbreaks were not homogeneous across the distribution range of the insect. Two groups of stands showed early- (1905–1930) and late-century (1968–1988) outbreaks of high severity and a mid-century (1935–1965) outbreak of moderate severity. This pattern is explained mainly by the presence of the insect within the balsam fir–yellow birch and balsam fir–white birch bioclimatic domains, areas where outbreaks tend to be most severe because of the abundance of balsam fir, the main SBW host species. However, these two models differ in terms of the duration of outbreaks. A third, more northern, cluster of stands experienced lower severity outbreaks over the 20th century, a pattern explained by a lower proportion of balsam fir trees in these landscapes. Our study shows that, on the one hand, these three groups of stands are defined by outbreaks of specific duration (an outbreak period beginning when more than 20% of the trees are affected and ending when <20% of the trees are affected) and severity (in terms of percentage of affected trees), and on the other hand they are spatially distinct and subject to different climatic conditions.

Keywords: insect outbreaks, spatiotemporal dynamics, disturbance severity, dendrochronology, multiscale interactions, climatic conditions, *Choristoneura fumiferana* (Clem.)

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LISTE DES ABRÉVIATIONS

TBE : Tordeuse des Bourgeons de l'Épinette

SBW : Spruce Budworm

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AVANT-PROPOS

Ce mémoire est un mémoire par article. L'article présenté est une recherche originale qui a été publié en 2021 dans la revue *Frontiers in Ecology and Evolution* et doit être cité comme suit dans la littérature :

BERGUET, Cassy, MARTIN, Maxence, ARSENEAULT, Dominique, *et al.* Spatiotemporal dynamics of 20th-century spruce budworm outbreaks in eastern Canada: Three distinct patterns of outbreak severity. *Frontiers in Ecology and Evolution*, 2021, vol. 8, p. 544088.

Plusieurs auteurs ont contribué à la confection de cet article. Cassy Berguet et Hubert Morin ont conceptualisé et mené l'étude à bien. Cassy Berguet a réalisé la collecte et l'analyse des données dendrochronologiques. Hubert Morin a fourni les ressources matérielles nécessaires et a contribué au financement. Cassy Berguet et Maxence Martin ont effectué les analyses statistiques, rédigé la première version du manuscrit et édité le manuscrit. Hubert Morin et Dominique Arseneault ont supervisé l'étude. Cassy Berguet, Maxence Martin, Hubert Morin et Dominique Arseneault ont révisé le manuscrit. Tous les auteurs ont contribué à l'article et ont approuvé la version soumise.

La vérification de la qualité de l'anglais de l'article a été vérifiée par Murray Hay.

Dans le mémoire, une introduction et une conclusion générale en français encadre l'article.

INTRODUCTION GÉNÉRALE

Les forêts, des systèmes dynamiques complexes

Les forêts sont des systèmes dynamiques complexes dont la variabilité structurale est reliée à différents facteurs tels que le climat, les caractéristiques physiographiques et les perturbations naturelles (Cook 1985; Gauthier 2009; Lebourgeois et Mérian 2012). Les perturbations naturelles comme les incendies et les épidémies d'insectes jouent un rôle important dans la dynamique forestière (Payette *et al.* 2000; Jasinski et Payette 2005; Girard *et al.* 2008). En effet, la structure spatio-temporelle des forêts est fortement influencée par les variables écologiques comme le type, l'étendue et la fréquence des perturbations naturelles (Campbell 2008). Pour comprendre comment vont évoluer les écosystèmes forestiers dans le futur, il est nécessaire de comprendre leur comportement passé et par conséquent les relations entre les écosystèmes, les perturbations qu'ils subissent et les conditions qui prédominent lors de ces perturbations. Ici, il s'agit de comprendre les relations entre les forêts du Québec, les épidémies de la TBE et les conditions dans lesquelles surviennent ces épidémies.

Les épidémies de la TBE

Les épidémies de la TBE font partie intégrante de la dynamique naturelle des forêts nord-américaines (Harvey 1985). Elles sont considérées comme l'une des perturbations les plus sévères dans l'Est de l'Amérique du Nord. Elles ont pour conséquences de forts taux de défoliation c'est-à-dire une destruction massive du feuillage des arbres à l'échelle du paysage. Suite à une défoliation, les arbres allouent principalement leur énergie à la création d'un nouveau feuillage dont ils ont besoin pour leur photosynthèse et mettent donc moins d'énergie dans leur croissance secondaire. On observe alors des réductions des cernes de croissance des arbres. Après plusieurs années de défoliation, de forts taux de mortalité sont observés dans les peuplements les plus vulnérables. Finalement, les épidémies ont un fort impact au niveau écologique d'une part, en termes de taux de mortalité des arbres, et au niveau économique d'autre part, à travers

les pertes financières de l'industrie du bois (Dymond *et al.* 2010; Chang *et al.* 2012; Pureswaran *et al.* 2015). Par exemple, l'épidémie qui a eu lieu entre 1974 et 1988 a affecté plus de 55 millions d'hectares de forêt et détruit entre 139 et 238 millions de mètres cubes d'épinettes et de sapins uniquement au Québec (Morin 1998; Morin *et al.* 2007).

La tordeuse des bourgeons de l'épinette

La Tordeuse des Bourgeons de l'épinette (TBE) ou *Choristoneura fumiferana* (Clem.) de son nom latin est une espèce de lépidoptère indigène d'Amérique du Nord. Son aire de répartition s'étend sur une grande partie de l'Amérique du Nord (Pureswaran *et al.* 2015) mais l'insecte est considéré comme le principal perturbateur de l'est de la forêt boréale. En effet, la TBE est un insecte herbivore qui se nourrit des bourgeons et des aiguilles de plusieurs conifères (Martineau 1985; Dorais *et al.* 1996; Campbell 2008). Le sapin baumier (*Abies balsamea* (L.) Mill.) est l'hôte principal de la TBE c'est-à-dire son alimentation préférentielle et ceci est dû à un synchronisme entre le débourrement des bourgeons de l'arbre et l'émergence des larves de l'insecte au printemps. L'épinette noire (*Picea mariana* Mill.), l'épinette blanche (*Picea glauca* (Moench) Voss) et l'épinette rouge (*Picea rubens* Sarg.) sont des hôtes secondaires de la TBE (Morin *et al.* 2010). Alors que les épinettes noires et rouges présentent un moins bon synchronisme avec l'insecte, l'épinette blanche subit une lignification rapide de ses aiguilles ce qui la rend moins appétante pour l'insecte (Nealis et Régnière 2004). Finalement, alors que le sapin baumier est très vulnérable aux attaques de la TBE et subit un taux de mortalité très élevé, les épinettes sont moins affectées par ses défoliations et vont simplement enregistrer les épidémies dans leurs cernes de croissance (MacLean 1980; Blais 1981; MacLean et Ostaff 1989; Bergeron *et al.* 1995; Morin *et al.* 2010).

La dendrochronologie pour retracer les épidémies

La dendrochronologie, soit l'étude des cernes de croissance des arbres, est une approche pour observer les variations temporelles de la croissance des espèces ligneuses (Fritts 1976; Hugues et al. 1982; Morin et Payette 1986). Il s'agit également d'une méthode efficace permettant de retracer les épidémies de la TBE avec une résolution annuelle (Lebourgeois et Mérian 2012). En effet, lors d'une épidémie, l'arbre va allouer son énergie à la reconstitution de son feuillage plutôt qu'à sa croissance secondaire ce qui a pour conséquence une réduction des cernes de croissance. Les réductions de croissance sont caractéristiques et apparaissent sous forme de « U » ou de « V » dans les chronologies de largeur de cernes (Morin *et al.* 2010). Les épinettes sont donc de bons enregistreurs des épidémies passées de la TBE car contrairement au Sapin Baumier, elles survivent aux épidémies et peuvent donc enregistrer plusieurs épidémies au cours de leur vie. De plus, l'étude spatio-temporelle des chronologies de largeurs de cernes apporte des explications complémentaires aux données de défoliation existantes (Brown 1970; Morin 1998).

