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Running head: RESEARCH ARTICLE

Interannual population dynamics of the green spruce aphid *Elatobium abietinum* (Walker) in France

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Keywords

Elatobium abietinum, *Picea sitchensis*, Population time series, Climate, Forest management, Environment

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Summary

- **Context** The hypothesis that similar processes govern interannual dynamics of green spruce aphid in the UK and France, is generally supported by the application of a general discrete model. A simple model based on relatively few parameters was able to closely characterise interannual population dynamics from completely independent aerial and arboreal samples of aphids. Long term field population estimates of the green spruce aphid *Elatobium abietinum* (Walker) in France have provided the

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3 opportunity to select and evaluate the generality of a model which was developed in
4 the UK to explain the year-to-year variations in peak abundance of the aphid.
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- 8 • **Aims** The objective was to observe the influence of the local climates and disturbing
9 climate factors on the population densities of the insect in two regions of France.
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 - 11 • **Methods** The model uses climate variables and aphid population data from regular
12 samples in the two regions that were investigated. A general discrete model was used
13 to predict aphid population densities.
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 - 15 • **Results** The model performed well in tracking the interannual patterns of population
16 but was less likely to predict absolute population density.
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 - 18 • **Conclusion** To improve predictions, further account would need to be taken of
19 additional site-specific climate variables and the strength of overcompensating density
20 dependence. Nevertheless it is clear that broadly similar processes are at work in the
21 population dynamics of this insect across its biogeographical range.
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1 | Introduction

The green spruce aphid *Elatobium abietinum* Walker 1949 (Homoptera: Aphididae) is one of the seven species of the genus *Elatobium* Mordvilko 1914 which belongs to the subfamily Aphidinae and tribe Macrosiphini (Remaudière and Remaudière 1997). Three of those species are conifer feeders (Blackman & Eastop, 1994). Of these, *E. abietinum* is the major pest of Sitka spruce *Picea sitchensis* (Bong.) Carr. throughout northern and western Europe where this tree species has been abundantly planted in reforestation areas since the early 1950s (Hanson, 1952; Carter, 1977; Parry, 1969; Day, 1984b; Day & Crute, 1990) (Fig. 1).

This sap-feeding insect was first described feeding on Norway spruce *Picea abies* (L.) Karst. which might be the original and normal host of *E. abietinum*. This host tree can tolerate heavy infestations without suffering severe defoliation and shows less reaction to its presence than does Sitka spruce (Carter & Nichols, 1988; Day & McClean, 1991). Norway spruce appears to have had time to evolve resistance mechanisms to the aphid forcing the insect to switch to a more susceptible host-plant.

The life cycle of the insect (Fig. 2) is dependent on the local climate and it is admitted that under maritime climates like in the UK but also in Normandy and Brittany, western France, anholocyclic populations are governed by low winter temperatures (Powell & Parry, 1976) while in more continental regions like the Limousin (France) and the Massif Central (France) or in Denmark (Harding & Carter, 1997) holocyclic populations overwinter as dormant eggs. In Brittany and Normandy, the aphids overwinter as wingless viviparous females but severe frost in these regions will result in high aphid mortality.

Parthenogenetic reproduction can continue at low temperatures and aphids are present in large numbers at the end of winter when temperatures become more favourable for the insect (Day et al. 2004). There is a period of maximum increase in the number of aphids

