

# Bottom-up factors contribute to large-scale synchrony in spruce budworm populations<sup>1</sup>

Mathieu Bouchard, Jacques Régnière, and Pierre Therrien

**Abstract:** Understanding the mechanisms that cause large-scale synchrony in insect population dynamics might yield key insights for predicting potential outbreak occurrence. Here, we evaluated which environmental factors best explain synchronous population fluctuations in the spruce budworm (*Choristoneura fumiferana* Clem.) (SBW), a major defoliator of coniferous forests in North America. SBW population levels were assessed with pheromone traps during the 1986–2014 period across a 625 000 km<sup>2</sup> territory located in the province of Québec (Canada). The populations were characterized by abundance fluctuations that were often synchronized across the whole study area. Interannual population fluctuations were correlated with host tree cone production (a source of food) and high May temperatures, suggesting that synchrony was influenced by food availability and phenological mismatch during shoot development. Cone production was itself correlated with low precipitation during the previous summer. This study indicates that bottom-up trophic factors can drive spatiotemporal synchrony in insect populations and contribute to explain important and sustained population increases during some years. We also suggest that several biological processes, all influenced by weather, are likely to interact to explain population synchrony during the different phases of the approximately 35 year SBW outbreak cycle, complicating the prediction of climate change effects on this insect.

**Key words:** spruce budworm, population synchrony, mast years, boreal forests, phenology.

**Résumé :** La compréhension des mécanismes qui causent le synchronisme à grande échelle dans la dynamique des populations d'insectes pourrait aider à mieux prédire l'occurrence des épidémies. Dans cette étude, nous avons évalué quels facteurs environnementaux expliquent le mieux les fluctuations synchrones des populations de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) (TBÉ), un défoliateur important des forêts conifériennes d'Amérique du Nord. Les niveaux des populations de TBÉ ont été évalués à l'aide de pièges à phéromones durant la période 1986–2014 dans un territoire de 625 000 km<sup>2</sup> localisé dans la province de Québec (Canada). Les populations de TBÉ étaient caractérisées par des fluctuations d'abondance souvent synchronisées sur l'ensemble du territoire. La fluctuation interannuelle des populations était corrélée avec la production semencière des arbres hôtes (une source de nourriture) et des températures élevées lors du mois de mai, suggérant que le synchronisme est influencé par la disponibilité de la nourriture et le décalage phénologique lors du débourrement. La production semencière était elle-même corrélée avec un faible niveau de précipitations durant l'été précédent. Cette étude indique que la disponibilité en ressources peut expliquer le synchronisme spatio-temporel chez les populations d'insectes, et contribuer à expliquer les hausses de populations importantes et soutenues lors de certaines années. Nous suggérons également que plusieurs processus biologiques, tous influencés par les conditions météorologiques, pourraient interagir pour expliquer la synchronisation lors de différentes phases du cycle épidémique de la TBÉ, compliquant la prédiction des effets des changements climatiques sur cet insecte.

**Mots-clés :** tordeuse des bourgeons de l'épinette, synchronisme des populations, années semencières, forêts boréales, phénologie.

## Introduction

Large-scale synchrony in population fluctuations has been described for many animal species, including small mammals, ungulates, and particularly insects (Liebhold et al. 2012; Myers and Cory 2013). Synchronous population increases have also been hypothesized to contribute to insect outbreak occurrence, for example by facilitating escape from natural enemy control (Liebhold et al. 2012). Population synchrony can take place across vast spa-

tial scales (e.g., >100 km) and is often thought to correlate with climatic perturbations, i.e., the so-called “Moran effect” (Moran 1953). However, the exact causal pathways through which climate and weather synchronize demography across large areas are still poorly understood. The mechanisms that have been proposed are varied and range from a direct effect of weather on animal populations to indirect effects through bottom-up and top-down factors or dispersal-related factors (Liebhold et al. 2012).

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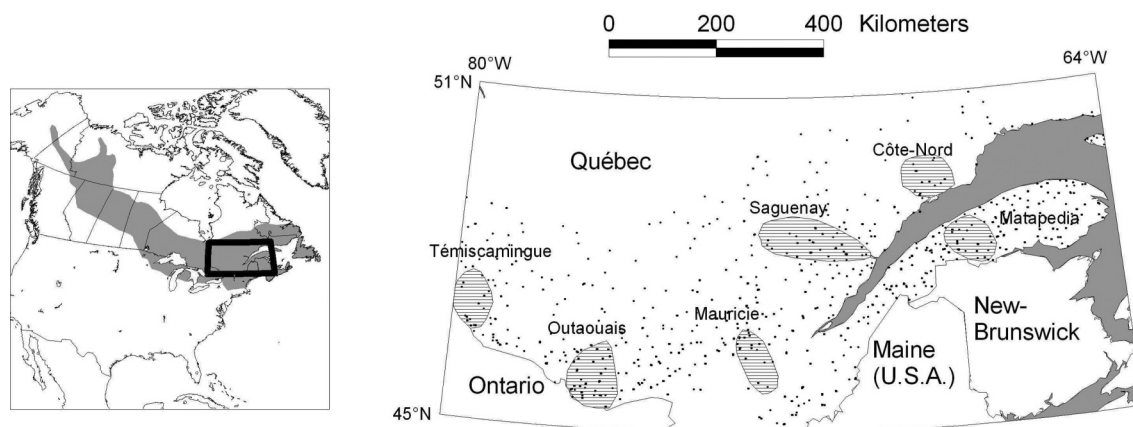
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**Fig. 1.** Location of the sample plots where pheromone traps were placed (dots). The shaded area in the left inset indicates the distribution of the spruce budworm (*Choristoneura fumiferana*) across North America. Cross-hatching in the right inset indicates the location of different outbreak epicenters that were observed during the 1986–2014 period.