Les épidémies du 20^{ème} siècle

Parmi tous les travaux connus concernant la dendrochronologie de la TBE, ceux de Robert Blais sont marquants. Cet auteur a travaillé pendant plus de 40 ans sur ce sujet et a réalisé un grand nombre de chronologies afin de détecter les épidémies. Grâce à lui, l'historique récent des épidémies de la TBE est bien connu dans plusieurs régions du Québec (Blais 1954; Blais 1961; Blais 1962; Blais 1964; Blais 1965). Par la suite, plusieurs autres études dendrochronologiques ont été menées au Québec (Morin *et al.* 1993; Morin 1994; Filion *et al.* 1998; Boulanger et Arseneault 2004; Bouchard et Pothier 2010). L'ensemble de ces études ont permis de mettre en évidence que les épidémies de la TBE sont apparues de façon cyclique tous les 30 à 40 ans durant le 20^{ème} siècle et ont duré en moyenne entre 10 et 12 ans. Ces études ont également mis en évidence les trois épidémies connues du 20^{ème} siècle. Toutefois, l'ensemble de ces études ont été menées de manière locale dans plusieurs régions du Québec et font

ressortir les épidémies de la TBE comme étant une perturbation ponctuelle dans le temps et l'espace.

Contexte et objectif

Dans un contexte de changements climatiques, il est nécessaire de connaître la dynamique des épidémies dans l'espace et dans le temps ainsi que les conditions dans lesquelles elles se sont produites. Ces connaissances sur la dynamique des épidémies permettraient de mieux comprendre les mécanismes impliqués et d'évaluer l'évolution des mosaïques forestières (Swetnam *et al.* 1999). Les changements climatiques prévus tendent à modifier les régimes de perturbation des insectes par des variations de leur phénologie (Pureswaran *et al.* 2015). En outre, le réchauffement du climat entraîne un bon nombre d'insectes phytophages à changer leur dynamique historique. En ce qui concerne la TBE, ces changements pourraient se traduire par une expansion vers le nord de son aire de distribution du fait d'une diminution du décalage phénologique entre l'insecte et son hôte secondaire : l'épinette noire (Logan *et al.* 2003). Depuis le début des années 2000, une nouvelle épidémie de la TBE se développe dans l'est de la forêt boréale, dans des secteurs plus nordiques que les épidémies précédentes où l'épinette noire est dominante. L'augmentation potentielle de la gravité des épidémies (en termes de pourcentage d'arbres affectés) et de la mortalité des arbres dans les forêts d'épinettes noires du nord soulèvent des inquiétudes concernant l'état futur de cet écosystème. En effet, les épidémies de la TBE peuvent affecter négativement l'approvisionnement en bois d'épinettes noires, qui est une des espèces commerciales les plus importantes en Amérique du Nord en raison de sa distribution transcontinentale et des bonnes propriétés de son bois (Giroud *et al.* 2016; Montoro Girona *et al.* 2016). Au Québec, les forêts d'épinettes noires couvrent une aire totale de 41Mha (Saucier *et al.* 2009) et cette espèce a toujours été très importante dans l'industrie forestière, anciennement pour la production de bois à pâte et aujourd'hui dans l'industrie de la production de bois d'œuvre. Il y a donc des intérêts, écologiques et économiques, à connaître et comprendre l'évolution spatio-temporelle des épidémies de la TBE à long terme. En fonction de l'évolution de la dynamique des écosystèmes forestiers face aux changements climatiques, on observera des changements de structure et de composition

des forêts, et par conséquent un changement de productivité des forêts qui aurait un impact direct sur le comportement de l'insecte (Pureswaran *et al.* 2015).

L'objectif principal de cette étude est de compléter les séries dendrochronologiques déjà existantes afin de retracer les épidémies de la TBE à l'échelle du Québec méridional au cours du 20^{ème} siècle. Pour cela, des échantillons d'arbres vivants ont été prélevés dans la portion sud et nord de l'aire de distribution de l'insecte dans le but de comparer les séries dendrochronologiques obtenues et comprendre la dynamique spatio-temporelle des épidémies à court terme soit au cours du 19^{ème} siècle. Pour cela, des variables telles que la durée (une période d'épidémie commençant lorsque plus de 20% des arbres sont touchés et se terminant lorsque moins de 20 % des arbres sont touchés) et la gravité (en termes de pourcentage d'arbres affectés) des épidémies ont été analysées. Nos hypothèses de recherche sont que : (1) la TBE malgré des périodes épidémiques plus intenses (en termes de gravité et de durée) exerce une influence continue dans le temps sur les forêts du Québec et que (2) l'influence de la TBE n'est pas homogène sur l'ensemble du territoire.

SPATIOTEMPORAL DYNAMICS OF 20TH-CENTURY SPRUCE BUDWORM OUTBREAKS IN EASTERN CANADA: THREE DISTINCT PATTERNS OF OUTBREAK SEVERITY

1. INTRODUCTION

The vulnerability and susceptibility of forest stands to SBW outbreaks depend on several factors. The first factor is the abundance of host species. Balsam fir (*Abies balsamea* (L.) Mill.) is the main host of SBW due to the synchronism in the spring between the bud flush period of the host and the emergence of the insect larvae; this synchronous timing enhances host vulnerability and increases its mortality rate (MacLean 1980; Blais 1981; MacLean and Ostaff 1989; Bergeron and *al.* 1995). Black (*Picea mariana* Mill.), white (*Picea glauca* (Moench) Voss), and red (*Picea rubens* Sarg.) spruce are secondary hosts of the insect (Morin and *al.* 2010) due to the highly lignified needles of white spruce and a lack of synchrony between insect emergence and the bud burst of black and red spruce (Nealis and Régnière 2004). Black, red, and white spruce are not equally susceptible to SBW outbreaks. Hennigar and *al.* (2008) put forward a susceptibility hierarchy of host species and quantified that when defoliation of balsam fir was 100%, the defoliation of white, red, and black spruce was 72, 41, and 28%, respectively. Consequently, spruce trees will often survive outbreaks and record these events in their growth rings (Blais 1957; Hennigar and *al.* 2008), which makes them suitable species for the dendrochronological analysis of outbreaks. A second factor of forest vulnerability is stand structure and age. SBW contributes to the dynamics of the forest mosaic (Bergeron and Archambault 1993; Martin and *al.* 2019; Martin and *al.* 2020) by eliminating mature trees (Bergeron and *al.* 1995). Preestablished regeneration survives insect attacks and forms the foundation of the replacement balsam fir stand (Kneeshaw and Bergeron 1998; De Grandpré and *al.* 2018). It then takes several decades for the stand to recover into a mature forest that would be sensitive to the next disturbance (Blais 1965; Martin and *al.* 2021). The third factor is the climate. Indeed, temperature has a major effect on the insect's development rate, while humidity has a greater influence on its survival rate (Reichenbach and Stairs 1984). In order for the insect to develop in all its phenological

stages, the average daily air temperature must be above 10°C (Pureswaran and *al.* 2019). Climatic conditions have hence a major role in restricting the extent and intensity of outbreaks (Gray and *al.* 2000; Volney and Fleming 2000; Volney and Fleming 2007). The capacity for SBW to cause damage depends on both insect population density and phenological timing in spring between emergence of SBW larvae and budding of host trees (Pureswaran and *al.* 2015; Pureswaran and *al.* 2019); both factors are dependent on climatic conditions.

Several studies show that SBW outbreaks behave differently depending on their geographic location; for example, outbreaks are more severe and longer lasting in the balsam fir–yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain (the transition zone between the northern temperate zone and the boreal zone; it extends between 47 and 48°N) and the balsam fir–white birch (*Betula papyrifera* Marsh) bioclimatic domain (an area in the southern part of the boreal zone, extending from 48 to 50°N) (Saucier and *al.* 2010) than within other regional domains (Gray and *al.* 2000; Jardon and *al.* 2003). The balsam fir–yellow birch bioclimatic domain represents the core of the SBW’s geographic distribution and is influenced to a much greater extent by SBW outbreaks than stands within the wetter coastal areas (Bouchard and Pothier 2010) and those found at the northern (Jardon and *al.* 2003; Tremblay and *al.* 2011; Martin and *al.* 2019) and southern margins of the insect’s range (Fraver and *al.* 2007). This geographic outbreak pattern may be related to unsuitable climatic conditions for SBW (Greenbank 1956; Régnière and *al.* 2012), although the lower abundance and limited continuity of host species in these marginal regions may also be contributing factors (Nealis and Régnière 2004; Campbell 2008; Gray 2008).

