



Bottom-up factors contribute to large-scale synchrony in spruce budworm populations

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Complete List of Authors:	Bouchard, Mathieu; Gouvernement du Quebec, Ministère de la Forêt, de la Faune et des Parcs Régnière, Jacques; Natural Resources Canada Therrien, Pierre; Gouvernement du Quebec, Ministère de la Forêt, de la Faune et des Parcs
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1 **Bottom-up factors contribute to large-scale synchrony in spruce budworm populations**

2 Mathieu Bouchard, Direction de la Recherche Forestière, Ministère des Forêts, de la Faune et des Parcs
3 du Québec, 2700 rue Einstein, Québec, QC, Canada G1P 3W8. E-mail:

4 Mathieu.Bouchard@mffp.gouv.qc.ca

5 Jacques Régnière, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, PO
6 Box 10380 Stn. Ste Foy, Quebec, Canada G1V 4C4. E-mail : Jacques.Regniere@Canada.ca

7 Pierre Therrien, Direction de la Protection des Forêts, Ministère des Forêts, de la Faune et des Parcs du
8 Québec, 2700 rue Einstein, Québec, QC, Canada G1P 3W8. E-mail: Pierre.Therrien@mffp.gouv.qc.ca

9 **Abstract**

10 Understanding the mechanisms that cause large-scale synchrony in insect population dynamics might
11 yield key insights for predicting potential outbreak occurrence. Here, we evaluated which environmental
12 factors best explain synchronous population fluctuations in the spruce budworm (SBW), a major
13 defoliator of coniferous forests in North-America. SBW population levels were assessed with pheromone
14 traps during the 1986-2014 period across a 625,000 km² territory located in the province of Québec
15 (Canada). The populations were characterized by abundance fluctuations that were often synchronized
16 across the whole study area. Interannual population fluctuations were correlated with host tree cone
17 production (mast years) and high May temperatures, suggesting that synchrony was influenced by food
18 availability and phenological mismatch during shoot development. Cone production was itself correlated
19 with low precipitation during the previous summer. This study indicates that bottom-up trophic factors
20 can drive spatiotemporal synchrony in insect populations, and contribute to explain important and
21 sustained population increases during some years. We also suggest that several biological processes, all
22 influenced by weather, are likely to interact to explain population synchrony during the different phases
23 of the ca. 35 years SBW outbreak cycle, complicating the prediction of climate change effects on this
24 insect.

25 Résumé

26 La compréhension des mécanismes qui causent le synchronisme à grande échelle dans la dynamique des
27 populations d'insectes pourrait aider à mieux prédire l'occurrence d'épidémies. Dans cette étude, nous
28 avons évalué quels facteurs environnementaux expliquent le mieux les fluctuations synchrones de
29 populations de tordeuse des bourgeons de l'épinette (TBÉ), un défoliateur important des forêts
30 conifériennes d'Amérique du Nord. Les niveaux de populations de TBÉ ont été évalués à l'aide de pièges
31 à phéromones durant la période 1986-2014 dans un territoire de 625 000 km² localisé dans la province de
32 Québec (Canada). Les populations de TBÉ étaient caractérisées par des fluctuations d'abondance qui
33 étaient souvent synchronisées sur l'ensemble du territoire. Les fluctuations interannuelles de populations
34 étaient corrélées avec la production semencière des arbres hôtes (un substrat alimentaire) et des
35 températures élevées lors du mois de mai, suggérant que le synchronisme était influencé par la
36 disponibilité en nourriture et le décalage phénologique lors du débourrement. La production semencière
37 était elle-même corrélée avec un faible niveau de précipitations durant l'été précédent. Cette étude
38 indique que la disponibilité en ressources peut expliquer le synchronisme spatio-temporel chez les
39 populations d'insectes, et contribue à expliquer des hausses de populations importantes et soutenues lors
40 de certaines années. Nous suggérons également que plusieurs processus biologiques, tous influencés par
41 les conditions météorologiques, pourraient interagir pour expliquer la synchronisation lors de différentes
42 phases du cycle épidémique de la TBÉ, compliquant la prédiction des effets des changements climatiques
43 sur cet insecte.

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46 Introduction

47 Large-scale synchrony in population fluctuations has been described for many animal species,
48 including small mammals, ungulates and particularly insects (Liebhold et al. 2012, Myers and Cory
49 2013). Synchronous population increases have also been hypothesized to contribute to insect outbreak
50 occurrence, for example by facilitating escape from natural enemy control (Liebhold et al. 2012).
51 Population synchrony can take place across vast spatial scales (e.g., >100 km), and is often thought to
52 correlate with climatic perturbations, i.e., the so-called 'Moran effect' (Moran 1953). However, the exact
53 causal pathways through which climate and weather synchronize demography across large areas are still
54 poorly understood. The mechanism that have been proposed are varied, and range from a direct effect of
55 weather on animal populations, to indirect effects through bottom-up and top-down factors, or dispersal-
56 related factors (Liebhold et al. 2012).

57 The spruce budworm (*Choristoneura fumiferana* Clem.; SBW) outbreak system represents an
58 interesting opportunity to explore the causal relationships that can explain synchronous population
59 fluctuations across large spatial scales. The spruce budworm is a defoliator of *Abies* spp. and *Picea* spp.
60 in North American boreal forests. In eastern Canada, SBW outbreaks have occurred every 30-40 years for
61 the last two centuries at least, and these cycles tend to be loosely synchronized at the regional level
62 (Royama 1984, Williams and Liebhold 2000, Morin et al. 2007). Cumulative defoliation by this insect
63 results in substantial tree mortality, and has cascading effects in boreal forest ecosystems (Bouchard et al.
64 2006). SBW population dynamics are driven by several processes such as competition for food, disease
65 propagation, predation, parasitism and migration (Régnière 1984, Royama 1984, Régnière and Nealis
66 2007). Some causal mechanisms have been proposed to explain large-scale synchrony, such as temporal
67 variation in apparent fecundity and natural enemies (Royama 1984) or moth dispersal (Régnière and
68 Lysyk 1995, Royama et al. 2005), but these hypotheses were not examined over large spatial scales, and
69 connections between year-to-year weather fluctuations and specific SBW population processes remain
70 little explored.

71 Temporal variation in feeding substrate availability could be important to explain spatial
72 synchrony in insect populations. For example, in the case of the gypsy moth (*Lymantria dispar*), it has
73 been suggested that episodic acorn production by oak trees could ultimately explain large-scale
74 synchronous outbreak occurrence (Haynes et al. 2013). In this case, acorn abundance affects the white-
75 footed mouse (*Peromyscus leucopus*), a predator of the gypsy moth, and the trophic relationship could
76 thus be better described as top-down than bottom-up (Haynes et al. 2013). In geometrid outbreaks in
77 Norway, Jepsen et al. (2009) found that the degree of synchrony between egg hatch and bud development
78 in the spring influences large-scale synchronization. Similarly, temporal variation in food quality was
79 found to be important for spatial synchrony in the jack pine budworm (*Choristoneura pinus pinus*), a
80 species that is closely related to the SBW. Short-duration outbreaks in this insect were associated with
81 pollen cone production episodes in its host species, jack pine (*Pinus banksiana*) (Nealis 2003). For the
82 SBW, the potential importance of balsam fir pollen cone availability for outbreak occurrence has been
83 suggested in a few studies (Blais 1952, Morris 1963). This resource constitutes an easily accessible and
84 nutritious food source in early spring, and provides a favorable micro-habitat for larvae emerging from
85 overwintering (Carisey and Bauce 1997). Pollen cones can alleviate the negative impact of phenological
86 mismatch between the insect and host tree shoot development, known to be highly variable in space and
87 time depending on early spring conditions (Greenbank 1963a, Nealis and Lomic 1994), and could
88 therefore have important repercussions on the insect's population dynamics.