The spruce budworm (*Choristoneura fumiferana* Clem.) (SBW) outbreak system represents an interesting opportunity to explore the causal relationships that can explain synchronous population fluctuations across large spatial scales. The SBW is a defoliator of *Abies* spp. and *Picea* spp. in North American boreal forests. In eastern Canada, SBW outbreaks have occurred every 30–40 years for the last two centuries at least, and these cycles tend to be loosely synchronized at the regional level (Royama 1984; Williams and Liebhold 2000; Morin et al. 2007). Cumulative defoliation by this insect results in substantial tree mortality and has cascading effects in boreal forest ecosystems (Bouchard et al. 2006). SBW population dynamics are driven by several processes such as competition for food, disease propagation, predation, parasitism, and migration (Régnière 1984; Royama 1984; Régnière and Nealis 2007). Some causal mechanisms have been proposed to explain large-scale synchrony, such as temporal variation in apparent fecundity and natural enemies (Royama 1984) or moth dispersal (Régnière and Lysyk 1995; Royama et al. 2005), but these hypotheses were not examined over large spatial scales, and connections between year-to-year weather fluctuations and specific SBW population processes remain little explored.

Temporal variation in feeding substrate availability can be important to explain spatial synchrony in insect populations. For example, in the case of the gypsy moth (*Lymantria dispar* Linnaeus), it has been suggested that episodic acorn production by oak trees could ultimately explain large-scale synchronous outbreak occurrence (Haynes et al. 2013). In this case, acorn abundance affects the white-footed mouse (*Peromyscus leucopus* Rafinesque), a predator of the gypsy moth, and the trophic relationship could thus be better described as top-down than bottom-up (Haynes et al. 2013). In geometrid outbreaks in Norway, Jepsen et al. (2009) found that the degree of synchrony between egg hatch and bud development in the spring influences large-scale synchronization. Similarly, temporal variation in food quality was found to be important for spatial synchrony in the jack pine budworm (*Choristoneura pinus pinus* Freeman), a species that is closely related to the SBW. Short-duration outbreaks in this insect were associated with pollen cone production episodes in its host species, jack pine (*Pinus banksiana* Lamb.) (Nealis 2003). For the SBW, the potential importance of balsam fir (*Abies balsamea* (L.) Mill. pollen cone availability for outbreak occurrence has been suggested in a few studies (Blais 1952; Morris 1963). This resource constitutes an easily accessible and nutritious food source in early spring and provides a favorable microhabitat for larvae emerging from overwintering (Carisey and Bause 1997). The presence of pollen cones during host species mast years can alleviate the negative impact of phenological mismatch between the insect and host tree shoot development,

known to be highly variable in space and time depending on early spring conditions (Greenbank 1963a; Nealis and Lomic 1994), and could therefore have important repercussions on the insect's population dynamics.

It is uncertain to what extent a large-scale synchronous increase in population density during a given year can persist during subsequent years. Density-dependent factors such as natural enemies or resource scarcity during the years following the increase are susceptible to drive insect populations back to pre-increase levels. Still, under some conditions, higher densities could persist over several years. In the case of the SBW, low-density populations can be subjected to mate-finding difficulties (Régnière et al. 2013a), which could generate a positive relationship between population density and population growth. Also, in insects, the likelihood that natural enemies are able to aggregate to suppress host populations is generally inversely related to the spatial extent and spatial homogeneity of the host population increases (Briggs and Hoopes 2004), suggesting that large-scale increases are also more likely to persist over time. Finally, the SBW also possesses foraging capabilities that allow it to cope with resource scarcity during less favorable years, for example by mining or feeding upon older foliage when optimal feeding substrates such as very young foliage or pollen cones are not available (Lawrence et al. 1997). Hence, population increases caused by large-scale pulses of resource during one year could potentially persist over subsequent years, leading to rising SBW populations and outbreak initiation in some cases.

