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Periodicity and synchrony of pine processionary moth outbreaks in France

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ABSTRACT

Although many forest Lepidoptera are known to exhibit cyclic outbreaks in temperate forests, this has never been formally demonstrated for the pine processionary moth (*Thaumetopoea pityocampa*), the main insect defoliator of southern Europe. Yet, the demonstration of periodicity in the population dynamics of forest defoliators is of great interest for developing predictive risk models. We took advantage of 32 years time series recorded on permanent plots throughout France to test for the cyclicity of *T. pityocampa* outbreaks, estimate the length of cyclic periods and investigate synchrony between regions. Spectral analysis revealed that a large majority of regions and clusters of monitoring plots show significantly periodic outbreaks with a return period of seven to nine years. Outbreaks were not synchronous across the whole country but in neighbouring regions. Several factors such as low host tree quality following defoliation, impact of natural enemies and prolonged diapause might drive the cyclicity of *T. pityocampa* outbreaks while the Moran effect, here the role of low temperatures, is likely to explain synchrony.

1. Introduction

Cyclic population dynamics is a common feature among forest moth defoliators (Myers and Cory, 2013). Liebhold and Kamata (2000) considered that almost fifty percent of moth defoliators would exhibit periodic outbreaks, i.e. dramatic increases in pest abundance from generation to generation (Barbosa et al., 2012). At least 15 Lepidoptera species have been reported to exhibit periodic outbreaks in both conifer and broadleaved forests of North America (Berryman, 1996; Parry et al., 2003; Nealis et al., 2004; Régnière and Nealis, 2008; Cory and Myers, 2009; Allstadt et al., 2013; Alfaro et al., 2014), Europe (Straw, 1996; Kendall et al., 2005; Dormont et al., 2006; Nilssen et al., 2007; Tenow et al., 2007; Kapeller et al., 2011; Klapwijk et al., 2013) and Asia (Kamata, 2000).

While the exact reasons for regular fluctuations in population abundance are still actively debated, there is a consensus to consider that they arise from trophic interactions or maternal effects that trigger delayed negative feedback (Liebhold and Kamata, 2000; Berryman, 2002; Esper et al., 2007; Büntgen et al., 2009; Liebhold et al., 2012). Recently Myers and Cory (2013) listed three main factors necessary for cyclic population dynamics: high fecundity to allow fast population growth; density dependent mortality factors to initiate decline in population at peak density; delayed-density dependent mechanisms that prolong population decline.

Another common feature in forest defoliators is that populations of spatially disjunct locations can fluctuate in a similar manner, *i.e.* exhibit synchrony (Liebhold and Kamata, 2000; Myers and Cory, 2013). Synchronous epidemic cycles have been observed for a long time in many forest Lepidoptera species such as *Lymantria dispar* (Haynes et al., 2013), *Operophtera brumata* (Nilssen et al., 2007), *Eppirita autumnata* (Klemola et al., 2006), *Choristoneura fumiferana* (Jardon et al., 2003), *Choristoneura occidentalis*, *Malacosoma disstria* and *Zeiraphera diniana* (Peltonen et al., 2002).

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Recently proper statistical methods have been developed that allow demonstrating spatial synchrony in pest outbreaks in spite of intrinsically non independent data (Liebhold et al., 2004; Gouhier and Guichard, 2014).

Periodic and even more, synchronous periodic, outbreaks of forest moths may result in dramatic loss in tree growth, carbon storage and even tree mortality such as those observed following the extended defoliation of spruce budworm (Kurz et al., 2008) or gypsy moth (Davidson et al., 1999). The demonstration of periodicity in the population dynamics of forest defoliators is then of great interest because it paves the way for the development of predictive models for risk assessment and implementation of preventive pest control measures. It also provides baseline of long term population dynamics that allows detecting departure from current patterns and identify possible drivers of change. For example the extraordinary well documented history of larch budmoth periodic outbreaks could be used to show that outbreaks stopped in the last decades, demonstrating the effects of recent climate warming on supposedly very stable ecological processes (Esper et al., 2007).

Thaumetopoea pityocampa (Denis & Schiffermüller) (Lepidoptera, Notodontidae), the pine processionary moth (hereafter referred to as PPM) is another important forest pest. It is considered the main pine forest defoliator in Southern Europe and North Africa, due to its long temporal occurrence, large geographic range and strong socioeconomic impact (Roques, 2015). It is currently spreading to higher latitudes, probably in response to increasing winter temperatures (Battisti et al., 2005; Robinet et al., 2007, 2014; Robinet and Roques, 2010). PPM larvae build silk nests and feed on pine needles during the fall and winter which results in tree growth loss, even at low levels of defoliation (Jacquet et al., 2012, 2013). In addition to this effect on forest health, PPM caterpillars have urticating hairs, causing allergic reactions in humans and domestic animals (Battisti et al., 2011). Monitoring and pest management actions are therefore required on a regular basis, to ensure the detection, evaluation and mitigation of potential risks associated with PPM outbreaks (Jactel et al., 2006; Cayuela et al., 2011).