89 It is uncertain to what extent a large-scale synchronous increase in population density during a
90 given year can persist during subsequent years. Density-dependent factors such as natural enemies or
91 resource scarcity during the years following the increase are susceptible to drive insect populations back
92 to pre-increase levels. Still, under some conditions, higher densities could persist over several years. In
93 the case of the SBW, low-density populations can be subjected to mate-finding difficulties (Régnière et
94 al. 2013a), which could generate a positive relationship between population density and population
95 growth. Also, in insects, the likelihood that natural enemies are able to aggregate to suppress host

96 populations is generally inversely related to the spatial extent and spatial homogeneity of the host
97 population increases (Briggs and Hoopes 2004), suggesting that large-scale increases are also more likely
98 to persist over time. Finally, the SBW also possesses foraging capabilities that allow it to cope with
99 resource scarcity during less favorable years, for example by mining or feeding upon older foliage when
100 optimal feeding substrates such as very young foliage or pollen cones are not available (Lawrence et al.
101 1997). Hence, population increases caused by large-scale pulses of resource during one year could
102 potentially persist over subsequent years, leading to rising SBW populations and outbreak initiation in
103 some cases.

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

111 **Methods**

112 **Data sources.** The study took place in the province of Québec (Canada), in an area approximately
113 625,000 km² in size (Figure 1). Annual variation in SBW abundance across the study area (Fig. 1) was
114 quantified with pheromone trap catch data from 1986-2014. Nonsaturating Multi-Pher traps (Distributions
115 Solida Inc., Saint-Ferréol-les-Neiges, QC) baited with spruce budworm pheromone were used to capture
116 males. The type of commercial lure that was used in the traps changed over the years; it included PVC
117 lures (manufactured by the New Brunswick Research and Productivity Council) between 1986 and 1989,
118 Biolure (2.8 mg load of pheromone released from a permeable membrane; Suterra Inc., Bend, OR)
119 between 1990 and 2010, and Flexlure (3.3 mg load of pheromone released from small PVC cylinders;

120 Contech Enterprises Inc., Victoria, BC) from 2011-2014. Each time the lure type was changed, calibration
121 was done to make sure that effectiveness was as comparable as possible across years (Sanders 1996,
122 Rhainds et al. 2016).

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

133 Balsam fir pollen cones are an important feeding substrate for the SBW. The abundance of
134 conifer pollen cones varies from year to year, depending on the occurrence of mast years, and tends to be
135 correlated across large areas (Koenig 2002). Annual variation in pollen cone abundance was estimated
136 using 1986-2014 seed collection data from provincial authorities. Seed collection is done annually in
137 natural forests and seed orchards located across the province to provide seeds for tree nurseries. Data
138 were more consistent and reliable for white spruce (*Picea glauca*) than for balsam fir, because this species
139 is well represented throughout the province and is in high demand for tree planting (and thus more closely
140 monitored by seed collectors). Cone production is known to be highly correlated among conifers,
141 including between white spruce and balsam fir (Rossi et al. 2012), and between male and female cones in
142 conifers in general (Moreira et al. 2014). Therefore, we used white spruce seed abundance as an estimate
143 of annual variation in host tree cone production (Supplementary material 3). A semi-quantitative metric
144 was used to assess cone production: null (0), low (1), moderate (2), high (3) and exceptional (4)

145 abundance. The most years identified using this method were also validated by looking at independent
146 field studies conducted across the province (Bauce and Carisey 1996, Houle 1999, Robert et al. 2012,
147 Rossi et al. 2012).

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

167 Large-scale synchrony in white spruce cone production has been associated with weather
168 conditions in the previous summer, during which cone primordia are initiated (Krebs et al. 2012). To

169 verify this relationship, we quantified weather (precipitation and cumulative degree-days) during the
170 period of June to August of the preceding year for each 1 x 1 degree cell.

171 **Statistical analyses.**

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

182 The effect of different environmental variables on the proportion of cells with population
183 increases in each year was examined with general linear models (GLMs). The three weather variables
184 mentioned above were used as predictors; for each variable, a province-level estimate for each year was
185 obtained by calculating the median value of all cells. The white cone production index was also used as
186 predictor. We compared several alternative statistical models to explain annual variation in the proportion
187 of cells, based on the Akaike Information Criterion for small sample sizes (AICc). Because the predicted
188 variable is a proportion, the data were assumed to follow a binomial distribution. No autoregressive term
189 was included in the models. The models were fitted with the glm function in R (Team 2013). Goodness of
190 fit of the models was also evaluated by calculating a pseudo R^2 value, which was done by comparing the
191 deviance of the model to the deviance of a null model (also designated as McFadden’s pseudo R^2)

192 (Hosmer et al. 2013). To examine whether the influence of the main explanatory variables was stationary
193 in time, we refitted the best model on a 10-year moving window subset along the 28-year dataset.

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

198 Finally, we examined how province-level population increases persist over time, and how they
199 contributed to the rise of local SBW populations inside outbreak epicenters that appeared during the
200 studied period. Epicenters were defined as the first locations where defoliation was detected from aerial
201 surveys (Bouchard and Auger 2014). We used aerial defoliation surveys to delineate the epicenters and
202 determine a date when outbreak population levels were reached in each of them, because these surveys
203 provide a finer spatial information on SBW populations compared with pheromone traps. The epicenters
204 were delineated by including a buffer zone surrounding the initial defoliation patches, to make sure that
205 they were large enough to include at least 10 pheromone traps, for a reliable estimate of pre-outbreak
206 population trends. Each epicenter was separated from the other ones by a distance > 50 km. Six epicenters
207 were thus delineated (Fig. 1), with defoliation starting between 1991 and 2011. In each of these, SBW
208 populations were thus at different stages of outbreak development during any given year. Population
209 abundance in each epicenter was assessed by averaging moth abundance in all pheromone traps located
210 therein. In each epicenter, the occurrence of persistent population increases was determined with the
211 following method. A release was defined as a 5-fold increase in mean SBW abundance per trap for one
212 year compared with the preceding year. This criterion represented the upper range of population increases
213 observed throughout the study period, and it would be extremely unlikely that such increases are due to
214 measurement error. To make sure that this increase was significant from a long-term population dynamics
215 standpoint, we considered it to be 'persistent' if abundance during both of the next two years remained

216 higher than during the year preceding the increase. Subsequently, we verified if these epicenter-level
217 persistent increases coincided with synchronous population increases at the province level.

218 **Results**

219 The proportion of cells with population increases was highly variable from year to year.
220 Population increases affecting more than 90% of the study area during a given year were observed in
221 1989, 1991 and 2006 (Figs. 2 and 3). Extensive population decreases were observed in 1987, 1990, 1993,
222 2002 and 2007 (Figs. 2 and 3). During the remaining years, synchrony at the scale of the study area was
223 less pronounced, even if visual examination indicates that increases and decreases in population
224 abundance were often clustered at finer spatial scales (Fig. 3).