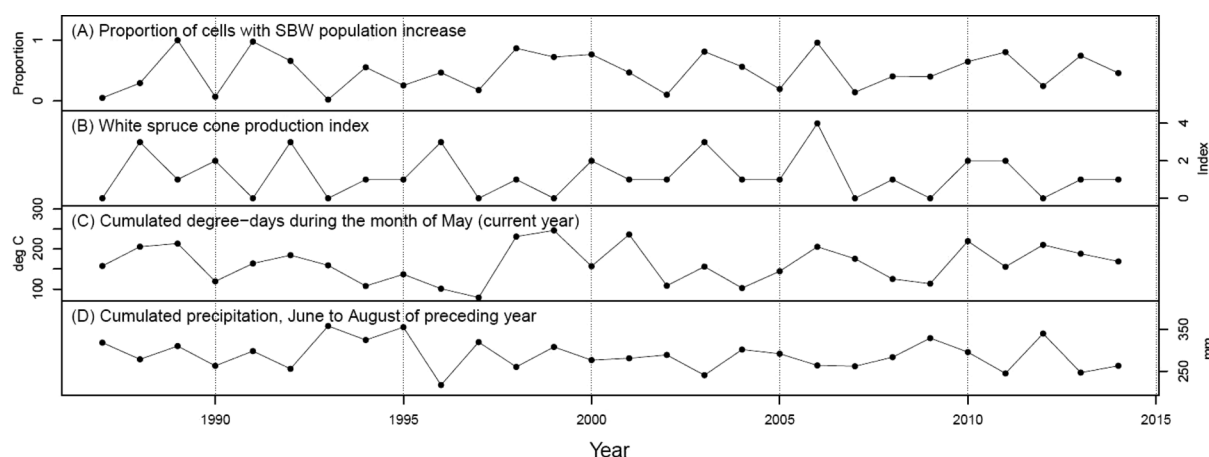
The main goal of this study was to clarify the causal pathways between environmental variability and large-scale fluctuations in insect populations, and to examine if these fluctuations could lead to persistent population increases. The SBW system, which has been thoroughly monitored over the years and for which an abundance of data has been collected, provides an ideal opportunity to look at these processes. Specifically, in this study, we examined whether regional-scale fluctuations in SBW populations were likely to be explained by variables associated directly or indirectly with weather, including synchronous host tree cone production.

## Methods

### Data sources

The study took place in the province of Québec (Canada) in an area approximately 625 000 km<sup>2</sup> in size (Fig. 1). Annual variation in SBW abundance across the study area (Fig. 1) was quantified with pheromone trap catch data from 1986 to 2014. Nonsaturating Multi-Pher traps (Distributions Solida Inc., Saint-Ferréol-les-Neiges,

**Fig. 2.** Year-to-year variations in (A) insect populations and (B–D) environmental variables. Variables in (B) and (C) are significant predictors of (A) (cf. Table 1), and (D) is a significant predictor of (B) (cf. Table 3).



Québec) baited with SBW pheromone were used to capture males. The type of commercial lure that was used in the traps changed over the years; it included PVC lures (manufactured by the New Brunswick Research and Productivity Council) between 1986 and 1989, Biolure (2.8 mg load of pheromone released from a permeable membrane; Suterra Inc., Bend, Oregon) between 1990 and 2010, and Flexlure (3.3 mg load of pheromone released from small PVC cylinders; Contech Enterprises Inc., Victoria, British Columbia) from 2011 to 2014. Each time the lure type was changed, calibration was done to make sure that effectiveness was as comparable as possible across years (Sanders 1996; Rhainds et al. 2016).

Traps were set up before the moth flight period and collected in the fall to determine the number of moths that were caught. A strip of insecticide (Vaportape II; Hercon Environmental, Emigsville, Pennsylvania) was placed at the bottom of the traps to kill captured moths. The traps were placed in plots located across the province (Fig. 1) and operated yearly. Three traps were placed in each plot, located 40 m apart in a triangle, at a height of 2 m on balsam fir trees. In further analyses, moth captures per trap were averaged for each plot and averaged again in each cell of a 1 degree  $\times$  1 degree grid covering the entire study area. Pooling data at the cell level was done to make sure that locations where a higher density of traps was installed for one reason or another were not given more weight in the analyses explaining spatial synchrony. Cell-level information on SBW populations, including the number of traps and mean moth abundance per cell, is presented in Supplementary materials 1 and 2<sup>2</sup>.

Balsam fir pollen cones are an important feeding substrate for the SBW. The abundance of conifer pollen cones varies from year to year, depending on the occurrence of mast years, and tends to be correlated across large areas (Koenig 2002). Annual variation in pollen cone abundance was estimated using 1986–2014 seed collection data from provincial authorities. Seed collection is done annually in natural forests and seed orchards located across the province to provide seeds for tree nurseries. Data were more consistent and reliable for white spruce (*Picea glauca* (Moench) Voss) than for balsam fir because this species is in high demand for tree planting (and thus more closely monitored by seed collectors). Cone production is known to be highly correlated among conifers, including between white spruce and balsam fir (Rossi et al. 2012) and between male and female cones in conifers in general (Moreira et al. 2014). Therefore, we used white spruce seed abundance to estimate annual variation in host tree cone production (Supplementary material 3<sup>2</sup>). A semiquantitative metric was used

to assess cone production: null (0), low (1), moderate (2), high (3), and exceptional (4) abundance. The mast years identified using this method were also validated by looking at independent field studies conducted across the province (Bauce and Carisey 1996; Houle 1999; Robert et al. 2012; Rossi et al. 2012).