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3 during the spring damaging period when the needles contain a high concentration of amino-
4 acids which is required by the insect (Carter & Nichols, 1988). Peak density is reached in
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6
7 May. After bud flush, nutrients are moved to the newly formed needles which remain
8
9 unattacked for up to 4 months after flushing. At the same time, in late spring, a winged
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11 viviparous female form (*alatae*) disperses and populations collapse until late summer, early
12
13 autumn when the tree produces hard terminal buds and is in a dormant shoot growth
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15 condition. Simultaneously, the aphid starts increasing in numbers (Day *op.cit.*).
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19 *Elatobium abietinum* only feeds on mature needles causing chlorotic bands while
20
21 current-year needles deter aphid feeding (Carter & Nichols, *op.cit.*). These old needles rapidly
22
23 become yellow and are prematurely abscised. Trees that have suffered heavy damage have
24
25 thin crowns and reduced annual rings. The aphid is especially damaging in winter on dormant
26
27 trees. Substantial needle losses can cause a reduction in growth and hence timber yield which
28
29 can be affected for two or three years after the attack (Straw & Green, 2001).
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33 With the economic consequences of green spruce aphid population growth in mind, a
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35 numerical model of long-term trends in peak population has been developed using relatively
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37 few parameters and incorporating knowledge of endogenous and exogenous factors
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39 influencing population dynamics (Day et al., 2009). This initiative was particularly promising
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41 because it robustly described field data derived not only from aphids feeding on trees in
42
43 Northern Ireland but also from alate aphids in suction traps from Scotland. The potential for
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45 describing geographically independent data sets suggested that this model might perform
46
47 equally well elsewhere in Europe.
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51 In this investigation we examine a time series obtained over 12 years in two French
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53 forests. We hypothesise that the essential features of spruce aphid interannual population
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55 dynamics, endogenous density dependent feedback and exogenous weather factors, will play
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57 out in a similar way wherever anholocyclic populations of the aphids are found on Sitka
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3 spruce in western Europe. Populations in northern and western France are a good test of the
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5 generality of this hypothesis, and are a considerable geographical distance from the regions
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8 for which the model we employ was originally developed.
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2 | Materials and methods

2.1 | Host-plant and aphid population data

A cartographic study of Sitka spruce plantations over the two regions has been carried using the IFN data set (Inventaire Forestier National, 1999) and regional vegetation maps (CORINE Land Cover France, 2009) and included an extensive field survey of Sitka spruce plantations. The aphid populations were assessed using the protocol as described below.

The aphid population time series was derived from estimates of aphid abundance on spruce needles at the forest of Monnaye (Normandy) (02°08 'W, 48°51'N, mean elevation 280 m) and forest of Malaunay (Brittany) (03°05 'W, 48°54' N, mean elevation 135m).

Both forests are privately owned and managed by private forest experts. The forest of Monnaye is located in the department of the Orne and covers 620.3 ha including 64 ha of Sitka spruce. The forest of Malaunay is located in the Côtes d'Armor on the north coast of Brittany and covers 672 ha including 296 ha of Sitka spruce.

Four forests compartments of different ages (forest plots planted in 1954 and 1967 in Monnaye; forest planted in 1965 and 1990 in Malaunay) have been selected in the two forests and sampled at regular intervals every two weeks from 1997 up to 1999 and four times per year from 2000 until 2008 providing a representation of year-to-year fluctuations in abundance (Day & Crute, 1990). The abundance of aphid populations within and between trees was assessed using a transect method called Central Point Quarter Method (CPQM) (Dahdouh-Guebas & Koedam, 2006) in the four forests plots that were visited. 80 trees per random transect were sampled using the modified plotless technique CPQM. This plot-less method involves measuring distances for a random sample of trees, typically along a transect, and recording the characteristics of interest for this sample. The advantage to using plot-less methods rather than standard plot-based techniques is that they tend to be more efficient. Plot-

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3 less methods are faster, require less equipment, and are not dependent on the size of quadrats.
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5 Many authors tested and stated that CPQM will highly recommended and used in forest
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7 inventory (Cottam & Curtis, 1956 ; Beasom & Haucke, 1975). For each tree, five branches
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9 were collected in a total of 400 samples per forest plot and date.
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12 Population estimates were expressed as mean total aphids per 100 needles and sample
13
14 shoot in order to standardize the results with existing protocols (Day, 1984b, 1986).
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17 In particular, the samples capture the point at which the aphid population reaches its
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19 annual maximum, and this has been used to represent annual populations in the analysis.
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22 23 24 2.2 | Climate variables