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

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

240 Inside the six studied epicenters, several persistent population increases were detected, including
241 in 1989 (2 epicenters), 1991 (4), 1996 (1), 2006 (4) and 2011 (1) (Fig. 5). These persistent increases often
242 corresponded to province-level population increases (e.g. 1989, 1991, 2006 and 2011) and white spruce
243 mast years (e.g. 1996, 2006 and 2011). In all epicenters but one (Mauricie), province-level synchronous
244 SBW population increases closely coincided with the triggering of outbreaks, as assessed from defoliation
245 surveys (Fig. 5).

246 **Discussion**

247 *Effect of bottom-up factors on synchrony*

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

256 The relatively simple approach developed in this study allowed us to establish a statistical
257 relationship between large-scale variations in SBW population abundance and two potential explanatory
258 variables, host tree cone production and weather during early larval development (in May). These
259 relationships provide a mechanistic explanation potentially connecting large-scale climatic variability
260 with insect population dynamics and synchrony. The first variable, host tree cone production, was related
261 to low precipitation during the previous summer (Table 3), which is known to synchronize the initiation
262 of reproductive buds and to favor high cone production in the following year (Krebs et al. 2012). In wind-
263 pollinated tree species, concentration of resources allocated to cone and seed production across large

264 areas during some years is thought to be an adaptation that increases fitness (Kelly and Sork 2002). The
265 SBW feeds on pollen cones when they are available, particularly those of balsam fir (Blais 1952,
266 Greenbank 1963b, Bauce and Carisey 1996). This resource is likely to reduce the need for larvae to
267 disperse in search of food during early larval stages (Blais 1952). Dispersal-related mortality in 2nd instar
268 larvae emerging from diapause can be very important (up to 85%) (Morris 1963, Régnière and Nealis
269 2008), and variation in mortality rates during this development stage may have major impacts on overall
270 SBW population dynamics (Volney and Fleming 2007, Régnière and Nealis 2008).

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

282 A true multi-scale perspective was not possible in this study, because the underlying
283 environmental information, particularly the pollen cone index, were available only at the province level. It
284 is likely that the relative influence of the various factors would have differed if they had been analysed at
285 other scales. For example, one would expect that the effect of weather on moth flight activity, which was
286 not significant in the province-level analyses (Table 1), may be significant if analysed across smaller
287 areas. Indeed, because the SBW flight period, like many other phenological events in its annual life cycle,
288 can vary by more than 1 month across the SBW's range in Québec (Régnière and Powell 2013), it is

289 unlikely that male moth flight activity is affected by similar weather conditions at both ends of this
290 gradient during any given year.

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

301 *Population synchrony and outbreak occurrence*

302 The same factors that synchronize population fluctuations at the province level also have the
303 potential to generate local population increases that persist for several years, and sometimes coincide with
304 outbreak initiation (Figure 5). Following outbreak initiation in an epicenter, the abundance of SBW
305 populations can increase rapidly, particularly when balsam fir is abundant, such as was the case in the
306 epicenters located in the eastern part of the province (Bouchard and Auger 2014). High population
307 densities generate migration and exodus flights (Greenbank et al. 1980), explaining the contagious
308 expansion patterns that are often observed in defoliation surveys (Bouchard and Auger 2014). Hence,
309 while density-independent factors (weather, pollen cone production) play an important role for
310 synchronization and potentially for outbreak triggering in low-density SBW populations, synchronization
311 through density-dependant processes (migration flights, E/M ratio) probably becomes prevalent once
312 outbreak conditions have been reached. A similar transition from bottom-up synchronizing agents acting

313 through weather, to a dispersal related contagious expansion during the outbreak phase was also proposed
314 for geometrid moths (Jepsen et al. 2009).

315 In insect population dynamics, population cycles are often implied to be caused by delayed
316 density-dependent, top-down trophic processes (Royama 1992). For example, fluctuations due to
317 interactions with natural enemies have been emphasized for various insects such as bark beetles (Turchin
318 et al. 1999), geometrid moths (Hagen et al. 2010) or the larch budmoth (Turchin et al. 2003), as well as
319 for the SBW (Royama 1984). However, as recognized indirectly by these authors and as pointed out
320 directly by others (Baltensweiler and Fischlin 1988), the assumption that insect population cycles are
321 mainly driven by one or a few top-down processes can be oversimplifying. Our study suggests that the ca.
322 35-year outbreak cycle that was historically observed for the SBW (Morin et al. 2007) is more likely to be
323 explained by a complex mix of factors including top-down, bottom-up and dispersal-related processes,
324 and that the relative influence of these factors is highly heterogeneous in space and time.

325 *Synchrony and climate change*

326 A mechanistic understanding of forest ecosystem disturbance processes, including of their
327 complex relationships with climatic factors or forest characteristics, is needed to obtain realistic
328 predictions about their future impacts (Williams and Jackson 2007). Our study shows that there are
329 several functional pathways through which climate and weather can influence insect population
330 dynamics. In the case of the SBW, length of the growing season has already been identified as an
331 important constraint on the northern and southern boundaries of potential outbreak occurrence (Régnière
332 et al. 2012). The current study shows that annual variation in weather conditions can also explain spatial
333 synchrony within this distribution, both directly (through their effect on larval development in early
334 spring) and indirectly (through their connection with host tree cone production). Furthermore, the
335 regional-level abundance of pollen cones available for insect consumption does not only change on an
336 annual basis, but also, on a longer time frame, as a function of variation in the abundance of populations

337 of host tree species, and in the age structure of these populations (Blais 1983). These complex interactions
338 indicate that predicting insect population dynamics and potential outbreak occurrence represents a
339 considerable challenge in the context of a changing climate and pervasive habitat modifications.

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474

475 **Table 1** – Relative support for candidate models describing the effect of environmental variables on
 476 synchrony, measured as the proportion of cells with increases in SBW abundance.

Model	K	AICc	Δ 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

477

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

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482 **Table 2** – Summary statistics of the best model (c.f. Table 1) analyzing the effects of environmental
483 variables on SBW population synchrony, measured as the proportion of cells with population increases.