The main objective of this study is to reconstruct the spatiotemporal dynamics of SBW outbreaks during the 20th century across the insect’s range in southern Quebec (Figure 1). The originality of our study stems, in part, from its spatial scale. Numerous regional-scale studies have focused on the dynamics of SBW in Quebec, including studies of the Abitibi (Morin and *al.* 1993), Saguenay (Morin and Laprise 1990; Morin 1994; Krause 1997), Outaouais (Blais 1981), Réserve des Laurentides (Blais 1962; Blais

1965), Gaspésie (Blais 1961), Quebec's (Bouchard and Pothier 2010), Estrie (Filion and *al.* 1998), and Lower St. Lawrence (Boulangier and Arseneault 2004) regions. Ours is a provincial scale study. The second part of this study's originality is our aim to obtain precise information on the spatial distribution, severity, and timing of outbreaks during the 20th century. This is in contrast to the Jardon and *al.* (2003) study, which estimated the periodicity of outbreaks, or the Navarro and *al.* (2018) study, which provided a more global understanding of outbreaks as an agent of disturbance and their important role in the history of landscapes, although neither focused the specific timing of these outbreaks. In our study, we use the percentage of affected trees to determine whether a stand experienced an outbreak and, if so, assess the severity of the outbreak (Jardon 2001; Morin and *al.* 2007). We hypothesized that (1) distinct SBW outbreak severity and temporality patterns can be observed during the 20th-century, and (2) different spatial locations and climatic characteristics distinguish these patterns.

2. MATERIALS AND METHODS

2.1 Study area

The study area (45.3–49.7°N, 68.1–79.5°W) in Quebec (Canada) covers nearly 350,000 km² (Figure 1) and overlaps the northern temperate zone, dominated by deciduous and mixed stands, and the boreal zone, characterized by evergreen coniferous stands. According to the provincial ecological classification system, the study area encompasses six bioclimatic domains (Saucier and *al.* 2010) under the influence of a north–south temperature gradient and an east–west precipitation gradient (Wilson 1971; Richard 1987). The study area is entirely south of the northern limit of commercial forests (Figure 1), beyond which harvesting is prohibited because of recurrent fires and low forest productivity (Jobidon and *al.* 2015). The regional climate is generally humid continental, i.e., a climate characterized by an average temperature of the four hottest months of the year above 10°C and an average temperature of the coldest month of the year below 3°C. East of the St. Lawrence River, however, the climate has a strong maritime influence characterized by higher temperatures and greater precipitation (Villeneuve 1959).

Table 1 | The dendrochronological data sets used in this study

| Data set | Sampling year | Species | Max. age | Mean age | SD age | No. of stands | No. of trees |
|---------------------------|---------------|---------------------------------|----------|----------|--------|---------------|--------------|
| Jardon project | 1995 | <i>P. mariana/glauca</i> | 248 | 161.8 | 35.4 | 38 | 760 |
| Overmature forest project | 2006 | <i>P. mariana</i> | 267 | 238.2 | 20.5 | 5 | 100 |
| Spruce budworm project | 2017 | <i>P. mariana/glauca/rubens</i> | 227 | 150.1 | 29.1 | 40 | 800 |
| Total | | | | | | 83 | 1660 |

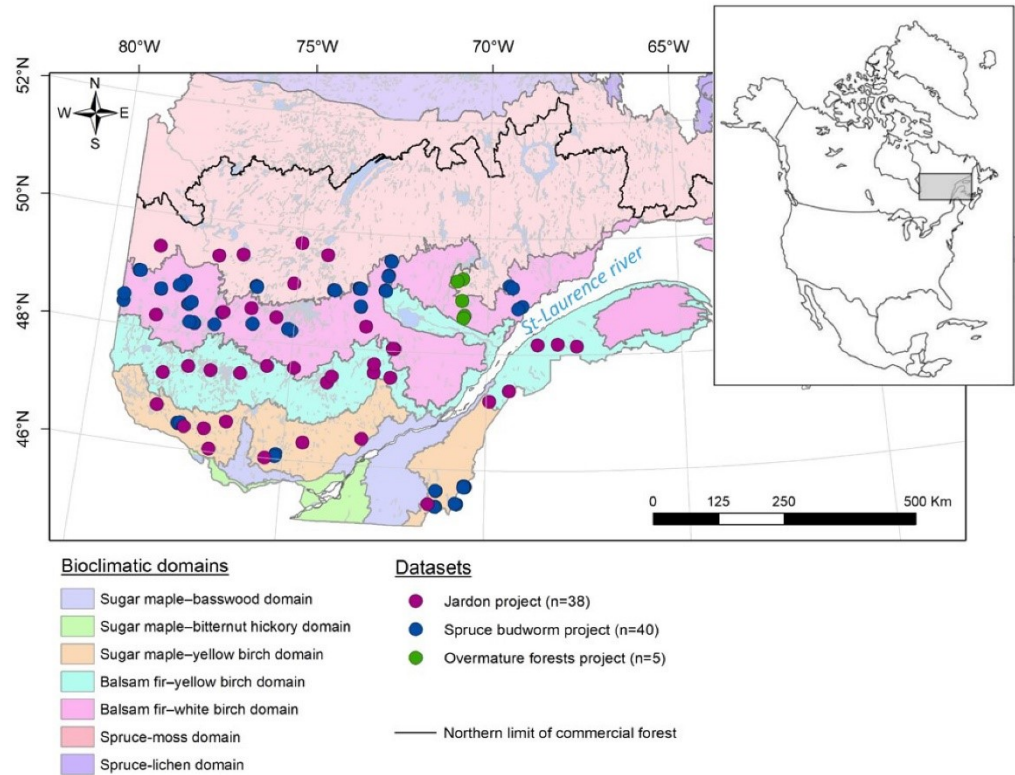


Figure 1 | Location of the studied forest stands in Quebec (Canada).

2.2 Sampling

We developed a tree-ring data set covering the entire study area, which included two pre-existing data sets and a new data set from cores collected in the field (Figure 1). This new data set (spruce budworm project) aimed to ensure an equal distribution of sample stands across the southern portion of the province. The first existing data set (the Jardon project) was developed by Jardon and *al.* (2003) and the second (the overmature forest project) originates from unpublished research (UQAC Plant Ecology Laboratory) (Table 1). Geographical gaps were filled using a random stratified sampling design based on forest age, relative spruce basal area, and proximity to a road to simplify sampling. Selected stands were ≥ 80 years old, had a relative spruce basal area $\geq 50\%$, and were located within 100m of a road.

We selected spruces trees to reconstruct the history of SBW outbreaks because these species are affected by defoliation, but with a lower mortality rate than balsam fir, thereby allowing us to extend the temporal scale of the outbreak record. Although balsam fir is the preferred host of SBW, it is usually used to reconstruct the history of outbreaks only over a relatively short period because of its high mortality during outbreaks (MacLean and Ostaff 1989; Bergeron and *al.* 1995; Morin and *al.* 2010). The three spruce species present in the study area (i.e., black, red, and white spruce) were used in this study to cover all of southern Quebec. Indeed, these three species have different spatial distributions, notably, red spruce is mostly present in the sugar maple (*Acer saccharum* Marsh.)- yellow birch domain while black and white spruce are more northerly. Within each stand, we randomly selected 20 dominant or codominant spruce trees and we cored each tree using a Pressler increment borer. We collected two cores per tree from opposing sides of the stem, 30 cm above the ground, to obtain the longest possible time series. The same sampling strategy was used for the Jardon and overmature forest projects.

2.3 Dendrochronological methods

Tree cores were dried and sanded before being measured. Tree ring widths were measured to the nearest 0.01mm using the semi-automatic LINTAB measuring bench coupled to the TSAPWin automatic recorder. Cores were cross-dated and averaged by tree using the PAST5 program. We standardized ring-width series to eliminate low- and medium-frequency signals by applying a negative exponential function and a cubic spline smoothing function, respectively (Cook and Peters 1981). We averaged the individual standardized series per stand. We then ran the program OUTBREAK to determine the percentage of trees affected by each outbreak for each stand chronology (Holmes and Swetnam 1996). We defined an outbreak event as a ring-width decrease lasting at least 5 years and having a maximum growth reduction >1.28 standard deviations from the mean (Blais 1962; Jardon 2001; Morin and *al.* 2010).