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26 The selection of climate variables and metrics was based on their known relationship to aphid
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28 population processes. The green spruce aphid passes the entire year anholocyclicly as nymph
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30 or adult and as such its rate of development, and that of its populations are at least partly
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32 temperature dependent. A decline in availability of plant sap nutrients following spruce
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34 budburst means that aphids can benefit most from higher temperature prior to this point.
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36 Thermal time (*phys*) accumulated through the months prior to budburst reflected the ability of
37
38 aphids to develop and reproduce, and hence was likely to be linked to population growth. On
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40 the other hand, spruce aphids are susceptible to subzero temperatures, despite their ability to
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42 supercool, and a metric reflecting this was incorporated in earlier versions of the population
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44 model. However, when tested with UK field data no signal of demographic effects from this
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46 metric was found in the model as winters in the areas from which UK data was derived were
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48 insufficiently severe. Another low temperature metric (*coma*) was derived to account for
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50 aphid mortality by starvation or chill coma experienced after prolonged periods when
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52 temperature is below the aphid developmental threshold. These two climate variables became
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3 the most successful metrics in generating a model applied to spatially heterogeneous
4 independent data (Day et al., 2009).
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10 2.3 | Model description and application

11 2.3.1 | *General description and background*

12 We employed a general discrete model of population dynamics (Turchin & Taylor, 1992)
13 where interannual per capita growth rate = $R_t = \ln(N_t / N_{t-1})$ where $N_t = N_{t-1} \times e^{R_t}$ (with $N_t =$
14 aphid abundance in late spring of year t). We also hypothesized that there would be negative
15 feedback (density-dependence) on aphid abundance i.e., $R_t = f(N_t) + \epsilon_t$, with ϵ representing
16 sampling error in density estimates plus exogenous (density-independent) effects on aphid
17 population dynamics. Thus we evaluated alternative models for climatic effects on aphid
18 populations by examining relations between ϵ and specific climate parameters.
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30 Alternative models for climatic effects were compared with respect to three criteria:
31 (1) the pattern with respect to climate should be consistent with theoretical expectations (e.g.,
32 extreme winter cold is expected to yield lower per capita growth rates); (2) a model that
33 includes one or more climatic drivers should be defensibly favoured over simpler alternative
34 models based upon information theory; (3) and we favoured models in which the regression
35 coefficients that were retained were statistically distinguishable from 0. Our rationale for the
36 latter criterion was that most of the statistical null hypotheses were nontrivial (e.g. spring rain,
37 a variable tested but discarded, might or might not matter to aphid populations). We began
38 analyses with shoot-based aphid abundance data collected over a period of 10 years in
39 Northern Ireland, identified the best models for this data set, tested those models against
40 independent 37 year time series data on aerial abundance from Scotland and then settled on a
41 single model, as follows, that could reasonably be applied to both situations.
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$$R = 4.74 (\pm 0.40) - 1.28 (\pm 0.11) \cdot \ln(N) - 0.047 (\pm 0.20) \cdot coma + 0.0045 (\pm 0.0014) \cdot phys,$$

[Eq.1]

This was the model used in the present study with mean daily temperature records obtained from the local Meteo France stations in Dinard and Côtes d'Armor for Brittany and Pré-en-ail, Orne for Normandy.

Population densities of aphids were predicted using this model for each year and forest area (Normandy and Brittany).

2.3.2 | Model parameters

phys

Physiological time (Campbell et al., 1974; Day, 1984a; Fisher & Dixon, 1986; Crute & Day, 1990; Day & Crute, *op.cit.*; Day et al., 2004, *op.cit.*) is the thermal time accumulated from 1 January to the approximate date of budburst respectively 20 April for Brittany and 30 April for Normandy. It has been assumed that growth and reproduction are temperature dependent (Day et al. 2004) and that 4°C is the threshold for aphid development. *Phys* expressed in degree days is then a function that accumulates degree days above 4°C over the period which is most favourable for aphid development. In the development of the model, values of physiological time were adjusted for each year relative to the site average to yield the metric *phys*.

coma

Prefreeze mortality is known to be potentially important for spruce aphids living in maritime climates (Powell & Parry, 1976; Bale et al., 1988; Dixon, 1998). To account for this the number of chill days with a daily mean temperature $\leq 5^{\circ}\text{C}$ from 1 October to budburst was

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3 recorded. The metric *coma* used in the model was then represented by the number of chill
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5 periods, each a consecutive run of 5 days with daily mean temperature of $\leq 5^{\circ}\text{C}$.
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3 | Results