484

Variable	Estimate	Std. Error	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

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

Model	K	AICc	Δ 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

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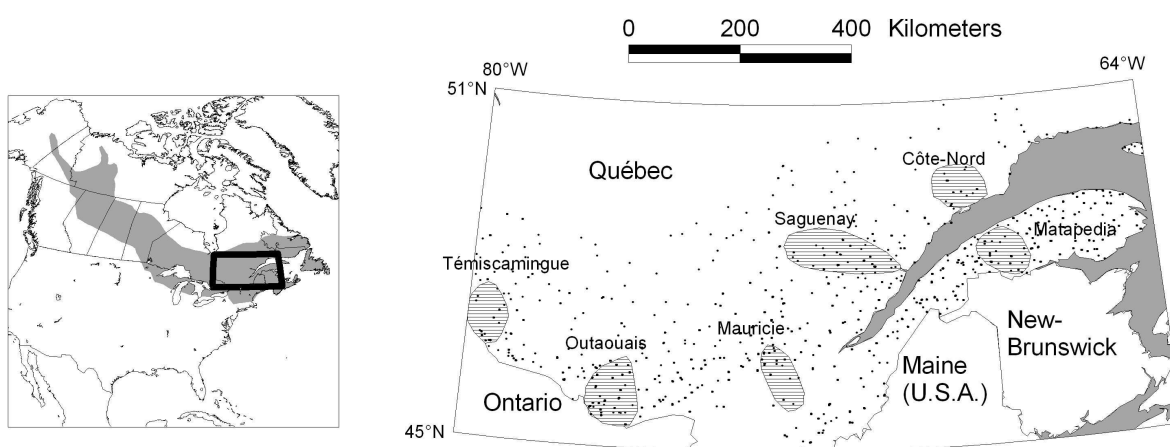
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495 Figures



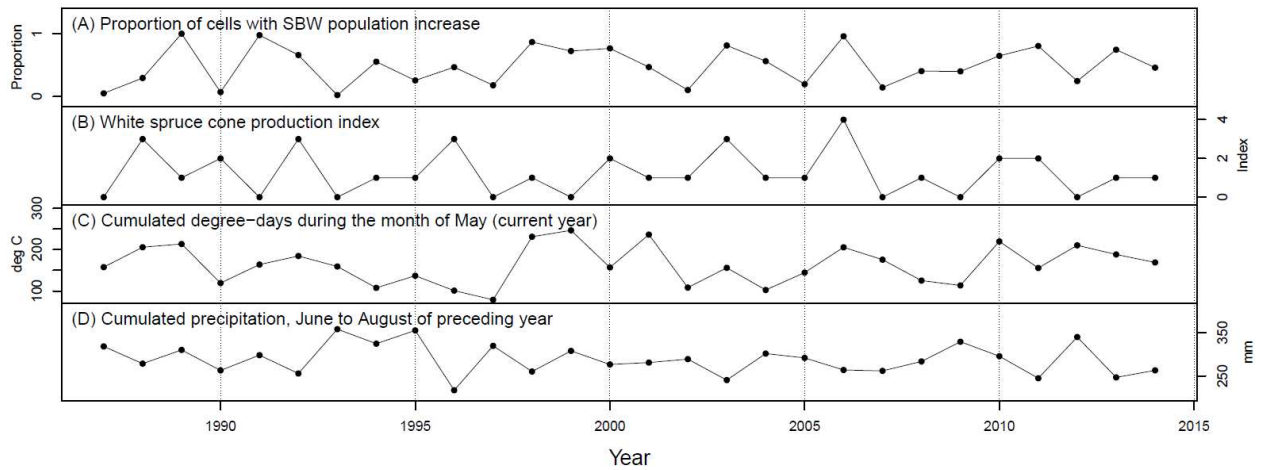
496

497 **Figure 1.** Location of the sample plots where pheromone traps were placed (red dots). The shaded area in
498 the left inset indicates the distribution of the SBW across North-America. Cross-hatching in the right inset
499 indicates the location of different outbreak epicenters that appeared observed during the 1986-2014
500 period.

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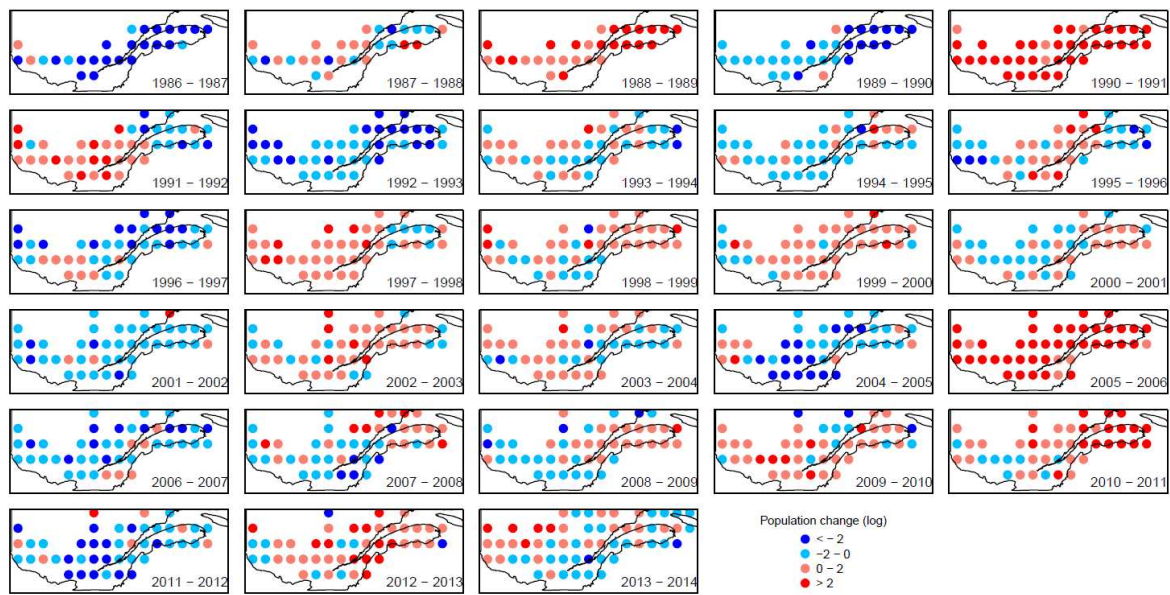


504

505 **Figure 2.** Year to year variations in the degree of synchrony (A) and environmental variables (B-D).
 506 Variables (B) and (C) are significant predictors of proportion of cells with population increase (A) (c.f.
 507 Table 1), and cumulated precipitation of preceding year (D) is a significant predictor of white spruce
 508 cone production index (B) (c.f. Table 3).

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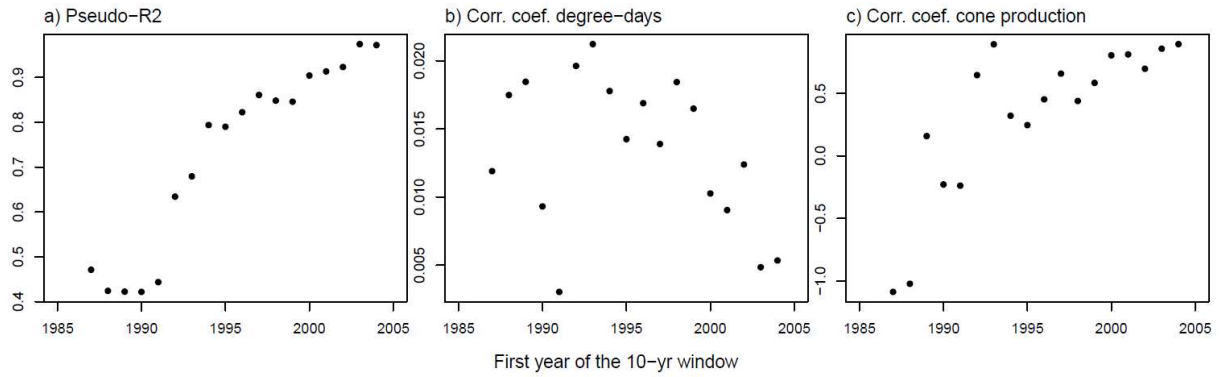


510

511 **Figure 3.** Annual changes in SBW population abundance. Each dot represents the difference between
512 years y and $y-1$ in the averaged number of moths ($\log_{10} [x+1]$) for a cell of 1 deg x 1 deg.