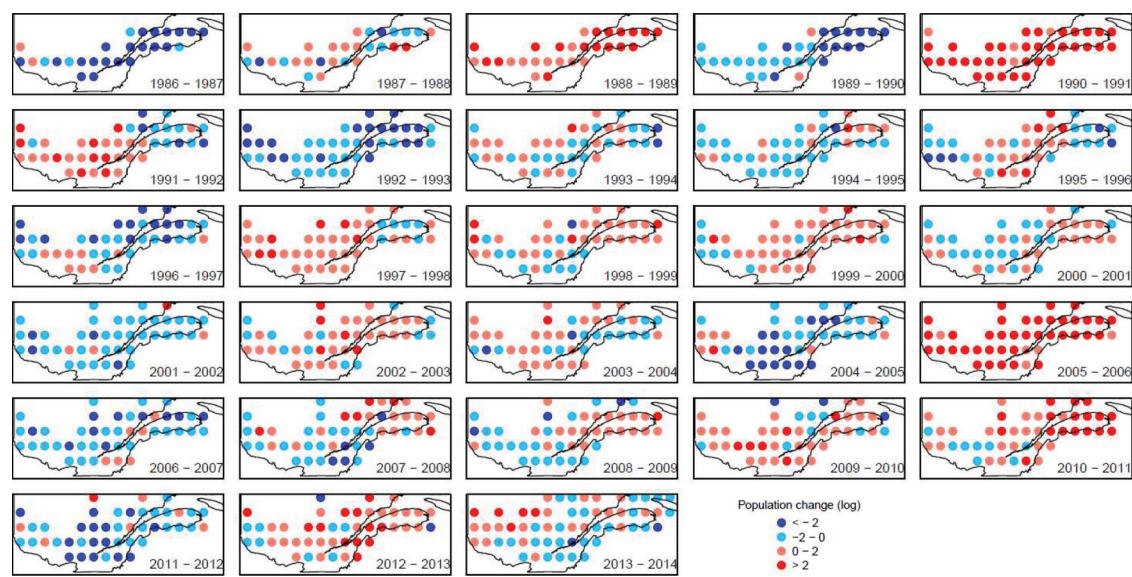
Weather is important with respect to its effect on local SBW populations, but the potential effects of annual variation in weather on landscape-level SBW population synchrony have never been examined. Summary weather variables that were potentially important to predict SBW development were obtained for each cell of the 1 degree  $\times$  1 degree grid covering the area where pheromone trap information was available. Meteorological information was interpolated from the eight weather stations nearest to the center of each cell with BioSIM (Régnière et al. 2013b). The effects of weather on SBW were quantified using three indices. First, we used total precipitation and total degree-days above 5 °C in May. This period coincides with the emergence of overwintering larvae. During this period, the larvae are very small (second or third instar), and they can be affected by weather in multiple ways, including through synchrony with host tree shoot development, exposure to extreme weather (rainstorms), or dispersal-related mortality (Rose and Blais 1954; Greenbank 1963a). Second, the mean maximum daily temperature during the flight period was calculated. High evening temperatures during the flight period (from late June to late July) could enhance SBW moth flight activity (Sanders et al. 1978) and influence population abundance estimated from pheromone trap captures. Finally, we determined the ordinal date that corresponded to the peak of egg hatch during the previous year, just before the beginning of larval diapause in late summer. Hatching that occurs too late in the season can cause high winter mortality (Régnière et al. 2012) and, therefore, a lower population abundance the following year. Even though egg hatch occurring too early can also have negative impacts on SBW populations, we assumed that this effect was negligible in the study area during the 1986–2014 period (Régnière et al. 2012).

Large-scale synchrony in white spruce cone production has been associated with weather conditions in the previous summer, during which cone primordia are initiated (Krebs et al. 2012). To verify this relationship, we quantified weather (precipitation and cumulative degree-days) during the period of June–August of the preceding year for each 1 degree  $\times$  1 degree cell.

<sup>2</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2017-0051>.



**Fig. 3.** Annual changes in spruce budworm (*Choristoneura fumiferana*) population abundance. Each dot represents the difference between years  $y$  and  $y - 1$  in the averaged number of moths ( $\log_{10}[x + 1]$ ) for a cell of 1 degree  $\times$  1 degree.



Statistical analyses

Population synchrony is defined as “coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations” (Liebhold et al. 2012). The proportion of cells with a higher moth abundance compared with the preceding year was used as an indicator of coincident change in population abundance at this scale. Very high (1) or very low (0) proportions indicate synchrony at the scale of the study area, with a proportion of 0.5 indicating no synchrony at this scale. It is noteworthy that a proportion of 0.5 could mask synchronous population fluctuations across distances smaller than the size of the study area. For example, a population increase in the eastern half of the territory coincident with a population decrease in the western half could result in an overall proportion of 0.5. However, finding an explanation for synchrony across all spatial and temporal scales was impossible because one of the explanatory variables (pollen cone abundance) was only available at the scale of the province.