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6 In Normandy, the forest of Monnaye belongs to the Seine biogeographical region. The
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8 average temperature of 10°C is lower and the moisture greater than in the neighbouring
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10 departments. The west winds are the most frequent and the rainfall, distributed over 160 up to
11
12 180 days annually, amounts to nearly 100 cm, or half as much again as the average for
13
14 France. Consequently, aphids experience cold winters and low temperatures which affect the
15
16 population dynamics by reducing the growth in winter (Carter, 1972; Day et al., 2009, *op.cit.*).
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18 Aphid physiological time (*phys*) was variable (between 290.5 and 606.6 day°C) as a result of
19
20 cold or mild winter and spring weather. Warm weather with a large accumulation of
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22 physiological time as observed in 1998, 1999, 2002, 2003 and 2007 allowed a rapid aphid
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24 recruitment and population growth. Periods showing a number of five consecutive chill days
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26 with a daily mean temperature $\leq 5^{\circ}\text{C}$ from 1 October to budburst (*coma*) had a negative effect
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28 on population growth (Powell & Parry, 1976; Day & Crute, 1990) as observed in 1997, 2005
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30 and 2006. The two metrics *phys* and *coma* were negatively correlated ($r = -0.65$) for this site.
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32 Aphid populations remained relatively low and below a threshold where visible damage to
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34 foliage would be widespread.
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40 The forest of Malaunay, on the north coast of Brittany is influenced by the Gulf
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42 Stream and by constant west winds bringing wet air from the Atlantic Ocean. The resulting
43
44 moderate oceanic climate is characterized by mild winters and lime summers. An average
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46 temperature of 12°C is observed on the coast and rarely come under zero while an average
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48 temperature of 10°C is recorded inland. Relative humidity remains high over the year. The
49
50 west wind blowing practically constantly brings wet air from the Atlantic Ocean that it rains
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52 relatively often even if rain quantities are not particularly important. Aphid physiological time
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54 (*phys*) was variable (between 280 and 508.9 day°C) as a result of cold or mild winter and
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56 spring weather. Warm weather with a large accumulation of physiological time as observed in
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3 1997, 1999, 2001, 2007 and 2008 allowed a rapid aphid recruitment and population growth
4 (Fig. 3a and b). As seen at Monnaye, periods showing a number of five consecutive chill days
5 with a daily mean temperature $\leq 5^{\circ}\text{C}$ from 1 October to budburst (*coma*) had a negative effect
6 on population growth (Powell & Parry, 1976; Day & Crute, 1990) as observed in 1999, 2005
7 and 2006. The two metrics *phys* and *coma* were negatively correlated ($r = -0.65$) for this site.
8 Climate metrics that were used in the model consistently explained the variations in field data
9 (Day et al., 2009).

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19 The annual populations of aphids predicted by the model and informed by local
20 meteorological data, were not close to observed values in absolute terms but the predicted
21 patterns of change from year to year were very similar to those observed (Fig. 4).
22 Endogenous, overcompensated regulation is strongly signaled by the “see-saw” fluctuation of
23 observed populations, something that is captured well in the model. While populations in
24 Normandy remained relatively low, and below a threshold where visible damage to foliage
25 would be widespread, populations in Brittany tended to fluctuate around a higher equilibrium
26 density and occasionally (4 out of 12 years) rose to a level at which needle loss would be
27 expected.
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4 | Discussion

Intra-annual population dynamics of green spruce aphid follow a familiar pattern in Western Europe and have been attributed to the combined influences of the thermal environment, host plant sap quality, aphid dispersal and predation (Day, 1984, 1986; Day et al., 2004, 2006; Straw et al., 2009). By contrast, the trajectory of populations across years was less studied until very long-term data became available through the Rothamsted Insect Survey (Harrington et al., 1992). Green spruce aphids suction-trapped during their early summer flight period across Great Britain became an accepted surrogate for aphid population density at a local level and with 40 years of data it was possible to assess the influence of the North Atlantic Oscillation (NAO), and latitudinal gradients in climate effects, on inter-annual changes (Saldana et al., 2007; Westgarth-Smith et al., 2007; Lima et al., 2008). Day et al. (2009) demonstrated similarities between the data obtained from suction traps and more intensively sampled foliar habitats where the aphids spend most of their lives. A simple model based on relatively few parameters was able to closely characterize interannual population dynamics from completely independent aerial and arboreal samples of aphids. This was made possible by a unique 9-year time series of forest aphid data (Day et al., 2009).