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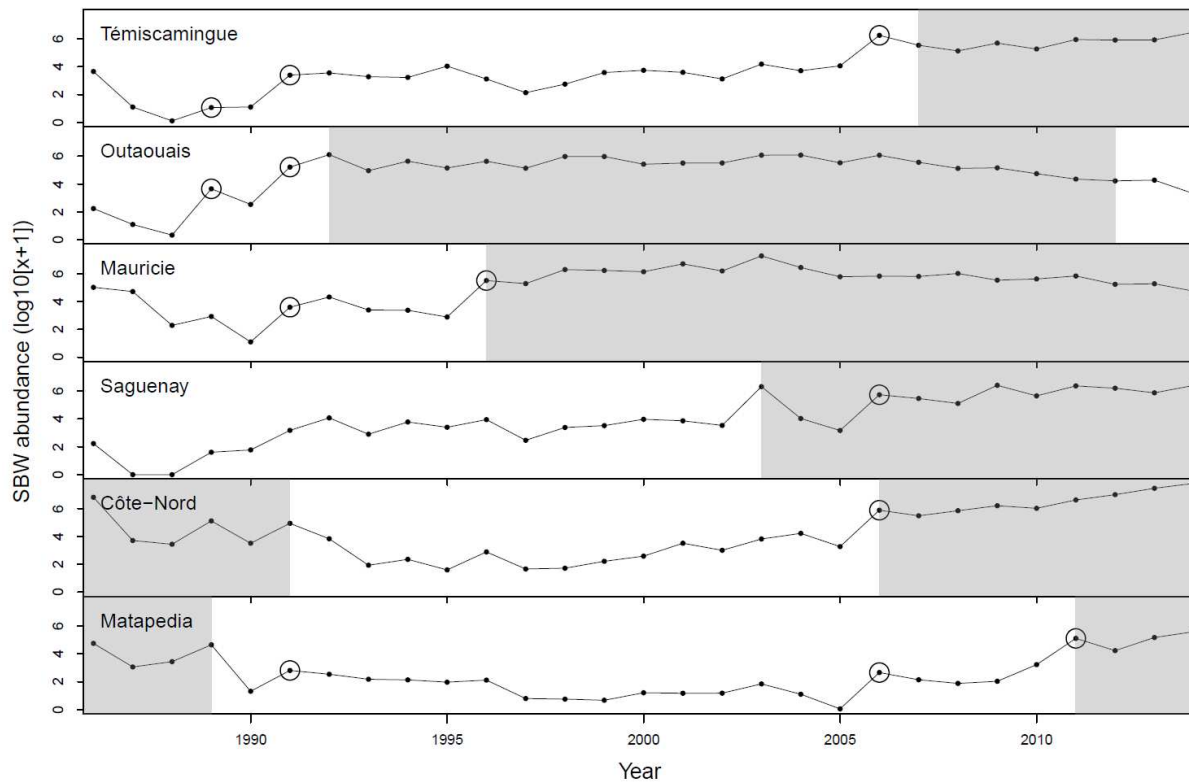


515

516 **Figure 4.** Temporal variation in statistics for the best model (Table 1) predicting changes in SBW
517 abundance at the province level. Separate models were fitted for each successive 10-year time window.

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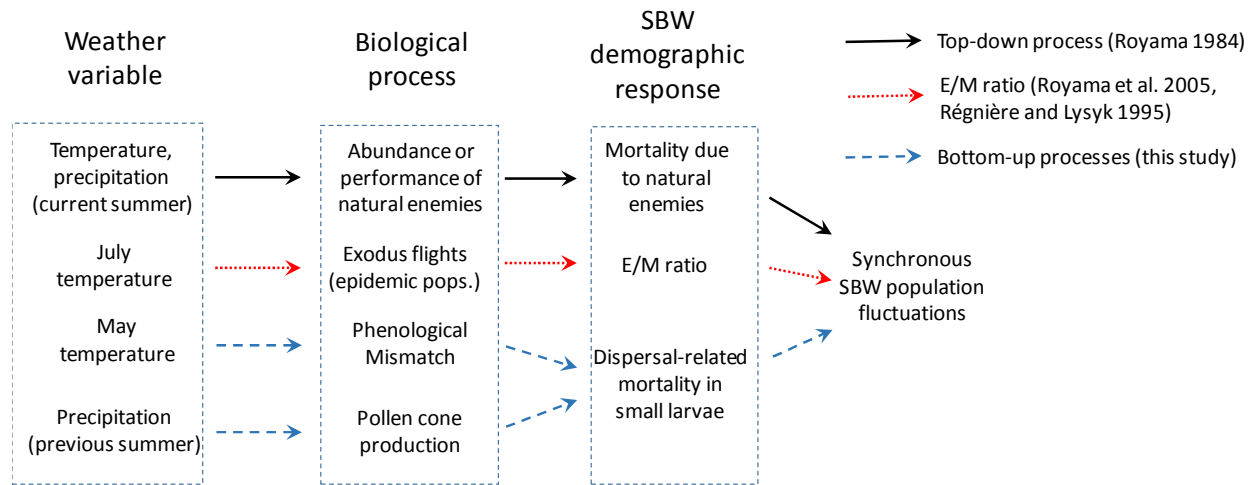
519

520 **Figure 5.** SBW population levels in six epicenters (c.f. Figure 1) where SBW outbreaks were detected
 521 during the 1986-2014 period. The shaded areas indicate the period during which defoliation could be
 522 detected from aerial surveys, corresponding to outbreak conditions. Larger circles indicate the beginning
 523 of a “persistent” population increase, defined as a 5x annual increase, with subsequent populations that
 524 remained above the pre-increase level for at least two years. Persistent increases were calculated from
 525 untransformed abundances, but log-transformed values are represented in the figure.

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530 **Figure 6.** Hypothetical biological pathways through which interannual variation in different weather
 531 variables could produce large-scale synchronized SBW population fluctuations.

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Supplementary material 1

Mean number of spruce budworms per trap in each 1 deg x 1 deg cell for each year.