2.4 Statistical analysis

We used k-means clustering to identify the activity patterns of SBW (Hartigan and Wong 1979), grouping the yearly percentage of trees affected by SBW outbreaks into several clusters. This approach was inspired by the studies of Moussaoui and *al.* (2019) and Martin and *al.* (2020), which used k-means clustering to classify patterns in the diameter distribution and radial growth of the sampled trees, respectively. These studies demonstrated that k-means clustering is an effective tool for discriminating complex patterns and can be successfully applied to outbreak chronologies. The k-means clustering algorithm defines total variation within each cluster as the sum of the squared Euclidian distances between the variables and the corresponding centroid. To ensure clustering robustness, we performed 1,000 iterations of the k-means algorithm. The optimal number of clusters was determined by the highest simple structure index (SSI) (Dolnicar and *al.* 2000). The SSI multiplicatively combines several elements that influence the interpretability of a partitioning solution, that is, “the maximum difference between the clusters for each variable, the sizes of the most contrasting clusters and the deviation of a variable in the cluster centers compared to its overall mean” (Dimitriadou and *al.* 2002). The maximum value determines the optimal partition, i.e., the number of clusters (Dimitriadou and *al.* 2002). We also verified whether the clusters contained a homogeneous and sufficient number of sites (i.e., ≥ 20 sites), thereby ensuring the robustness of the subsequent analyses and the representativeness of the results at the scale of the study area. Moreover, this verification ensures representativeness of the different patterns and thus avoids overly specific clusters that would only concern a small number of stands. We performed k-means clustering with the R software, version 3.3.2 (Team 2018) using the *vegan* (Oksanen and *al.* 2007) package and applying a p-threshold of 0.05.

We mapped the resulting clusters. To understand the spatial variation between clusters, we tested for differences in the latitudes and longitudes of the corresponding

stands between the clusters using permutational ANOVA (PERMANOVA; (Anderson 2001) based on Euclidian distances and 10,000 iterations. When the results were significant, we then performed pairwise PERMANOVA, using Euclidian distances, 10000 iterations, and a Bonferroni adjustment for pairwise comparisons. PERMANOVA was performed using the R software and the pairwiseAdonis (Martinez Arbizu 2017) package, and we applied a p-threshold of 0.05.

We then assigned the mean monthly cumulative precipitation and average temperatures (1901–1995) to each stand from the corresponding grid cell of the CRU.TS.v.4.03 data set provided by the Climatic Research Unit at the University of East Anglia (Harris and *al.* 2014). This model is based on an updated gridded climate data set across the global land area (excluding Antarctica). The available data for our study area were provided by the Canadian Historical Temperature Database (Vincent and Gullett 1999).

To understand how stand-scale temporal variations of outbreaks varied between and within the clusters, we carried out an analysis of the onset, end, and duration of the SBW outbreaks. For each cluster, we defined outbreaks as periods where more than 20% of trees were affected, a value used as a threshold for distinguishing also minor outbreaks which are often underestimated (Morin and *al.* 2010).

Finally, to determine outbreak severity, we used 20th-century outbreak periods that had been previously identified at the scale of the study area, namely O1 from 1905 to 1930, O2 from 1935 to 1965, and O3 from 1968 to 1988 (Navarro and *al.* 2018). We assessed outbreak severity for each stand using the average, median, and the 75th and 95th percentiles of the yearly percentage of trees affected.

For all analyses, attributes were compared between the clusters using PERMANOVA and relying on the same methodology as described above. We present our results using various techniques. Boxplots and maps highlight the climatic differences between clusters. A Gantt diagram offers a visualization of the detailed timing of the outbreaks in each cluster. Finally, two tables present the differences in the severity of outbreaks within and between clusters.

3. RESULTS

The k-means clustering showed that the partition having the highest SSI included three clusters of 24, 30, and 29 stands, respectively (Figures 2A,B). The clusters presented specific patterns of outbreak severity based on the percentage of affected trees between 1900 and 1995 (Figure 2A) with three outbreak peaks at the beginning, middle, and end of the 20th century. Clusters 1 and 3 presented strong outbreak peaks at the beginning and end of the century and a relatively weaker mid-century outbreak. Although these two patterns are similar in terms of severity, they differ in terms of the duration of outbreaks. Cluster 2 on the other hand, showed outbreak peaks of intermediate severity during the 20th century and is similar in duration to Cluster 1.

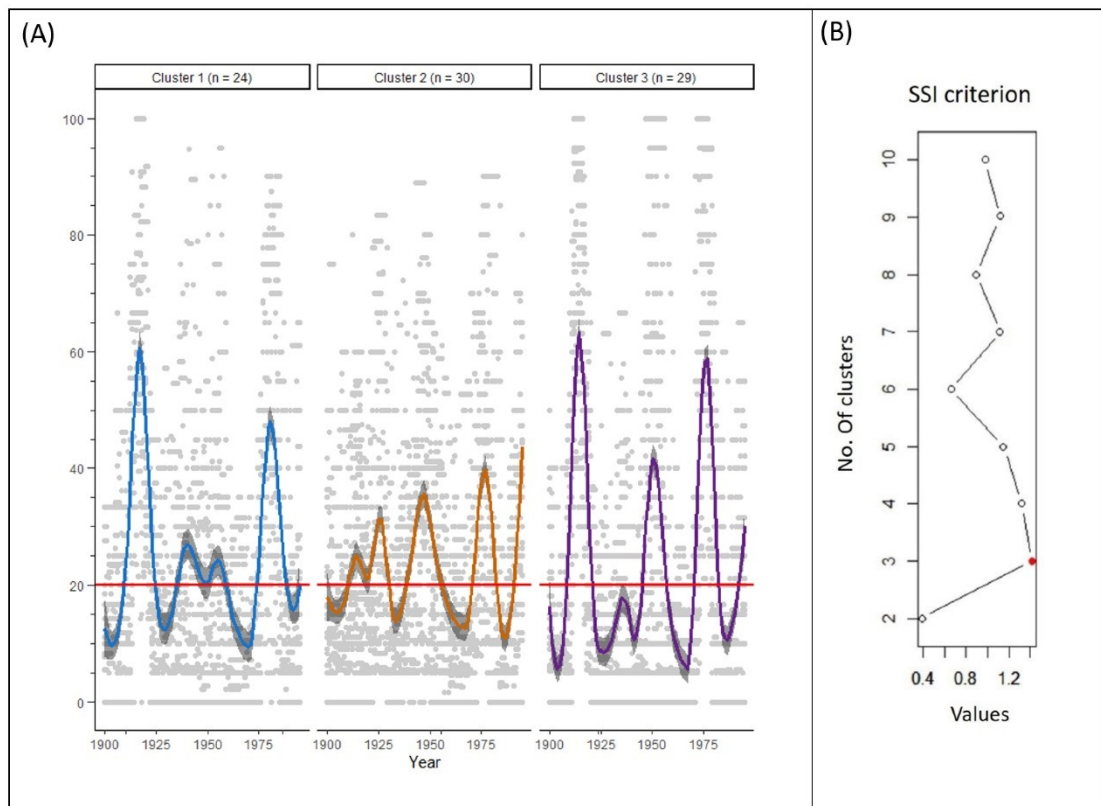


Figure 2 | (A) Annual percentage of affected trees in the studied stands for the three clusters identified by k-means clustering. The curves are a LOESS (locally estimated scatterplot smoothing) of the annual percentage of trees affected per year, using a *smoothing of 10%*. The gray band around the curves corresponds to a 95% confidence interval. The red line corresponds to a percentage of affected trees of 20%. (B) Values of the SSI criterion according to the number of clusters. The red dot indicates the optimal SSI criterion for the partition of clusters.

The analysis of stand coordinates highlighted significant differences (Annexe 1) in latitude ($F,2= 5.135; 0.008^{**}$) and longitude ($F,2=10.515;<0.001^{***}$) between clusters (Figures 3B,C), although the three clusters overlapped in the center of the study area (Figure 3A). Cluster 1 stands are located mainly in eastern and southeastern Quebec, particularly east of the St. Lawrence River, and in the northern section of the study area. Cluster 2 members are located mainly in the northwestern sector with a few stands found in the south. Cluster 3 contains stands located in southwestern Quebec and a few northern stands.