Although the regularity of PPM outbreaks has been long noticed by forest managers and entomologists, surprisingly few studies intended to demonstrate cyclicity in *T. pityocampa* dynamics. Geri and Millier (1985) evoked a cycle of 8–10 years in a single locality, Robinet (2006) suggested a 6-year periodicity in the outbreak cycle on the basis of 31 plot-level time series in Central France whereas Tamburini et al. (2013) found no regular cycles in the Italian Alps. The absence of robust analysis of PPM temporal dynamics is most probably due to the lack of adequate time series that need to be several times longer than the length of outbreak cycles, typically in the order of several tens of years, to allow statistically testing periodicity (Liebhold and Kamata, 2000). Furthermore, to our knowledge, the synchrony of PPM outbreaks has never been studied.

Here we took advantage of the long-term monitoring of PPM defoliations made by the French Department of Forest Health to verify the periodicity of *T. pityocampa* outbreaks. Started in 1981 on permanent plots, this survey provided us with time series of 32 years across the entire distribution range of PPM in France. Our objectives in this study were:

(1) to test the cyclicity of PPM outbreak dynamics with spectral analyses;
(2) to fit autoregressive models to empirical data and estimate return intervals (periods) between consecutive outbreaks;
(3) to assess the synchrony of outbreaks across regions;
(4) to explore the potential role of several factors in the geographical variation of the cyclicity and periodicity of PPM outbreaks.

2. Material and methods

2.1. Construction of time series

In 1981 was set up a network of permanent plots in pine forests specifically dedicated to the monitoring of pine processionary moth damage in France (Abgrall and Bouhot, 1990). The plots were randomly distributed in all regions with the presence of host trees (mainly *Pinus nigra subsp nigra* and *subsp. laricio*, *Pinus sylvestris*, *Pinus pinaster* and *Pinus halepensis*) within the natural range of the insect. The number of permanent plots per region was set to be roughly proportional to the forest area covered by pines. Each plot consisted in an area of 0.25 ha where all trees were observed from the ground. Most of the time plots were sampled within pure pine stands. The following variables were recorded each year at the end of winter, when defoliation and winter nests are more visible: total number of trees, of attacked trees, total number of winter nests per plot, and an estimate of mean defoliation based on categories. In this study we used the percentage of attacked trees per plot as variable to model PPM population dynamics because it was the most accurate. Counts of larval nests or measures of defoliation were not used because detection is particularly difficult on tall trees and in dense stands and estimates are imprecise, especially at low population densities such as at incipient stages of outbreaks (Jactel et al., 2006).

Due to the difficulty to detect larval nests on tall trees, plots that were too old (e.g. older than 40 years) were progressively excluded and replaced by new plots. The same was done with plots damaged by forest fires, windstorms or harvested. New plots were also regularly established to follow the range expansion of PPM (Battisti et al., 2005), notably at higher elevation (in the Massif Central and the Alps) and higher latitude (in Bretagne, Centre and Bourgogne).

We discarded the plots where PPM infestations were never observed (110) and those which were sprayed with insecticide (139). A total number of 1353 plots (11,816 time data) were then used in our study, with an average of 380 "active" plots per year (standard deviation 52 plots) during the 1981–2012 period of time. Due to these reasons, only one individual permanent plots was monitored for 32 years in a row. Most of them (84.5%) had less than 15 years of data (mean = 8.6 years), a too low number to achieve the objective of detecting periods longer than 3 years. Therefore analyzing the raw data set was not an option and a preliminary step was necessary to build up almost complete series of 32 years.

We started with a grouping of plots based on biogeographical attributes using the GRECO (Grandes Régions ECOlogiques) classification developed by the French National Forest Inventory (http://inventaire-forestier.ign.fr/spip/spip.php?article773) which defined large eco-regions with homogeneous soil, climate conditions and vascular plants diversity. We used 8 of these regions of continental France where PPM was present and eventually ended up with 9 regions when we split the south-western one (GRECO F) in two distinct areas, separating the large plantation forest of the Landes (10,000 km^2) from the rest (Aquitaine) to get a more balanced number of plots per region.

Then, within the 9 selected regions, we grouped together neighbouring plots based on agglomerative hierarchical clustering. The geographic distance between plots was used for building clusters of plots and then we applied a *k*-means method in order to readjust loosely classified plots. The number of clusters, *k*, was chosen in order to satisfy a good compromise between two criteria: minimise the average distance within cluster and minimise the percentage of missing data in the time series.