LON	LAT	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
-80	48						117.3	86.0	38.7	31.7	45.3	20.7	2.7	11.7
-79	47	28.4	1.5	0.2	2.6	1.5	27.5	36.3	25.5	24.1	55.5	21.5	7.4	14.5
-79	48	0.0	0.0	0.0	11.7	4.0	21.7	120.5	37.7	60.0	45.0	41.3	11.7	15.3
-79	49					51.5	73.3	436.5	42.7	37.7	36.0	30.3	3.0	9.3
-78	46	3.0	0.0	0.0	7.0	0.0	63.4	58.3	25.8	27.6	36.6	34.4	12.9	24.7
-78	47	2.0	2.3	0.0	3.7	1.0	15.2	31.6	22.8	27.7	59.5	19.8	8.5	25.3
-78	48						59.3	59.0	18.3	22.3	21.3	13.3	4.3	11.7
-77	46	9.8	1.4	0.6	38.8	20.6	205.0	397.5	190.4	278.7	220.1	85.4	93.8	242.5
-77	47	0.7	0.0	0.0	2.0	0.2	48.5	68.3	18.3	42.9	35.1	11.3	13.3	66.3
-77	48					5.3	50.5	113.3	35.8	43.8	36.0	20.3	5.8	26.3
-76	45	29.7	9.0	8.0	159.0	131.7	4.7	2424.0	3459.3	1920.3	1263.3	1147.0	783.0	2705.3
-76	46	6.5	2.0	0.3	26.3	4.2	135.0	390.5	86.6	219.4	99.9	334.4	178.8	401.1
-76	47	3.1	0.2	0.1	1.5	0.6	46.0	166.2	35.0	32.1	25.3	25.4	26.8	65.0
-75	46	1.6	0.1	0.0	4.7	0.4	45.5	98.9	38.7	48.2	23.2	35.0	52.7	72.1
-75	47	0.5	0.0	0.0	1.9	0.8	37.9	52.6	32.4	33.1	29.1	21.4	19.8	37.1
-74	46	54.4	2.3	0.1	2.1	0.0	13.6	45.7	33.6	21.0	12.4	11.6	22.9	27.9
-74	47	28.0	0.0	0.0	0.8	0.0	6.2	13.2	10.4	7.9	9.5	6.9	8.9	18.9
-74	48		0.0	0.0	4.0	1.0	6.2	14.8	6.0	10.0	13.0	12.5	5.8	7.0
-73	46	47.0	0.0	0.0	12.2	0.9	23.9	51.5	22.1	22.7	13.4	321.8	247.8	580.9
-73	47	284.7	60.8	4.4	4.7	0.4	14.9	42.7	12.5	14.1	9.9	22.5	19.8	72.6
-73	48					0.3	4.2	24.8	15.4	27.2	16.2	27.3	7.0	12.5
-73	49												1.3	9.7
-73	50													
-72	45				5.3	0.3	27.8	58.3	15.3	38.1	22.8	35.3	23.9	31.4
-72	46					0.0	5.2	17.6	8.7	22.5	7.2	7.7	6.3	12.8
-72	47	20.3	0.0	0.0	1.5	0.1	2.8	14.6	9.9	7.5	3.4	5.0	7.2	13.9
-72	48	17.0	0.0	0.0	4.0	0.2	1.8	5.3	2.3	11.2	6.8	9.5	2.6	7.6
-71	46				0.0	0.0	3.5	7.0	3.9	3.1	1.6	6.3	3.1	13.4
-71	47	6.7	0.6	0.1	1.6	0.0	3.7	16.6	5.4	3.7	2.7	5.3	12.9	12.7
-71	48		0.0	0.0	1.3	2.8	13.4	25.9	9.2	14.0	13.3	19.1	6.3	11.2
-71	49					2.0	20.3	57.0	26.7	74.7	35.3	59.3	9.3	46.7
-70	46													
-70	47	52.7	0.0	0.0	1.7	0.0	15.7	18.9	7.7	6.4	2.9	5.7	4.8	8.1
-70	48	8.3	0.0	0.0	4.0	2.9	12.2	29.2	9.7	11.9	11.2	16.2	3.3	14.7
-70	49	0.3	0.0	0.0	1.3	6.3	26.2	12.7	3.1	5.8	5.8	40.0	7.8	9.6
-69	47				23.7	0.0	3.0	8.0	1.2	2.0	0.4	0.0		
-69	48	25.9	0.3	0.0	32.0	0.3	15.0	20.7	7.2	8.7	2.6	5.5	1.3	2.1
-69	49	1280.7	72.7	60.0	261.7	63.8	160.1	37.5	5.7	4.9	3.1	7.5	1.9	3.0
-69	50						115.3	40.7	6.7	11.3	7.3	36.3	9.3	9.7
-68	48	47.4	32.6	34.3	74.6	1.5	13.8	8.3	7.6	5.5	3.4	3.4	1.0	0.8
-68	49	279.2	10.8	3.5	67.3	6.0	75.3	29.2	9.2	11.7	3.3	11.3	1.7	1.0
-67	48	124.3	18.8	33.2	119.2	11.8	92.5	17.8	10.8	9.1	11.9	5.9	0.9	1.1

-67	49	80.6	7.0	5.4	114.0	5.5	32.5	22.0	2.3	2.4	15.2	10.3	1.4	0.7
-67	50						24.7	22.7	2.7	1.5	3.3	2.7	0.3	1.0
-66	48	78.5	53.5	218.7	376.5	55.4	220.1	80.9	11.3	8.9	4.5	3.7	0.8	1.3
-66	49	154.5	12.7	18.8	139.3	11.3	52.7	47.8	7.9	3.2	9.1	5.5	1.2	0.5
-65	48					20.2	290.8	102.9	19.7	5.1	4.0	3.3	0.2	0.0
-65	49	23.7	1.0	0.3	83.3	6.7	36.5	39.7	8.3	4.6	6.7	1.0	0.9	0.8
-64	48					40.7	178.3	42.7	16.0	4.0	2.3	0.0	0.0	0.0
-64	49	7.7	0.3	2.3	90.7	5.3	37.5	33.0	23.0	1.3	4.0	2.0	0.3	0.7
-62	47								349.9	107.4	304.6	145.8	5.9	1.2