The effect of different environmental variables on the proportion of cells with population increases in each year was examined with general linear models. The three weather variables mentioned above were used as predictors; for each variable, a province-level estimate for each year was obtained by calculating the median value of all cells. The white cone production index was also used as predictor. We compared several alternative statistical models to explain annual variation in the proportion of cells based on the Akaike information criterion for small sample sizes (AICc). Because the predicted variable is a proportion, the data were assumed to follow a binomial distribution. No autoregressive term was included in the models. The models were fitted with the glm function in R (R Development Core Team 2013). Goodness of fit of the models was also evaluated by calculating a pseudo- $R^2$  value, which was done by comparing the deviance of the model with the deviance of a null model (also designated as McFadden’s pseudo- $R^2$ ) (Hosmer et al. 2013). To examine whether the influence of the main explanatory variables was stationary in time, we refitted the best model on a 10 year moving window subset along the 28 year data set.

Alternative statistical models looking at the respective effects of precipitation and temperature of the preceding year on white spruce cone production were also formulated. In this case, we assumed that the response variable (cone production index) followed a Poisson distribution. The models were fitted with the glm function in R.

**Table 1.** Relative support for candidate models describing the effect of environmental variables on synchrony measured as the proportion of cells with increases in spruce budworm (*Choristoneura fumiferana*) abundance.

Model	K	AICc	$\Delta$ AICc	Pseudo- $R^2$
MayW + cones + flight + hatch	6	416.07	0.00	0.42
MayW + cones + flight	5	418.11	2.04	0.41
MayW + cones	4	430.86	14.79	0.38
MayW + cones + hatch	5	431.34	15.27	0.38
MayW	3	516.90	100.83	0.20
Cones	2	541.95	125.88	0.15
Hatch	2	602.41	186.34	0.04
Flight	2	610.30	194.23	0.02

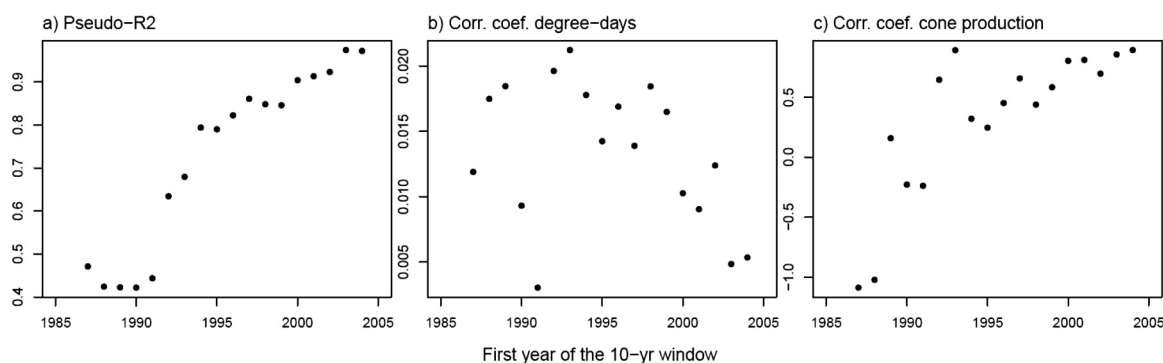
**Note:** “MayW” includes precipitation and cumulative degree-days during the month of May, “flight” corresponds to mean maximal daily temperature during the adult flight period, and “hatch” corresponds to the date at which egg hatch peaked during the preceding year (late summer).

**Table 2.** Summary statistics of the best model (cf. Table 1) analysing the effects of environmental variables on spruce budworm (*Choristoneura fumiferana*) population synchrony measured as the proportion of cells with population increases.

Variable	Estimate	SE	z value	Pr(> z )
(Intercept)	−3.07	2.02	−1.52	0.1296
May degree-days	0.02	0.00	10.41	<0.0001
May precipitation	0.02	0.00	6.71	<0.0001
Cones	0.46	0.06	7.76	<0.0001
Flight	5.80	1.36	4.25	<0.0001
Hatch	−0.02	0.01	−2.30	0.0215

Finally, we examined how province-level population increases persist over time and how they contributed to the rise of local SBW populations inside outbreak epicenters that appeared during the studied period. Epicenters were defined as the first locations where defoliation was detected from aerial surveys (Bouchard and Auger 2014). Aerial defoliation surveys were used to delineate epicenters because they provide a finer spatial information on SBW populations compared with pheromone traps. The epicenters were delineated by including a buffer zone surrounding the initial defoliation patches, to make sure that they were large enough to include at least 10 pheromone traps, for a reliable

**Fig. 4.** Temporal variation in statistics for the best model (Table 1) predicting changes in spruce budworm (*Choristoneura fumiferana*) abundance at the province level. Separate models were fitted for each successive 10 year time window.



estimate of pre-outbreak population trends. Each epicenter was separated from the other ones by a distance of >50 km. Six epicenters were thus delineated (Fig. 1), with defoliation starting between 1991 and 2011. In each of these, SBW populations were thus at different stages of outbreak development during any given year. Population abundance in each epicenter was assessed by averaging moth abundance in all pheromone traps located therein. In each epicenter, the occurrence of persistent population increases was determined with the following method. A release was defined as a fivefold increase in mean SBW abundance per trap for one year compared with the preceding year. This criterion represented the upper range of population increases observed throughout the study period, and it would be extremely unlikely that such increases are due to measurement error. To make sure that this increase was significant from a long-term population dynamics standpoint, we considered it to be “persistent” if abundance during both of the next two years remained higher than during the year preceding the increase. Subsequently, we verified if these epicenter-level persistent increases coincided with synchronous population increases at the province level.