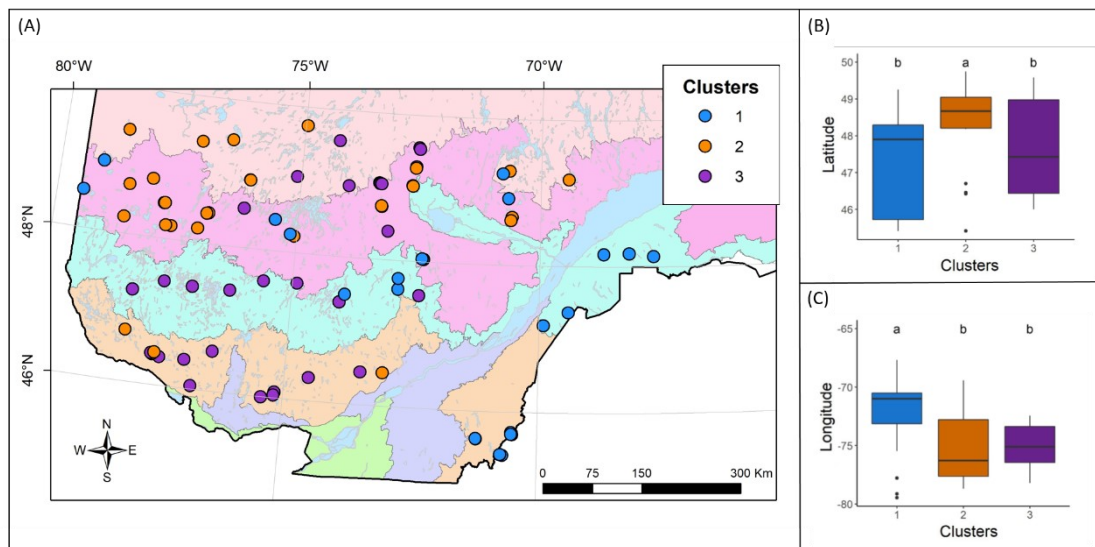


Figure 3 | (A) Spatial distribution of the three observed clusters. For the background map legend see Figure 1. Boxplots representing (B) the mean latitude and (C) longitude for each cluster, presented with the post-hoc test results ($a > b$).

Climate variables revealed patterns of decreasing temperature from south to north and a northwest–southeast gradient of increasing precipitation (Annexe 1). Consequently, temperatures were significantly ($F,2= 4.762; 0.012^{*}$) lower in cluster 2 (average annual temperature of 0.7°C) than in clusters 1 and 3 (average annual temperatures of 1.8 and 1.6°C , respectively) (Figures 4A,B). Precipitation was significantly ($F,2= 11.157; <0.001^{***}$) higher in cluster 1 (average annual precipitation

84.4mm) than in clusters 2 and 3 (average annual precipitation 76.4 and 76.7mm, respectively) (Figures 4C,D).

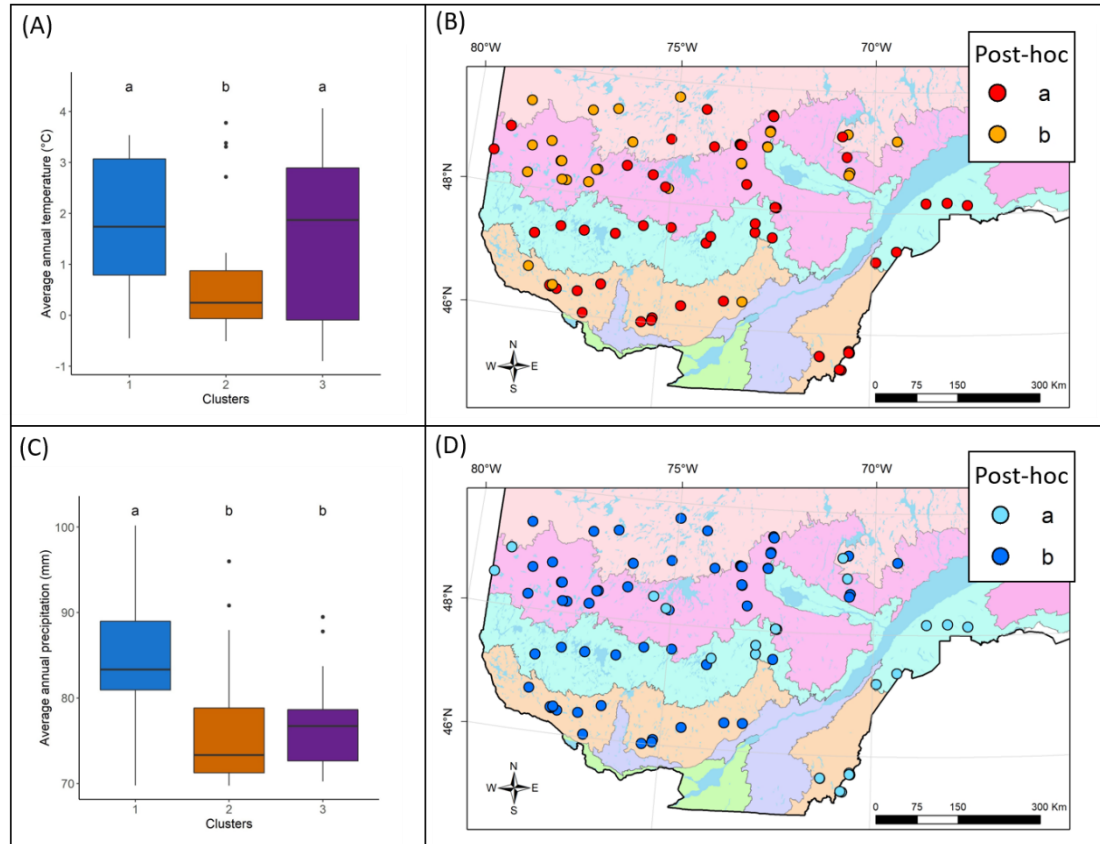


Figure 4 | (A) Boxplot representing the mean annual temperature (°C) for each cluster presented with the post-hoc test results ($a > b$) and (B) maps showing these post-hoc results. (C) Boxplot representing the mean annual precipitation (mm) for each cluster presented with the post-hoc test results ($a > b$) and (D) maps showing these post hoc results. For the background map legend see Figure 1.

The onset date of the outbreaks did not differ between the clusters for all three outbreaks (Figure 5, Annexe 1); the three outbreaks of the 20th century began ca. 1909, 1939, and 1972. However, the end date for the outbreaks differed between clusters. Outbreak O1 ended significantly ($F,2 = 10.818; <0.001***$) later for clusters 1 and 2 than for cluster 3. Outbreak O1 ended ca. 1926 for clusters 1 and 2 and ca. 1922 for cluster 3. The end date of the O2 outbreak did not differ significantly between clusters, ending ca. 1959, 1959, 1955 for clusters 1, 2, and 3, respectively. Outbreak O3 ended significantly ($F,2 = 4,315; 0.019*$) later for cluster 1 (ca. 1985) than for cluster 2 (ca. 1982) and ended at an intermediate date for cluster 3 (ca.1983).

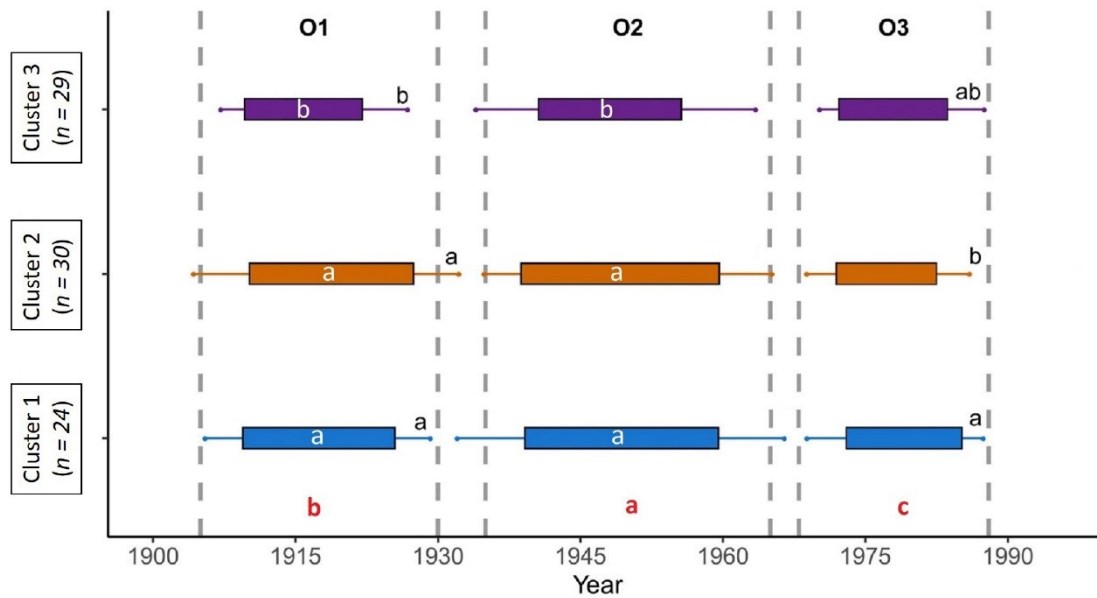


Figure 5 | Gantt chart representing the timing of outbreaks for the three clusters. The boxes represent the average duration of outbreaks and the dashes represent the standard deviations of these durations for O1, O2, and O3 in each cluster. Different letters indicate significant differences at $p < 0.05$ between end dates (black letters) and duration (white letters) for each cluster ($a > b$). Red letters indicate significant differences in duration, at $p < 0.05$, between each outbreak ($a > b > c$). Dotted lines indicate the onset and end dates of each outbreak, according to Navarro et al. (2018).