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1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
67.3	101.0	54.7	20.3	19.3	35.3	197.0	155.3	50.7	47.7	34.0	55.0	25.7	19.0	42.7
34.7	40.9	35.2	21.6	64.4	39.7	56.7	515.3	252.4	167.8	294.9	192.8	381.3	366.1	324.0
55.0	50.3	51.0	19.0	13.3	23.7	46.3	566.7	232.3	113.7	34.3	82.0	78.3	118.5	94.7
62.0	50.7	24.0	12.7	10.0	15.0	15.8	82.8	60.1	34.2	24.3	29.7	41.8	10.1	41.5
26.6	23.3	41.7	8.5	14.8	13.9	46.5	112.3	44.8	91.3	35.7	31.1	86.0	66.2	44.3
33.5	32.3	49.2	19.7	41.4	13.0	37.8	120.1	109.3	106.7	34.6	55.8	113.4	120.1	72.1
6.7	38.3	30.7	4.7	6.7	9.3	19.0	36.0	12.3	47.3	27.0	28.0	48.7	48.0	56.3
304.1	201.8	220.1	311.5	444.1	357.7	256.5	297.2	209.0	146.9	112.1	63.8	61.2	62.9	73.3
47.5	43.0	39.3	21.8	33.5	23.0	11.3	55.6	27.8	56.8	22.1	27.3	27.2	38.3	73.2
27.3	46.5	21.0	19.2	16.6	18.5	23.5	108.0	37.8	54.7	25.2	43.0	71.2	35.4	54.0
1072.0	525.0	524.7	156.6	505.7	1012.7	471.3	1150.0	339.0	201.7	110.5	88.3	163.5	54.3	150.0
370.9	188.6	199.9	144.9	394.6	364.6	172.6	382.7	209.1	128.4	172.7	113.2	59.1	62.3	63.9
53.2	48.8	25.8	21.6	38.6	90.1	18.9	161.8	66.9	54.8	31.7	94.7	37.2	27.2	38.3
68.5	47.2	45.8	20.1	46.5	85.8	20.4	71.3	39.4	25.3	16.2	28.3	26.4	5.0	12.7
51.8	76.0	27.2	33.8	39.9	102.5	39.7	121.2	29.7	34.8	17.7	57.4	39.6	11.7	13.6
33.0	51.1	51.6	41.0	34.2	45.2	17.2	78.1	35.3	30.3	13.2	25.8	53.2	9.7	8.6
21.6	39.5	16.5	11.3	14.5	17.3	2.0	25.2	15.2	6.7	4.9	26.3	20.6	8.3	9.3
14.5	21.5	14.8	6.5	11.8	20.2	3.3	47.8	19.3	10.0	11.7	17.4	21.0	6.0	31.3
518.3	314.3	530.0	238.5	892.2	443.6	335.7	313.3	165.4	131.7	26.7	14.2	40.5	11.5	20.9
73.3	123.1	187.5	201.1	612.2	207.1	74.9	82.7	124.8	164.9	121.7	107.3	189.4	87.9	111.5
18.7	46.9	55.3	17.8	23.0	28.8	2.5	56.6	19.3	17.9	6.8	9.1	52.9	8.3	32.8
16.0	37.3	18.8	7.7	25.8	84.5	73.5	647.7	148.7	109.2	14.8	32.3	201.3	37.8	146.8
		1.7	1.4	7.2	14.3	9.7	70.0	30.5	29.5	43.2	3.5	4.0	45.2	9.0
35.6	59.1	52.2	18.7	35.9	87.3	4.8	36.5	23.5	1.3	4.5	14.0	14.2	5.3	2.3
11.7	23.2	18.2	10.1	10.7	27.4	7.4	23.6	26.8	1.9	0.3	12.6	13.3	5.1	3.6
20.0	33.4	22.1	14.7	32.4	21.2	4.5	61.6	9.2	13.4	10.3	11.1	15.1	2.5	10.2
9.2	24.3	22.7	13.6	42.7	47.8	25.9	195.1	133.4	132.0	378.7	195.0	417.2	153.8	134.7
8.0	12.3	19.6	5.7	5.6	16.2	2.7	6.9	8.6	1.5	1.1	2.7	7.9	1.4	3.5
6.2	9.2	13.7	7.4	13.5	27.0	12.2	21.4	11.6	3.5	4.6	13.8	9.5	7.2	92.8
32.8	38.6	30.5	25.9	671.3	31.8	17.9	263.9	225.7	129.3	568.0	249.8	445.9	312.5	234.6
16.8	36.1	31.3	19.3	50.5	17.8	14.6	140.8	41.0	248.3	81.0	29.9	54.3	37.0	152.6
6.0	9.7	6.3	2.7	1.3	3.7	0.0	2.0	3.0	1.3	0.0	1.7	3.7	0.0	4.7
6.4	10.0	15.7	5.4	15.0	8.7	7.0	14.3	22.1	6.2	5.8	14.0	26.0	7.4	164.1
19.5	31.9	31.0	21.4	40.8	40.5	10.0	101.6	82.7	59.6	148.5	85.6	166.2	386.0	298.0
12.3	22.0	28.4	9.1	21.8	31.3	6.7	87.7	34.3	180.1	177.0	105.5	295.2	48.4	320.7
								12.3	3.0	1.7	5.7	13.3	9.3	39.8
3.9	6.9	4.6	4.0	4.1	1.4	1.2	21.2	20.4	11.4	13.7	14.1	50.3	49.5	241.3
5.2	13.3	24.1	12.5	29.0	42.6	13.5	218.8	58.6	192.3	245.6	165.7	849.0	783.3	1716.3
11.0	18.7	51.0	40.0	76.3	97.7	42.0	306.7	170.7	546.0	335.3	146.2	300.7	496.0	1766.2
1.0	1.7	2.2	1.4	2.9	0.6	0.4	8.3	3.4	4.3	8.0	14.8	129.5	38.7	233.4
1.3	4.2	6.2	4.3	5.2	13.3	8.3	162.8	326.3	103.2	357.9	511.8	590.3	685.5	519.5
1.2	2.6	3.0	2.0	4.9	1.6	0.5	8.4	2.0	2.3	5.4	7.9	153.8	69.9	159.6

2.2	2.3	3.7	2.5	5.5	4.5	1.4	21.8	5.7	7.4	18.4	58.4	246.1	284.8	499.1
1.5	6.0	2.0	8.0	5.7	14.7	6.7	88.0	201.9	484.5	97.7	152.2	1317.6	867.5	1611.7
1.3	9.2	7.3	3.8	6.3	2.1	0.9	7.8	3.5	1.8	6.1	4.5	27.5	20.1	58.5
0.7	1.8	3.4	2.8	3.9	4.6	3.2	29.3	6.0	13.4	33.9	75.0	234.5	445.4	668.9
0.3	1.5	2.2	1.3	1.3	0.5	0.2	4.0	1.3	1.2	4.3	7.0	20.8	12.4	63.4
1.1	2.2	4.6	2.7	6.8	4.0	4.3	36.1	13.6	30.8	23.0	61.5	178.2	169.7	333.4
0.7	0.0	0.0	0.3	0.0	0.0	0.0	1.7	1.0	11.0	28.5	15.0	80.0	144.0	49.0
4.0	5.0	4.3	1.7	1.8	0.2	0.0	7.7	2.5	5.5	29.2	5.3	49.2	21.8	86.5
1.1	3.3	6.5	7.9	4.0		0.5	11.4	1.3	5.2	3.6	6.1		82.5	56.7

Draft

2014

52.3
474.7
250.3
104.3
42.9
109.3
132.9
30.0
51.6
122.1
112.3
20.7
36.2
9.4
36.6
8.3
5.5
20.2
7.9
70.5
42.9
168.3
27.3
2.3
2.8
3.9
48.0
1.3
21.0
312.3
69.8
1.8
77.0
423.8
191.5
35.0
168.3
1984.6
2107.1
280.1
708.3
190.9

Draft

619.4
2052.8
38.3
546.7
18.6
391.1
11.5
63.2

Draft

Supplementary material 2

Number of plots located in each cell (three pheromone traps are present in each plot).