## Results

The proportion of cells with population increases was highly variable from year to year. Population increases affecting more than 90% of the study area during a given year were observed in 1989, 1991, and 2006 (Figs. 2 and 3). Extensive population decreases were observed in 1987, 1990, 1993, 2002, and 2007 (Figs. 2 and 3). During the remaining years, synchrony at the scale of the study area was less pronounced, even if visual inspection indicates that increases and decreases in population abundance were often clustered at finer spatial scales (Fig. 3).

Comparison of the alternative statistical models indicates that the proportion of cells with an increase in SBW populations during a given year was best explained by a model that included host tree cone production and weather during early larval development (in May) (Table 1). May temperature had more impact on SBW population fluctuations than May precipitation, as shown by a higher  $z$  value in the best model (Table 2). Temperature during the flight period and date of hatching are included in the best model, but these variables do not appear to play a major role, as indicated by their marginal effect on the AICc and pseudo- $R^2$  (Table 1). We further verified whether the influence of environmental factors on SBW populations tended to vary during the 29 year period by looking at general linear model statistics in a 10 year moving window. This analysis suggested that the influence of environmental variables was not stationary in time. Notably, the influence of host tree cone production increased during the latter part of the 29 year series (Fig. 4c), and model fit improved accordingly (Fig. 4a).

**Table 3.** Relative support for candidate models describing the effect of weather of the preceding ( $y - 1$ ) year on the white spruce (*Picea glauca*) cone production index.

Model	$K$	AICc	$\Delta$ AICc	Pseudo- $R^2$
Precipitation $^{y-1}$	2	75.04	0	0.353
Degree-days $^{y-1}$ + precipitation $^{y-1}$	3	77.41	2.37	0.357
Degree-days $^{y-1}$	2	82.70	7.66	0.124

Host tree cone production was best explained by precipitation during the preceding year (Table 3). Integrating cumulative degree-days of the preceding year in the model did not improve model fit (Table 3).

Inside the six studied epicenters, several persistent population increases were detected, including in 1989 (two epicenters), 1991 (four), 1996 (one), 2006 (four), and 2011 (one) (Fig. 5). These persistent increases often corresponded to province-level population increases (e.g., 1989, 1991, 2006, and 2011) and white spruce mast years (e.g., 1996, 2006, and 2011). In all epicenters but one (Mauricie), province-level synchronous SBW population increases closely coincided with the triggering of outbreaks, as assessed from defoliation surveys (Fig. 5).