The duration of the outbreaks also varied between clusters (Annexe 1). Outbreaks O1 ($F,2 = 5,673; 0.004^{**}$) and O2 ($F,2 = 4,084; 0.021^{*}$) lasted longer for clusters 1 (16 and 20 years, respectively) and 2 (17 and 21 years, respectively) than for cluster 3 (12 and 15 years, respectively). We observed no difference in the duration of the O3 outbreak between clusters. The O3 outbreak lasted 12, 10, and 11 years for clusters 1, 2, and 3, respectively. For all clusters, the duration of the three outbreaks differed significantly ($F,2 = 25.551; <0.001^{***}$). Outbreak O1 had a mean duration of 16 years, followed by O2, which lasted an average of 21 years—the longest outbreak of the century. Outbreak O3 lasted 11 years on average, the shortest outbreak of the 20th century. Considering the average duration of outbreaks and their standard deviations, the three clusters were more often in an outbreak state than in a non-outbreak state. Similarly, the time between outbreaks was very short, especially for C1 and C2.

Table 2 | Mean and standard deviation of severity attributes (mean, median, 75th and 95th percentile of the percentage of trees affected by SBW for each of study sites and outbreak period) between clusters for each SBW outbreak. The different letters indicate significant differences between clusters for each outbreak period at $p \leq 0.05$.

| Outbreak period | Severity attributes | Cluster 1 ($n = 24$) | Cluster 2 ($n = 30$) | Cluster 3 ($n = 29$) |
|-----------------|---------------------|------------------------|------------------------|------------------------|
| O1 (1905–1930) | Mean (%) | 36.15 ± 7.39 a | 24.48 ± 8.54 b | 33.15 ± 8.82 a |
| | Median (%) | 31.48 ± 11.21 a | 20.8 ± 10.92 b | 23 ± 8.85 b |
| | 75th percentile (%) | 58.48 ± 14.73 a | 36.4 ± 13.25 b | 61.83 ± 19.2 a |
| | 95th percentile (%) | 72.22 ± 15.89 a | 49.19 ± 16.79 b | 72.95 ± 19.61 a |
| O2 (1935–1965) | Mean (%) | 23.51 ± 12.64 | 26.07 ± 8.79 | 24.15 ± 12.27 |
| | Median (%) | 20.71 ± 11.99 | 22.82 ± 10.56 | 16.32 ± 7.94 |
| | 75th percentile (%) | 35.1 ± 19.9 | 38.81 ± 13.02 | 43.11 ± 25.9 |
| | 95th percentile (%) | 45.87 ± 24.56 | 51.37 ± 17.2 | 55.06 ± 29.32 |
| O3 (1968–1988) | Mean (%) | 33.57 ± 11.14 ab | 28.96 ± 12.68 b | 37.49 ± 11.86 a |
| | Median (%) | 36.07 ± 17.33 | 27.57 ± 17.79 | 33.83 ± 20.88 |
| | 75th percentile (%) | 52.38 ± 19.73 b | 44.74 ± 18.29 b | 64.45 ± 20.74 a |
| | 95th percentile (%) | 59.93 ± 19.98 ab | 52.58 ± 19.19 b | 70.81 ± 19.95 a |

Outbreak severity varied significantly between clusters (Table 2, Annexe 1). During outbreak O1, the percentage of affected trees was lower in cluster 2 (24.48% of trees affected on average) than in clusters 1 and 3 (36.15 and 33.15%, respectively), except when using the median as a measure (Table 2). During outbreak O2, all clusters shared a similar percentage of affected trees, with no observed significant differences, regardless of the considered parameters. Indeed, clusters 1, 2, and 3 had averages of 23.5, 26.1, and 24.2% affected trees, respectively. In contrast, the severity of outbreak O3 was greater in cluster 3 (37.5%) than cluster 2 (29.0%), with intermediate values in cluster 1 (33.6%). The within cluster severity of outbreaks also varied (Table 3). Cluster 1 had similar yet more severe outbreaks in O1 and O3 (36.2 and 33.6%, respectively) than observed for outbreak O2 (23.5%). Outbreak severity within cluster 2 remained consistent over the century; outbreaks O1, O2, and O3 had respective percentages of affected trees of 24.5, 26.1, and 29.0%. Cluster 3, like cluster 1, had outbreak severities for O1 and O3 (33.2 and 37.5%, respectively) being significantly greater than that observed for outbreak O2 (24.2%).

Table 3 | Results of the pairwise comparisons of severity attributes (mean, median, 75th and 95th percentile of the percentage of trees affected by SBW for each of study sites and outbreak period) between the different SBW outbreaks per cluster, where a > b > c.

| Clusters | Severity attributes | O1 (1905–1930) | O2 (1935–1965) | O3 (1968–1988) |
|---------------------|---------------------|-------------------|-------------------|-------------------|
| Cluster 1 (n=24) | Mean (%) | a | b | a |
| | Median (%) | a | b | a |
| | 75th percentile (%) | a | b | a |
| | 95th percentile (%) | a | b | c |
| Cluster 2 (n=30) | Mean (%) | - | - | - |
| | Median (%) | - | - | - |
| | 75th percentile (%) | - | - | - |
| | 95th percentile (%) | - | - | - |
| Cluster 3 (n=29) | Mean (%) | a | b | a |
| | Median (%) | a | b | c |
| | 75th percentile (%) | a | b | a |
| | 95th percentile (%) | a | b | a |

4. DISCUSSION

In this study, we identified three spatiotemporal patterns of SBW disturbance during the 20th century in our study area. The three obtained clusters are defined by outbreaks of specific duration and severity, supporting our first hypothesis. Moreover, the three clusters are spatially distinct and subject to different climatic conditions, a finding that supports our second hypothesis.

4.1 SBW Outbreak patterns were spatially and climatically distinct

We ran k-means clustering using the percentage of affected trees within a stand based on tree-ring chronologies. We observed three spatially distinct outbreak patterns. The majority of the stands constituting cluster 1 are located in eastern Quebec, east of the St. Lawrence River. The cluster 2 stands are mainly located in the northern reach of our study area in southern Quebec, and cluster 3 stands are mainly located along a southwest– northeast transect across the central part of southern Quebec. Admittedly, the resulting clusters also include isolated stands; for example, cluster 1 contained some outlier stands situated in western Quebec, and cluster 2 included some stands in southern Quebec. Nevertheless, the presence of stands having a location distinct from those stands making up the majority of a cluster is not incongruent given the methodology and the data used, i.e., the k-means clustering algorithm and dendrochronological data. Despite these few outliers, our approach was effective in improving the understanding of SBW outbreaks in space and time. Indeed, patterns similar to those of cluster 1, characterized by a high percentage of affected trees during outbreaks O1 and O3, were observed by Boulanger and Arseneault (2004) and Boulanger and *al.* (2012) in regional studies conducted south of the St. Lawrence River. Cluster 2 was characterized by outbreaks having similar percentages of affected trees, in agreement with reconstructions of past outbreaks north of Lac Saint-Jean (Morin and Laprise 1990). Similarly, the cluster 3 pattern,

characterized by a moderate (O2) to high (O1 and O3) severity and by stands located at the heart of the insect's distribution, has been highlighted previously, in particular by Jardon and *al.* (2003) and Bouchard and *al.* (2006). Therefore, the use of kmean clustering to identify large-scale SBW outbreak patterns produced spatially well-defined results that are consistent with earlier local-scale studies. Finally, the results of this study help to explain the differences in outbreaks patterns between local studies conducted in different locations. The recording of outbreak periods therefore depends on the spatial scale under consideration. It is likely that at a small spatial scale, recorded outbreaks are often shorter in duration because the insect changes location on the basis of available resources (Pureswaran and *al.* 2016). The shorter duration of outbreaks at a local scale may explain why, at the local level, outbreaks are generally considered as punctual events or as peaks of disturbance (Martin and *al.* 2019). At the provincial level, on the other hand, despite the presence of peaks in severity, outbreak periods appear continuous over time.