The hypothesis that similar processes govern interannual dynamics of green spruce aphid in the UK and France, is generally supported by the application of a general discrete model developed for aphid data in the north of the UK, to aphid populations in northern France. The model had a tendency to overestimate population density in France because values of *phys* in France (12 year means, Normandy 332,5; Brittany 412) are understandably well above those experienced in Northern Ireland and Scotland (78 year mean East Craigs, 239). We deduce that aphid populations in the *Phys* period (January to April) did not increase at a rate anticipated by the model which was derived from lower UK *Phys* values. Despite

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3 warmer spring conditions in France, aphids were unable to take advantage by developing
4 more quickly, probably because needle sap nutrients remained low for a greater proportion of
5 the *Phys* period.
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10 The effects of winter temperature on aphids in France was probably similar to that in
11 the northern UK. Aphids in Northern Ireland and Scotland showed no demographic effects
12 from accumulated degree days below -7°C (Day et al., 2009) but were sensitive to sustained
13 « chill periods ». The *coma* metric showed that the French forests were not colder in winter
14 than those in Scotland included in the model (mean *coma* values, Normandy 3.7, Brittany 7.6
15 and East Craigs 11.2) (Fig. 5). The observed French populations demonstrate the “see-saw”
16 fluctuations resulting from overcompensated density dependence. This type of behaviour is
17 common in aphid populations associated with trees (Sequeira & Dixon, 1997) and arises from
18 a number of processes such as discussed by Day et al. (2009).
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30 Records in western France show that the aphid has existed on non-indigenous spruce
31 forests like Sitka spruce plantations since the 1950s (Joly, 1961). This pattern did not seem to
32 affect the dispersal ability of aphid populations. It has been assumed that increases in mean
33 temperatures at local and regional scales might increase the abundance of aphid populations
34 over the next 50–100 years and that newly planted trees might experience more severe
35 defoliations (Straw, 1995; Straw et al. 1998a,b).
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44 Green spruce aphid outbreaks that have affected the health and growth of Sitka spruce
45 through successive regular defoliations, as observed in the UK (Carter & Nichols, 1988;
46 Thomas & Miller, 1994) have occurred in Normandy and Brittany every 10 years as
47 confirmed by our study and by historical records in 1958 (Joly, 1961), 1968 (Leroy &
48 Malphettes, 1969). Heavy defoliations were also observed in the Limousin in 1968 by Leroy
49 & Malphettes (1969) and in 1999 during our survey.
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3 Sitka spruce has been successfully introduced in the two regions by foresters since the
4 middle of the 19th century (Leroy & Malphettes, *op.cit.*) and more intensively planted
5 following major projects of wetland afforestation and/or reforestation since the 50s covering a
6 total surface of nearly 20 000 ha for the two regions. Changes in land use including forest and
7 conservation issues have had a quick and deep impact on the plantations of Sitka spruce and
8 consequently aphid populations in the two regions. A major change in the management of
9 public forests has led to the restoration of wetlands while private forestry is still using Sitka
10 spruce in reforestation areas (Lemperiere et al., in prep.). As a result, the patches that have
11 been formed by the Sitka spruce plantations within large agricultural landscapes follow a
12 pattern which is linked with the nature of the soil. Most of those patches are not connected
13 and could then be considered as biogeographical islands (Woiwod & Hanski, 1992).
14 Metapopulations of the green spruce aphid that were mostly distributed throughout the Sitka
15 spruce growing areas seem to follow this general patchiness which was observed in the two
16 regions.

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19 Another major impact on aphid distribution could be a shift from Sitka spruce to
20 Norway spruce which is considered as its normal host in northern Europe (Austara et al.,
21 1997; Halldorsson et al., 2004) and causing more cryptic damages as observed in some parts
22 of the Alps (Fig. 6). An interesting complementary study could be carried out to improve the
23 model since the observed outbreaks that have occurred after the last field assessments in 2008
24 (local annual reports for Normandy and Brittany from the Département de Santé des Forêts
25 surveys on forest pests) confirm that the general model performs well in tracking the
26 interannual trajectories of the populations from 2008 up to 2018 with outbreaks in 2012 and
27 2015 in Brittany and 2014 and 2017 in Normandy.