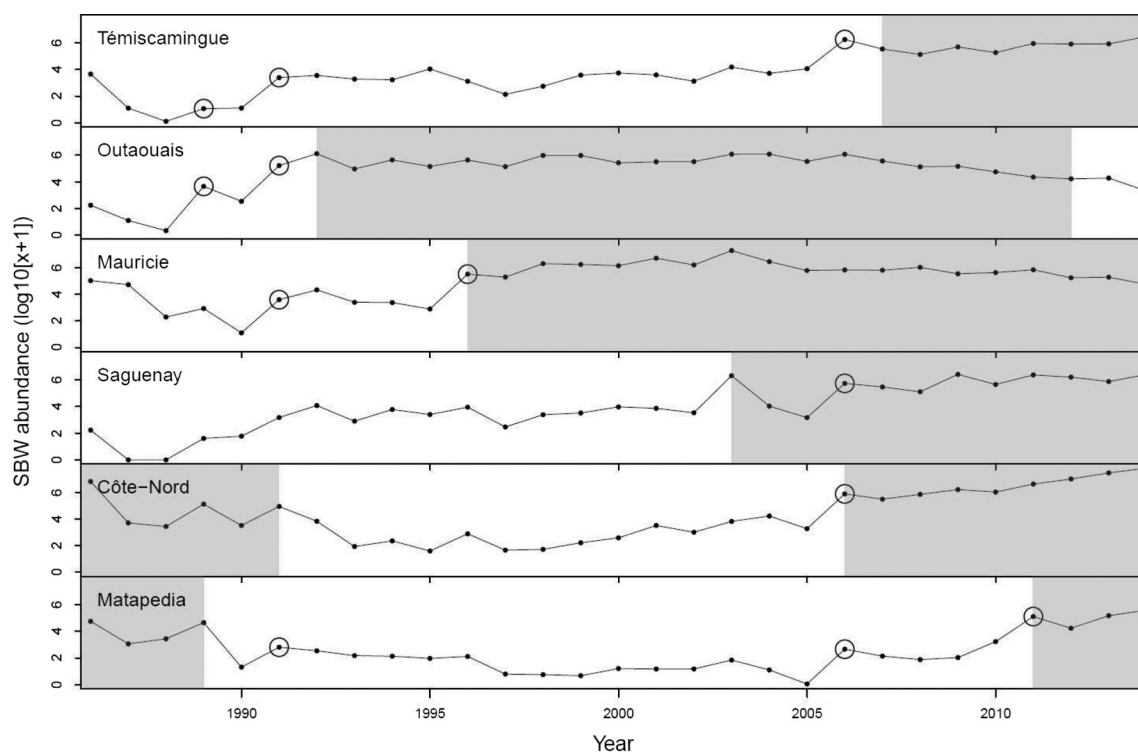
## Discussion

### Effect of bottom-up factors on synchrony

Even though detecting and describing synchrony in animal populations has become a relatively straightforward process thanks to the availability of appropriate statistical techniques (Bjørnstad and Falck 2001), explaining synchrony is still exceptionally challenging for several reasons. First, it is difficult to sample at the same time population abundances and meaningful environmental drivers across representative spatiotemporal scales. Second, when explanatory variables are available, they are usually weather related, but the exact biological pathways through which weather affects population dynamics are rarely identified. Third, there is a general lack of recognition for the fact that multiple causes are usually involved and that these causes might act at different scales.

The relatively simple approach developed in this study allowed us to establish a statistical relationship between large-scale variations in SBW population abundance and two potential explanatory variables, host tree cone production and weather during early larval development (in May). These relationships provide a mechanistic explanation potentially connecting large-scale climatic variability with insect population dynamics and synchrony. The first variable, host tree cone production, was related to low precipitation during the previous summer (Table 3), which is known to synchronize the initiation of reproductive buds and to

**Fig. 5.** Spruce budworm (*Choristoneura fumiferana*) population levels in six epicenters (cf. Fig 1) where spruce budworm outbreaks were detected during the 1986–2014 period. The shaded areas indicate the period during which defoliation could be detected from aerial surveys, corresponding to outbreak conditions. Larger circles indicate the beginning of a “persistent” population increase, defined as a fivefold annual increase with subsequent populations that remained above the pre-increase level for at least 2 years. Persistent increases were calculated from untransformed abundances, but log-transformed values are represented in the figure.



favor high cone production in the following year (Krebs et al. 2012). In wind-pollinated tree species, concentration of resources allocated to cone and seed production across large areas during some years is thought to be an adaptation that increases fitness (Kelly and Sork 2002). The SBW feeds on pollen cones when they are available, particularly those of balsam fir (Blais 1952; Greenbank 1963b; Bause and Carisey 1996). This resource is likely to reduce the need for larvae to disperse in search of food during early larval stages (Blais 1952). Dispersal-related mortality in second-instar larvae emerging from diapause can be very important (up to 85%) (Morris 1963; Régnière and Nealis 2008), and variation in mortality rates during this development stage may have major impacts on overall SBW population dynamics (Volney and Fleming 2007; Régnière and Nealis 2008).

SBW populations were also directly influenced by spring temperature during the current year. Warm, sunny, and dry conditions are generally favorable to SBW larval development (Greenbank 1956; Pilon and Blais 1961). Spring conditions also influence the degree of mismatch between insect development just after the larvae emerge from overwintering and the phenology of the current-year foliage on which the SBW feeds preferentially. In the case of the SBW, a better match is expected when conditions are warmer (Greenbank 1963a; Thomson et al. 1984). As with pollen cone abundance, a good phenological match with the young developing foliage is expected to reduce the risk of starvation (Trier and Mattson 1997) and dispersal-related mortality while foraging (Nealis and Lomic 1994; Lawrence et al. 1997). Because the population increases observed during some years in our study are very high (more than fivefold in some cases) (Fig. 5), it is also possible that survival or dispersal during later development stages was also indirectly impacted by early spring conditions.

A true multiscale perspective was not possible in this study because the underlying environmental information, particularly

the pollen cone index, was available only at the province level. It is likely that the relative influence of the various factors would have differed if they had been analysed at other scales. For example, one would expect that the effect of weather on moth flight activity, which was not significant in the province-level analyses (Table 1), may be significant if analysed across smaller areas. Indeed, because the SBW flight period, like many other phenological events in its annual life cycle, can vary by more than 1 month across the SBW's range in Québec (Régnière and Powell 2013), it is unlikely that male moth flight activity is affected by similar weather conditions at both ends of this gradient during any given year.