LON	LAT	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
-80	48						1	1	1	1	1	1	1	1	1	1	1
-79	47	4	4	4	4	2	5	6	4	4	4	4	4	4	4	4	4
-79	48	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
-79	49					1	1	1	1	1	1	1	1	1	1	1	1
-78	46	1	1	1	2	2	3	3	3	3	3	3	3	3	3	3	3
-78	47	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4
-78	48						1	1	1	1	1	1	1	1	1	1	1
-77	46	8	8	8	8	7	9	10	9	10	10	10	9	9	8	9	9
-77	47	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
-77	48					1	2	2	2	2	2	2	2	2	2	2	2
-76	45	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
-76	46	12	12	11	12	13	14	14	14	14	14	17	13	13	13	13	13
-76	47	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
-75	46	5	5	8	8	8	8	7	8	8	8	8	8	8	9	9	8
-75	47	2	2	1	3	3	3	3	3	3	3	3	3	3	3	3	3
-74	46	3	3	3	3	5	6	6	6	6	6	6	5	5	6	6	6
-74	47	1	1	1	2	3	5	6	6	6	6	6	6	6	5	5	5
-74	48		1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
-73	46	1	1	1	2	3	3	3	3	3	3	4	4	4	4	4	4
-73	47	3	4	4	5	9	11	16	16	15	16	15	16	16	16	16	16
-73	48					2	3	3	3	3	3	3	3	3	3	3	3
-73	49												1	1	2	2	2
-73	50																2
-72	45				2	4	4	4	4	4	4	4	4	4	4	3	4
-72	46					2	2	3	3	2	3	2	2	2	2	3	3
-72	47	2	2	2	2	4	6	6	6	7	7	7	7	7	8	7	8
-72	48	1	1	1	1	2	2	2	2	2	2	2	3	3	4	4	4
-71	46				2	5	5	6	6	5	5	5	5	5	5	5	5
-71	47	3	3	3	3	5	6	6	6	6	6	6	5	5	6	6	5
-71	48		1	1	1	4	4	4	4	4	4	4	4	4	7	7	7
-71	49					1	1	1	1	1	1	1	1	1	4	4	4
-70	46														1	3	1
-70	47	1	1	1	1	5	6	6	6	6	5	3	3	3	3	3	3
-70	48	1	1	1	1	4	5	5	5	5	5	6	6	6	7	8	7
-70	49	1	1	1	1	3	3	3	3	2	2	1	2	2	3	3	3
-69	47				1	1	1	2	2	2	2	1					
-69	48	3	3	3	4	6	7	13	12	12	12	11	11	11	10	10	11
-69	49	1	1	1	1	3	4	4	5	5	5	5	5	4	4	4	4
-69	50						1	1	1	1	1	1	1	1	1	1	1
-68	48	4	7	7	7	7	8	10	10	10	9	10	9	8	8	9	9
-68	49	2	2	2	2	2	3	3	2	2	2	2	2	2	2	2	2
-67	48	3	3	3	3	4	6	6	6	6	6	5	5	6	6	6	6

-67	49	4	4	3	4	5	5	5	5	5	3	4	3	3	3	3	2
-67	50						1	1	1	1	1	1	1	1	1	1	1
-66	48	2	2	2	2	3	3	4	4	5	6	6	6	6	6	6	6
-66	49	5	5	5	5	7	7	6	6	6	7	8	6	9	5	5	9
-65	48					4	4	4	4	3	3	2	2	2	2	2	2
-65	49	1	1	1	1	4	4	4	4	4	4	3	3	6	5	6	6
-64	48					1	1	1	1	1	1	1	1	1	1	1	1
-64	49	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
-62	47									3	3	4	3	3	3	3	4

Draft

2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
1	1	1	1	1	1	1	1	1	1	1	1	1
4	4	4	4	7	6	4	4	3	3	3	10	12
1	1	1	1	1	1	1	1	1	1	1	12	15
1	1	2	2	3	3	3	3	3	3	3	4	4
2	3	3	2	3	3	2	2	2	2	2	5	5
5	4	4	4	5	5	4	3	3	3	3	6	6
1	1	1	1	1	1	1	1	1	1	1	6	7
11	13	9	9	9	9	9	8	9	8	9	13	14
2	2	2	2	2	3	3	3	3	3	3	8	8
2	2	2	2	2	2	2	2	2	2	2	2	4
2	1	1	1	1	1	1	1	1	1	1	1	1
16	21	13	13	12	12	12	12	12	9	9	11	12
3	3	3	3	3	3	3	2	3	2	2	7	8
9	9	9	9	9	9	9	9	9	9	9	12	15
3	3	3	3	3	3	3	3	3	3	3	7	7
7	6	6	7	7	7	7	7	7	7	7	10	10
5	5	5	4	4	4	4	4	4	3	3	8	9
2	2	2	2	2	2	2	2	2	2	1	2	3
5	5	4	4	4	4	4	4	2	2	4	4	3
17	19	17	17	17	17	17	17	17	13	17	17	15
5	4	4	4	4	4	4	4	4	4	3	7	8
2	2	2	2	2	2	2	2	2	1	2	6	6
2	2	2	2	2	2	2	2	2	1	2	1	2
4	4	4	4	4	4	3	4	4	4	4	7	7
3	3	3	3	3	3	3	3	3	3	3	6	7
8	8	8	8	8	8	8	8	8	6	8	11	11
3	3	3	3	3	3	3	3	2	3	3	8	8
5	5	5	5	5	5	5	5	5	5	5	7	8
5	5	5	4	5	4	5	5	5	5	5	8	8
8	11	7	7	7	7	7	7	7	7	7	14	16
4	4	4	4	4	4	5	4	3	3	4	6	11
1	1	1	1	1	1	1	1	1	1	1	3	3
3	3	3	3	3	3	3	3	3	3	3	8	12
7	7	7	7	7	7	7	7	7	6	7	15	18
3	3	3	3	3	4	4	4	4	4	4	7	9
					1	1	1	1	1	1	2	3
10	10	10	8	8	9	8	10	10	9	10	11	17
4	4	4	4	4	5	4	4	4	4	4	5	7
1	1	1	1	1	1	1	1	2	1	1	2	3
9	9	9	9	9	9	8	8	8	8	8	12	15
2	2	2	2	2	4	2	2	2	2	2	8	8
7	7	7	8	8	8	8	8	8	8	8	8	12

7	7	7	7	7	9	9	8	8	8	8	12	11
1	1	1	1	1	4	4	2	2	2	2	4	4
6	6	6	6	6	7	7	7	7	7	7	7	7
10	10	10	10	10	9	9	8	10	10	10	13	14
3	3	2	3	3	3	3	3	3	3	3	4	4
8	8	8	8	8	8	7	8	8	7	7	9	13
1	1	1	1	1	1	1	1	1	1	1	1	1
2	2	2	2	2	2	2	2	2	2	2	2	2
4	4		4	4	4	4	3	3		3	3	

Draft

Supplementary material 3

White spruce cone collection data in Québec for the 1980s (Plants Forestiers (Quebec Government)). Because the quality of tree farms during any given year or period, the qualitative

Year	Assess. ¹	Harvest ²	Index ³
1986	Nul	0	0
1987	Nul	0	0
1988	Ab	1,820	3
1989	We	781	1
1990	Mo	1,180	2
1991	Nul	0	0
1992	Ab	510	3
1993	Nul	0	0
1994	We	179	1
1995	We	21	1
1996	Ab	867	3
1997	Nul	0	0
1998	We	108	1
1999	Nul	0	0
2000	Mo	429	2
2001	We	35	1
2002	We	121	1
2003	Ab	824	3
2004	We/Mo	429	1
2005	We	52	1
2006	Ab/Vab	757	4
2007	Nul	1	0
2008	We	132	1
2009	We/Nul	5	0
2010	Mo	104	2
2011	Mo	223	2
2012	We/Nul	14	0
2013	We	36	1
2014	We/Mo	151	1

Notes:

1 Overall province-level semi-quantitative assessment made each year

2 Volume of cones harvested, in hectolitres (1 hl = 100 litres)

3 Quantitative index used in the analyses

6-2014 period. Data is provided by the Direction Générale de la Production de Semences et de quantitative assessment (volume of cones harvested) is somewhat biased by the demand expressed by the assessment was used as a predictor in the statistical analyses performed in this study.

Draft

each year: Vab : cone production very abundant, Ab : abundant, Mo : moderate, We : weak, Nul : nul.