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4
5 European Union.
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21 22 **Figure Legends**

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26 Fig. 1 Distribution of the green spruce aphid *Elatobium abietinum* (Walker) (in grey) and
27 Norway spruce (hatched) in Europe. After Halldorsson *et al.*2004, redrawn from (Anon.,
28 1966) and Sigurgeirsson & Szmidt, 1992.
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31 Fig. 2 Life cycles of *Elatobium abietinum* after Carter & Halldorsson (1998).
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33 Fig. 3 Population time series for *Elatobium* at Monnaye (Normandy) (a) and Malaunay
34 (Brittany) (b), France. Mean aphid population density (n= 400 samples) at annual peak
35 population (April/June) each year.
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37
38 Fig. 4 Population time series for *Elatobium* at Monnaye (Normandy) (a) and Malaunay
39 (Brittany) (b), France. Mean aphid population density (n= 400 samples) at annual peak
40 population (April/June) each year.
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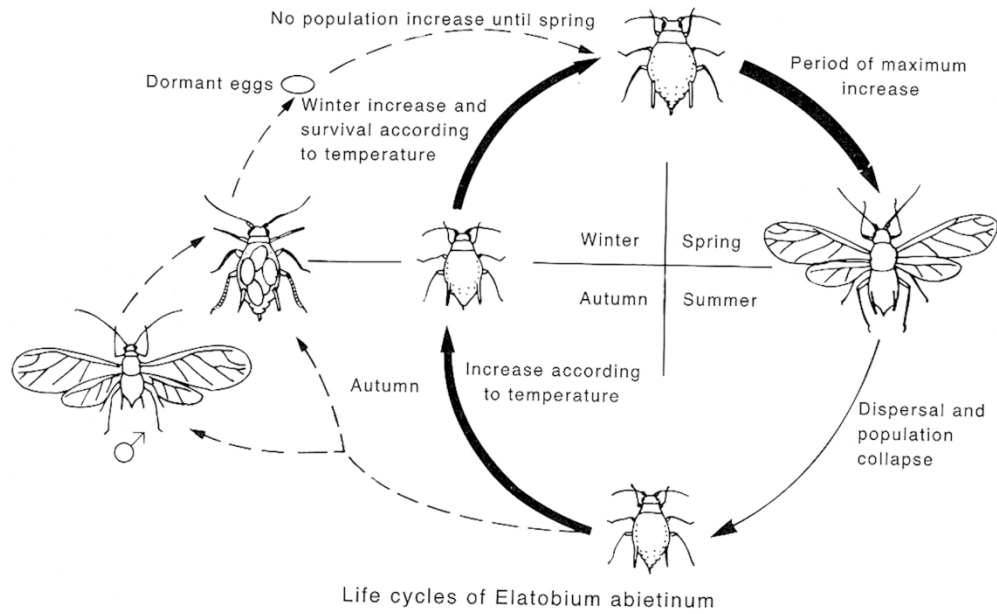
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43 Fig. 5 Historical patterns in two climatic metrics relevant to the population dynamics of
44 *Elatobium abietinum* patterns near Monnaye (Normandy) and Malaunay (Brittany) and East
45 Craigs, Scotland (1951–2007).
46

47 Fig. 6 Distribution of Sitka spruce in France and location of study sites with presence and
48 absence of *Elatobium abietinum* (1997–2008).
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Distribution of the green spruce aphid *Elatobium abietinum* (Walker) (in grey) and Norway spruce (hatched) in Europe. After Halldorsson et al. (2004), redrawn from Anon. (1966) and Sigurgeirsson & Szmidt (1992).