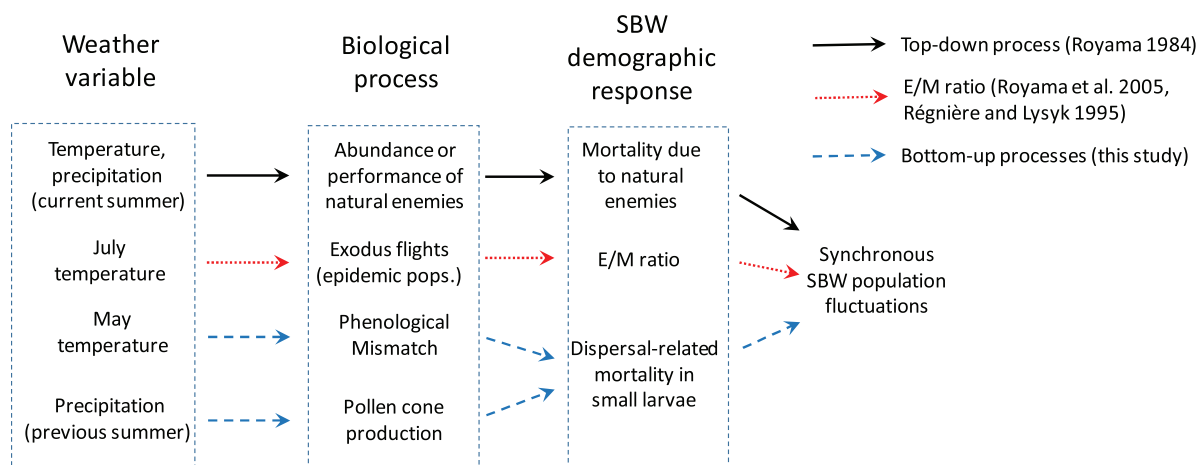
Different processes than those identified in our study could also explain large-scale synchronous population oscillations in some situations. Short-frequency oscillations in late epidemic, collapsing populations were also attributed to weather, but through an interaction with the natural enemies that build up when host population density increases, a top-down trophic process (Royama 1984; Régnière and Nealis 2007). Year-to-year variations in the emigration/migration ratio also has been mentioned as a potential explanation (Régnière and Lysyk 1995; Royama et al. 2005). These other factors might explain why annual oscillations were relatively poorly predicted by the selected variables during the early portion of the time series (e.g., 1986–1995) (Fig. 4), which coincides with the collapse of the previous outbreak cycle (Morin et al. 2007). Natural enemies as well as the emigration/migration ratio could thus represent alternative pathways through which weather could affect insect synchrony (Fig. 6).

#### Population synchrony and outbreak occurrence

The same factors that synchronize population fluctuations at the province level also have the potential to generate local population increases that persist for several years, and sometimes



**Fig. 6.** Hypothetical biological pathways through which interannual variations in different weather variables could produce large-scale synchronized spruce budworm (*Choristoneura fumiferana*) population fluctuations.



coincide with outbreak initiation (Fig. 5). Following outbreak initiation in an epicenter, the abundance of SBW populations can increase rapidly, particularly when balsam fir is abundant, such as was the case in the epicenters located in the eastern part of the province (Bouchard and Auger 2014). High population densities generate migration and exodus flights (Greenbank et al. 1980), explaining the contagious expansion patterns that are often observed in defoliation surveys (Bouchard and Auger 2014). Hence, while density-independent factors (weather, pollen cone production) play an important role for synchronization and potentially for outbreak triggering in low-density SBW populations, synchronization through density-dependent processes (emigration/migration ratio) might become prevalent once outbreak conditions have been reached. A similar transition from bottom-up synchronizing agents acting through weather to a dispersal-related contagious expansion during the outbreak phase was also proposed for geometrid moths (Jepsen et al. 2009).

In insect population dynamics, population cycles are often implied to be caused by delayed density-dependent, top-down trophic processes (Royama 1992). For example, fluctuations due to interactions with natural enemies have been emphasized for various insects such as bark beetles (Turchin et al. 1999), geometrid moths (Hagen et al. 2010), and the larch budmoth (Turchin et al. 2003) as well as for the SBW (Royama 1984). However, as recognized indirectly by these authors and as pointed out directly by others (Baltensweiler and Fischlin 1988), the assumption that insect population cycles are mainly driven by one or a few top-down processes can be oversimplifying. Our study suggests that the approximately 35 year outbreak cycle that was historically observed for the SBW (Morin et al. 2007) is more likely to be explained by a complex mix of factors including top-down, bottom-up, and dispersal-related processes, and that the relative influence of these factors is heterogeneous in space and time.

### Synchrony and climate change

A mechanistic understanding of forest ecosystem disturbance processes, including their complex relationships with climatic factors or forest characteristics, is needed to obtain realistic predictions about their future impacts (Williams and Jackson 2007). Our study shows that there are several functional pathways through which climate and weather can influence insect population dynamics. In the case of the SBW, length of the growing season has already been identified as an important constraint on the northern and southern boundaries of potential outbreak occurrence (Régnière et al. 2012). The current study shows that annual variation in weather conditions can also explain spatial synchrony within this distribution, both directly (through their

effect on larval development in early spring) and indirectly (through their connection with host tree cone production). Furthermore, the regional-level abundance of pollen cones available for insect consumption does not only change on an annual basis but also, on a longer time frame, as a function of variation in the abundance of populations of host tree species and in the age structure of these populations (Blais 1983). These complex interactions indicate that predicting insect population dynamics and potential outbreak occurrence represents a considerable challenge in the context of a changing climate and pervasive habitat modifications.

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