Indeed, the continuous presence throughout the 20th century of at least a number of affected trees in Quebec suggests that SBW is an continuous disturbance agent across the province. The identified spatial patterns corresponded to specific climatic conditions. Cluster 1 included stands having a higher average annual precipitation than those in clusters 2 and 3. The mean annual temperatures of stands in cluster 2 were significantly lower than for clusters 1 and 3. The climatic conditions of cluster 3 were intermediate between clusters 1 and 2. These results are generally consistent with large-scale patterns of Quebec climate. Villeneuve (1959) pointed out that although there is a humid temperate climate throughout southern Quebec, a more maritime climate can be observed in the St. Lawrence estuary, and a drier continental climate is present across the remainder of the province. This supports our results that show greater precipitation in cluster 1 (stands generally located in eastern Quebec) relative to the drier climate in the more continental clusters 2 and 3. However, Villeneuve (1959) also highlighted the existence of several climatic regions within the continental climate category, which occur because of the influence of inland water

masses, latitude, and altitude. These climatic patterns match the spatial distribution of our two continental clusters; cluster 2 has colder temperatures than cluster 3. SBW is also a climate-dependent species (Greenbank 1956; Williams and Liebhold 1995; Williams and Liebhold 1997; Williams and Liebhold 2002; Pureswaran and *al.* 2015; Pureswaran and *al.* 2019), and climatic conditions can both directly affect SBW, such as influencing survival, reproduction, and the displacement of populations, and indirectly affect SBW, including through changes in the upper (predators and parasites) and lower (host trees) trophic levels. As a result, the various outbreak patterns identified in our study can be clearly associated with various known climatic regions. Hence, our approach could discriminate SBW outbreak patterns on the basis of consistent climatic gradients.

4.2 Variability in outbreak severity and timing within the SBW outbreak patterns

The outbreaks of each cluster were defined by varying severities and timings. Nonetheless, we observed, for each cluster, three outbreak peaks—at the beginning, middle, and end of the century—and these three outbreak peaks correspond well to the three known outbreak periods of the 20th century (Blais 1965; Jardon and *al.* 2003; Boulanger and Arseneault 2004; Morin and *al.* 2007; Navarro and *al.* 2018). Yet, the severity of these outbreaks differed between clusters. In clusters 1 and 3, the severity of outbreaks O1 and O3 was significantly greater than that of outbreak O2. It is therefore likely that the severity of outbreak O1 led to a landscape characterized by a scarcity of mature host trees, thereby leading to a less severe O2 outbreak. As time passed, the abundance of mature trees and balsam fir progressively increased (MacLean 1984; MacLean and Ostaff 1989); as a result, the O3 outbreak was as severe as the O1 outbreak. Morin and *al.* (2007) highlighted this succession of alternating high-low-high severities for 20th-century outbreaks. Our results underscore that this alternating pattern of outbreak severity is common to large and continuous areas in Quebec for forest stands that have remained unburned for an extended period.

The severity of each outbreak also varied between clusters. The severity of the O1 outbreak was higher in clusters 1 and 3 than within cluster 2. For the less severe O2 outbreak, however, the severity was similar for each cluster. Finally, during the O3 outbreak, cluster 2 experienced a lower severity outbreak than clusters 1 and 3, which had outbreaks of intermediate severity. The pronounced severity of outbreaks O1 and O3 within clusters 1 and 3 likely stemmed from the greater abundance of mature host species, in contrast to cluster 2 stands, which are located further north in a zone characterized by a lower proportion of balsam fir (Bergeron and *al.* 1995; MacLean and MacKinnon 1997). During outbreak O2, clusters 1 and 3 experienced lower severity outbreaks owing to the high-low-high alternating pattern of severity highlighted above. Cluster 2, having stands located further north, lies in an area having a higher proportion of black spruce. Black spruce is less responsive to SBW outbreaks than red and white spruce (Hennigar and *al.* 2008) , and this difference in sensitivity could explain the lower severity of the O1 and O3 outbreaks observed within cluster 2. Nevertheless, we did not observe any significant differences in the severity of the O2 outbreak between clusters, which suggests that the proportion of black spruce in the landscape plays a smaller role in determining outbreak severity than balsam fir availability and climate.

The duration of the three outbreaks also varied. For all clusters, the O3 outbreak was significantly shorter than outbreaks O1 and O2. This reduced duration relates to the O3 outbreak, which occurred in the 1980s, representing the most severe outbreak ever recorded. This outbreak destroyed between 139 and 238 million m³ of timber on public lands in Quebec (Dorais and *al.* 1996). Its severity led to more a rapid defoliation and death of host individuals. The degree of severity of this outbreak can be linked to the insect's population dynamics. Explosive population growth of SBW over the entire territory causes extensive damage to host trees (Morris 1963; Royama 1984); however, this massive population increase leads, in turn, to the explosive growth of predator and parasite populations, leading to the crash of SBW populations.

In addition, the O2 outbreak was significantly longer than the O1 and O3 outbreaks. Noting that the O2 outbreak was also the least severe of the 20th century, this pattern of a long, less severe outbreak supports the hypothesis that a low outbreak severity is related to the population dynamics of the insect. A slow SBW population growth and a gradual dispersal across the territory causes predator and parasite populations to increase slowly as well, lengthening the duration of the outbreak. These duration-intensity relationships suggest least severe outbreaks are longer lasting and are in contrast to the short, intense outbreaks, such as outbreak O3. Our temporal analysis of outbreaks shows that, despite variations in severity, the three 20th-century outbreaks began synchronously in all clusters. Several authors have suggested that the 20th-century epidemics developed initially in the southern areas of mixed forest and then spread to the coniferous forests further north (Hardy and *al.* 1983; Hardy and *al.* 1986; Gray and *al.* 2000). Others hypothesized that these outbreaks spread from southern regions, characterized by a high proportion of balsam fir, to northern regions, which have a lower proportion of balsam fir (Royama 1984; Blais 1985; Morin and Laprise 1990; Morin and *al.* 1993). Our results refute this northward expansion hypothesis. Our findings indicate that the onset of all three outbreaks was synchronous over the entire study area. The synchronicity between the more northern stands in cluster 2 and the more southern stands in clusters 1 and 3 suggests that these more northerly SBW populations were already present at the turn of the century, as suggested previously (Morin 1994; Morin and Laprise 1997). These remote populations may result from the overflow of more southern populations toward the end of the 19th century (Royama 1984; Blais 1985; Morin and *al.* 1993).

The end of outbreaks and therefore their duration, however, vary from one cluster to another. O1 and O2 outbreaks were indeed longer in clusters 1 and 2 than in cluster 3. This longer duration can be explained by the relatively moderate climatic conditions (Greenbank 1956) and the continuous presence of host species (Nealis and Régnière 2004; Campbell 2008; Gray 2008) within the various bioclimatic domains represented by cluster 3. All these factors favor the insect and its wide dispersal. This pattern

suggests that cluster 3 is spatially the most appropriate area for SBW outbreaks and that in cluster 3, SBW consumes resources faster and attains an outbreak peak earlier, thereby facilitating the rapid growth of predators and parasites, as well as depleting host trees; when combined, these factors precipitate the collapse of the insect population (Royama 1984; Royama 1992). Our results also indicate that for all clusters, the 1980s outbreak was shorter in duration than the two previous 20th-century outbreaks. Various authors have hypothesized that a tri-trophic relationship between host trees, insects and their natural enemies, and late 20th-century climate change explains this change in duration (Dale and *al.* 2001; Pureswaran and *al.* 2015). In addition, Dale and *al.* (2001) illustrate that climate change can lead to increases in insect populations and alter the intensity and frequency of outbreaks. This shift also produces several indirect effects, including the loss of host species and increased populations of insect predators. It is therefore possible that an increase in SBW populations owing to climate change contributed to the more rapid decline of insect host species during the O3 outbreak.

Overall, we highlighted in this study that the characteristics of SBW outbreaks are dependent on three factors: spatial location, climate, and forest composition (Gray 2008). However, we used indirect data (i.e., reconstruction of outbreak patterns using dendrochronological data), which means that we are unable to reconstruct in detail the specific local climate, vegetation, and stand structure at the time of the various outbreaks. Hence, the direct influence of these factors requires further assessment; in particular, it demands a better understanding of the influence of stand characteristics on outbreaks. The identification of those factors most strongly related to the obtained clusters would (i) help identify the local environmental, ecological, and climatic conditions able to explain the obtained patterns of duration, severity, and timing, and (ii) test hypotheses related to the dynamics of insect populations at several space and time scales. Moreover, studying these local factors would bolster predictions of the effects of changes in insect distribution on forest stands and the associated ecological resources.