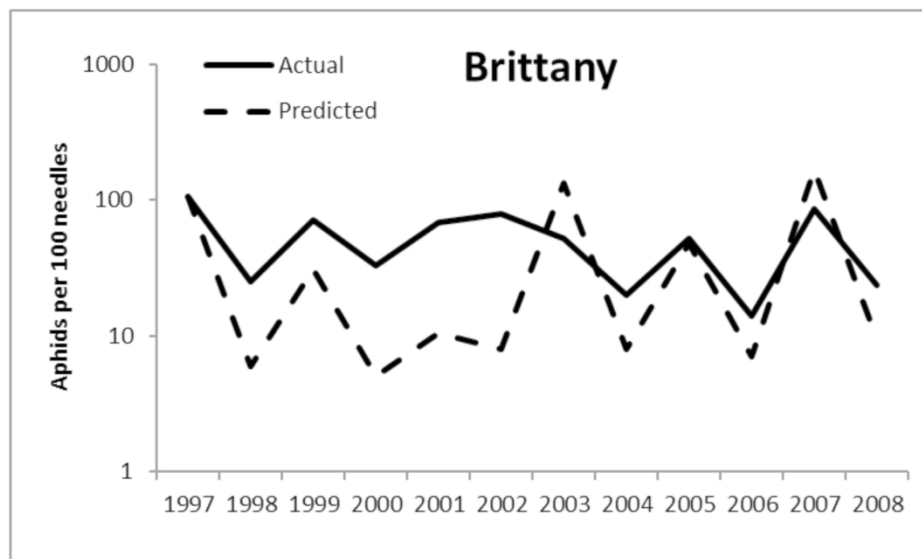
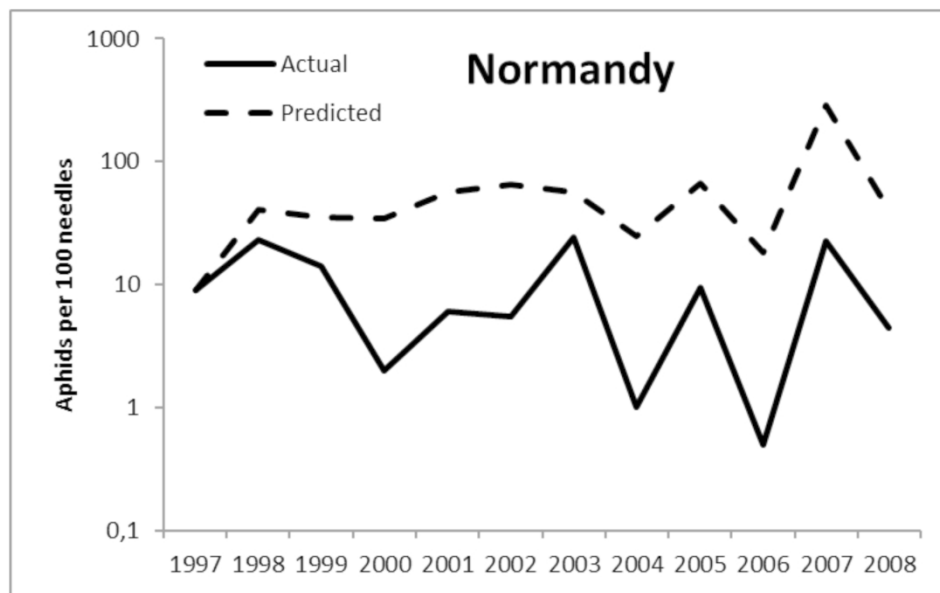
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Life cycles of *Elatobium abietinum* after Carter & Halldorsson (1998).

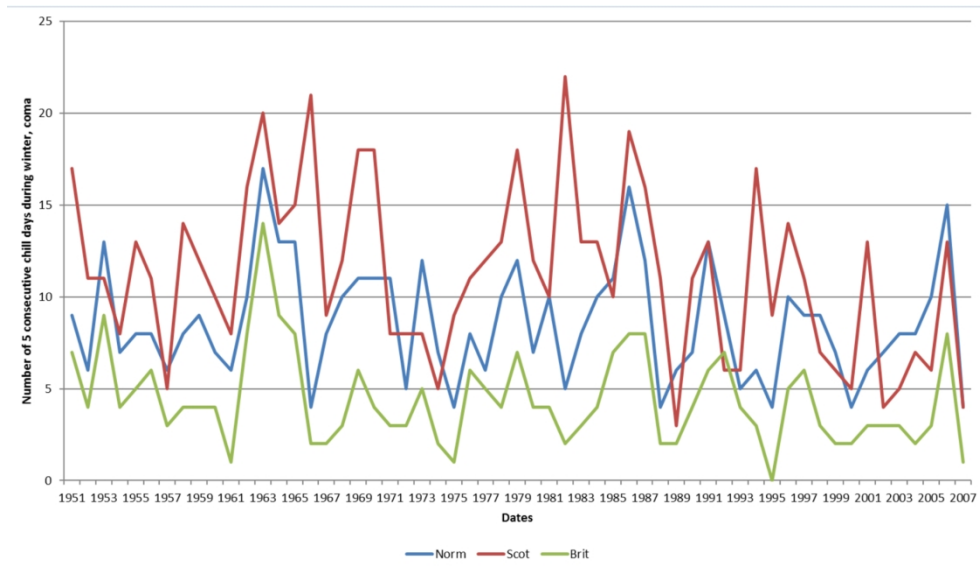


Population time series for *Elatobium* at Monnaye (Normandy) (a) and Malaunay (Brittany) (b), France. Mean aphid population density (n= 400 samples) at annual peak population (April/June) each year.



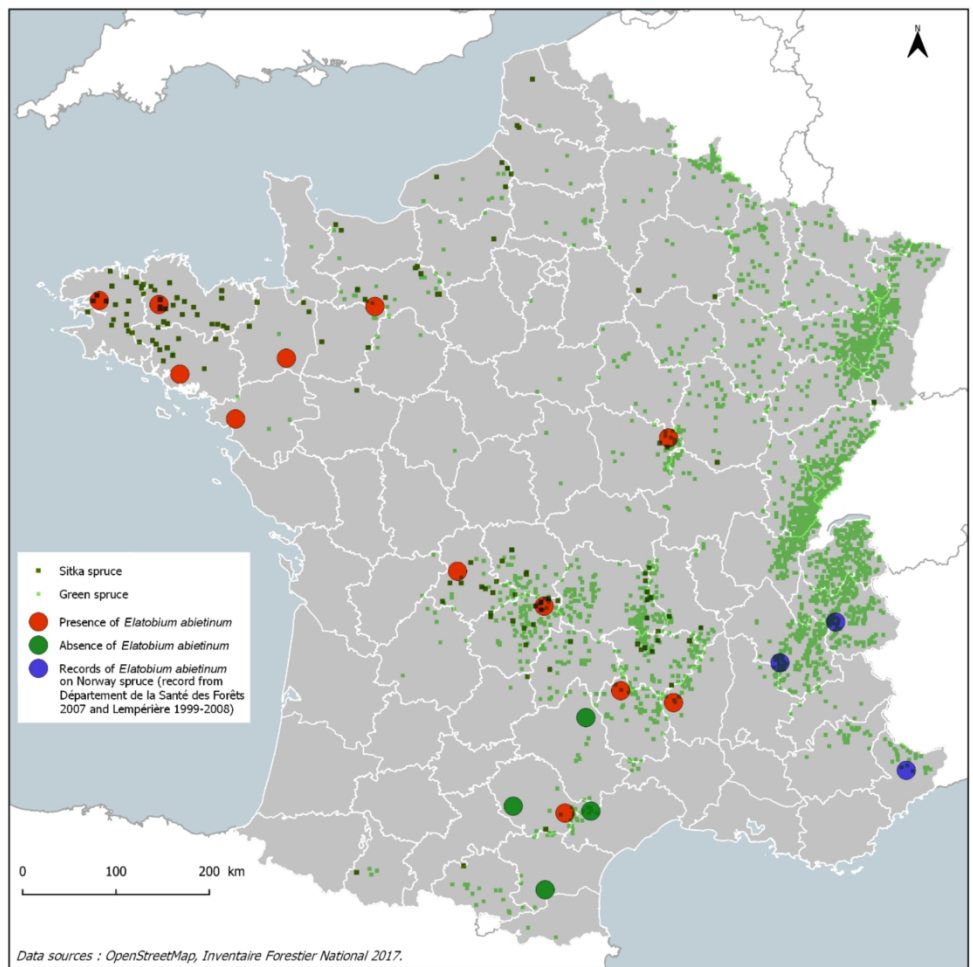
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Observed (solid) and predicted (open) annual maximum population densities of the green spruce aphid in two forests, a) Monnaye forest (Normandy) and b) Malaunay forest (Brittany). Population estimates were derived from spruce needle samples. The predictions were based on the preferred model (equation 1) in Day et al. (2009), developed for northerly UK aphid populations.



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Distribution of Sitka spruce in France and location of study sites with presence and absence of *Elatobium abietinum* (1997–2008).