CONCLUSION GÉNÉRALE

Dans cette étude, nous avons utilisé la dendrochronologie, soit l'étude des cernes de croissance des arbres, dans le but de retracer les épidémies du Lépidoptère *Choristoneura fumiferana* (Clem.), la tordeuse des bourgeons de l'épinette (TBE). Pour ce faire nous avons échantillonné des arbres du genre *Picea* qui enregistrent les épidémies dans leurs largeurs de cernes. L'échantillonnage a été fait sur une zone recouvrant l'ensemble du Québec méridional et sur des arbres assez âgés pour permettre l'obtention de chronologies recouvrant l'ensemble du 20^{ème} siècle. Ceci nous a permis d'une part de compléter la base de données dendrochronologiques que de nombreux auteurs ont contribué à constituer depuis plusieurs années au Québec et d'autre part de retracer les trois épidémies connues de la TBE qui ont eu lieu au cours du 20^{ème} siècle.

L'objectif principal de cette étude était de mieux comprendre la dynamique spatio-temporelle des épidémies de la TBE à court terme (1900-2000). L'idée est ici de regarder les épidémies à une échelle spatiale plus large que ce que les précédents auteurs ont fait et de s'interroger sur le type d'influence que l'insecte a sur le paysage. Les épidémies sont-elles des événements ponctuels ou des événements continus? Les épidémies ont-elles une influence homogène ou hétérogène sur un territoire aussi vaste que le Québec méridional?

Afin de répondre à ces questions, une approche novatrice qui consiste à discriminer mathématiquement et non subjectivement les patrons d'éclosion a été utilisée. Cette approche a permis l'obtention d'une image globale de la dynamique spatio-temporelle des épidémies de la TBE. Pour la première fois, nous avons mis en évidence trois patrons épidémiques distincts que nous avons comparés grâce à des variables telles que la distribution spatiale, la gravité et la durée des épidémies.

L'obtention de ces trois modèles épidémiques corrobore l'hypothèse de l'hétérogénéité du comportement des épidémies de la TBE et démontre la complexité de ce phénomène écologique. En effet, le climat a un impact sur la végétation et les taux de perturbations lesquels influencent ensuite les épidémies de la TBE en termes de sévérité et de timing. Toutefois, ces relations corrélatives, bien que mentionnées plusieurs fois de manière hypothétiques et parfois spéculatives pour discuter certains points, n'ont pas été testées dans cette étude.

De plus, l'analyse de ces patrons a permis de mettre en évidence que malgré des périodes épidémiques plus intenses, la TBE exerce une influence continue dans le temps puisque le pourcentage d'arbres affectés n'est jamais nul. Cette étude a donc permis de mettre en avant l'importance de considérer les épidémies de la TBE comme un agent de perturbation continu à l'échelle du paysage plutôt que ponctuel.

ANNEXE 1

Table of statistical results for the different PermANOVAs realized in this study

| Analysis | Variable | D.f. | Sum of squares | R ² | F-statistic | p |
|------------------------------------|------------------------|------|----------------|----------------|-------------|-----------|
| Outbreak severity between clusters | O1, mean | 2 | 2043,049 | 0,268 | 14,714 | <0.001*** |
| | O1, median | 2 | 1644,294 | 0,161 | 7,697 | 0.001** |
| | O1, standard deviation | 2 | 1992,191 | 0,309 | 17,965 | <0.001*** |
| | O1, 5th percentile | 2 | 79,476 | 0,033 | 1,395 | 0.248 |
| | O1, 75th percentile | 2 | 11103,099 | 0,352 | 21,766 | <0.001*** |
| | O1, 95th percentile | 2 | 10527,079 | 0,298 | 17,012 | <0.001*** |
| | O2, standard deviation | 2 | 99,291 | 0,009 | 0,392 | 0.683 |
| | O2, standard deviation | 2 | 643,444 | 0,071 | 3,098 | 0.053 |
| | O2, standard deviation | 2 | 430,885 | 0,054 | 2,303 | 0.108 |
| | O2, 5th percentile | 2 | 301,886 | 0,095 | 4,201 | 0.021* |
| | O2, 75th percentile | 2 | 851,528 | 0,025 | 1,038 | 0.361 |
| | O2, 95th percentile | 2 | 1113,61 | 0,023 | 0,957 | 0.39 |
| | O3, standard deviation | 2 | 1075,801 | 0,085 | 3,755 | 0.025* |
| | O3, standard deviation | 2 | 1081,667 | 0,036 | 1,529 | 0.221 |
| | O3, standard deviation | 2 | 1204,152 | 0,151 | 7,144 | 0.001** |
| | O3, 5th percentile | 2 | 16,28 | 0,006 | 0,254 | 0.777 |
| | O3, 75th percentile | 2 | 5801,793 | 0,158 | 7,558 | <0.001*** |
| | O3, 95th percentile | 2 | 4942,561 | 0,137 | 6,375 | 0.002** |
| Outbreak severity within clusters | Mean, O1 | 2 | 2141,08 | 0,215 | 9,486 | <0.001*** |
| | Mean, O2 | 2 | 308,851 | 0,033 | 1,489 | 0.233 |
| | Mean, O3 | 2 | 2686,475 | 0,206 | 10,917 | <0.001*** |
| | Median, O1 | 2 | 2984,715 | 0,185 | 7,856 | <0.001*** |
| | Median, O2 | 2 | 724,72 | 0,043 | 1,985 | 0.142 |
| | Median, O3 | 2 | 4531,523 | 0,218 | 11,774 | <0.001*** |
| | 5th percentile, O1 | 2 | 8,291 | 0,002 | 0,091 | 0.914 |
| | 5th percentile, O2 | 2 | 75,592 | 0,024 | 1,097 | 0.344 |
| | 5th percentile, O3 | 2 | 189,45 | 0,107 | 5,06 | 0.009** |
| | 75th percentile, O1 | 2 | 7063,741 | 0,234 | 10,568 | <0.001*** |
| | 75th percentile, O2 | 2 | 1104,784 | 0,053 | 2,438 | 0.097 |
| | 75th percentile, O3 | 2 | 7859,95 | 0,16 | 8,022 | <0.001*** |
| | 95th percentile, O1 | 2 | 8349,901 | 0,224 | 9,979 | <0.001*** |
| | 95th percentile, O2 | 2 | 177,716 | 0,006 | 0,281 | 0.757 |
| | 95th percentile, O3 | 2 | 5538,573 | 0,107 | 5,057 | 0.009** |
| | Standard deviation, O1 | 2 | 1328,893 | 0,205 | 8,931 | <0.001*** |
| | Standard deviation, O2 | 2 | 33,837 | 0,007 | 0,324 | 0.72 |
| | Standard deviation, O3 | 2 | 1004,685 | 0,1 | 4,695 | 0.013* |

| | | | | | | |
|------------------|----------------|---|---------|-------|--------|-----------|
| Coordinates | Longitude | 2 | 149,58 | 0,208 | 10,515 | <0.001*** |
| | Latitude | 2 | 14,659 | 0,113 | 5,135 | 0.008** |
| Meteo | Precipitations | 2 | 1063,6 | 0,218 | 11,157 | <0.001*** |
| | Temperatures | 2 | 18,144 | 0,106 | 4,762 | 0.012* |
| Outbreak timings | Duration, O1 | 2 | 373,284 | 0,124 | 5,673 | 0.004** |
| | Duration, O2 | 2 | 565,401 | 0,095 | 4,084 | 0.021* |
| | Duration, O3 | 2 | 35,913 | 0,02 | 0,826 | 0.453 |
| | Beginning, O1 | 2 | 7,191 | 0,004 | 0,199 | 0.824 |
| | Beginning, O2 | 2 | 50,623 | 0,019 | 0,769 | 0.47 |
| | Beginning, O3 | 2 | 15,367 | 0,021 | 0,854 | 0.435 |
| | End, O1 | 2 | 437,659 | 0,212 | 10,818 | <0.001*** |
| | End, O2 | 2 | 280,142 | 0,073 | 3,052 | 0.052 |
| | End, O3 | 2 | 95,656 | 0,098 | 4,315 | 0.019* |

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