The weighted mean distance for *k* clusters is

$$D(k) = \frac{\sum_{i=1}^{k} d(C_i) \times n_{C_i}}{\sum_{i=1}^{k} n_{C_i}}$$

where C_i denotes the ith cluster, $d(C_i)$ is the average distance within-cluster C_i and n_{C_i} is the number of plots included in cluster C_i, so $\sum_{i=1}^{k} n_{C_i}$ is the total number of studied plots.

The time series corresponding to a given cluster i was obtained by averaging the percent of damaged trees of the plots included in the cluster for a given year t:

$$Z_{i,t} = \frac{1}{n_{i,t}} \sum j \in B(i) \frac{A_{j,t}}{N_{j,t}}$$

where $n_{i,t}$ is the number of plots in cluster i with a non missing data at year t, $B(i)$ the set of plots within cluster i, $A_{j,t}$ the number of PPM attacked trees in plot j at year t and $N_{j,t}$ the total number of sampled trees in plot j at year t. The same method was used to produce a time series for each of the nine regions.

The alternative computation using the numbers of damaged trees in place of their proportions gave very similar results (data not shown) because the number of trees were similar between plots.

A logarithmic transformation has then be used: $X_t = \log(Z_t + 0.01)$, where $\{Z_t,\ t = 1981, \ldots, 2012\}$ is the reconstructed series and X_t is its transformed form which has been analyzed in this study. The term 0.01 in this expression avoids the possibility of log(0). The logarithmic transformation is known as a simple and often effective way to stabilize the variance across time, it reduces the difference between high peaks and low levels. Moreover the logarithmic transformation avoids negative predictions for the proportion.

2.2. Testing the cyclicity of PPM outbreaks

As in Price et al. (2006), spectral analyses were used to explore cyclical patterns of PPM outbreaks. A periodic time series is considered a sum of cosine waves with varying amplitudes and frequencies. In spectral analysis, by applying a Fourier transformation of the variance to the series, a spectral density is obtained which helps to decompose the series into different frequencies present in the cyclic process. The spectral density can be plotted by a periodogram which quantifies the relative importance of the different frequency values that might explain the periodic pattern of observed data. The computational method implies that the frequency identified by the periodogram is an integer. Note that the corresponding period, which is the inverse of the frequency, is most often not an integer but can be seen as an approximation of true integer value (Shumway and Stoffer, 2010).

Because the estimate of the true periodogram had a high variance, it was necessary to smooth it. Here we used the method of Daniel's windows (weighted moving average) with 5-year width (Bloomfield, 2004).

We used the language *R* to make this analysis and the function “spectrum” in the R Package “stats” (R Development Core Team, 2012) to plot the spectrum estimated by a smoothed periodogram and function “periodogram” to generate the periodogram. The periods were identified by visual inspection of the smoothed periodogram, as more than one period may be good candidates (for examples those which were multiple of shorter ones).

Kolmogorov–Smirnov tests were used to test the null hypothesis that series were non periodic (see Brockwell and Davis, 2009). A small *P* value for this test (<0.05) meant that the periodic behaviour of the series was statistically significant. This test did not assess one specific period but the periodic behaviour. The test was applied to time series made at both the cluster and regional scales.

2.3. Modelling the temporal dynamics of PPM

Once we have shown the cyclicity of PPM outbreaks, we developed a statistical model to fit empirical data, based on a sinusoidal pattern.

$$X_t = a\sin\left(\frac{2\pi t}{T}\right) + b\cos\left(\frac{2\pi t}{T}\right) + c + \varepsilon(t) \tag{1}$$

where X_t is the time series, T is the period, a, b and c are constants to estimate and $\varepsilon(t)$ is an autoregressive process of order 1:

$$\varepsilon(t) = \rho\varepsilon(t-1) + \delta(t) \tag{2}$$

The independent random variables had a Gaussian distribution with mean equal to 0 and variance equal to 1. Because the residuals may be correlated, we modelled the correlation with the autoregressive term.

For each time series, different models with different values for T have been estimated and compared. For example, for a complete time series with 32 years, a set of periods $\{T = 2, \ldots, 15\}$ has been used, corresponding to 14 models.

The parameters of model (1) have been estimated using generalized least squares (GLS) estimators (Fox, 2002) and the function gls in the R package nlme (Pinheiro et al., 2007).

The period which corresponds to the best R^2 for the sinusoidal model (1) was retained for each series. R^2 was calculated as the square of the correlation between observed and predicted series.

The significance test for the periodic term was based on the comparison of the deviances of two models: model (1) and model (1) without the sinus and cosinus terms. Under the null hypothesis the difference of deviances was approximately distributed as a χ^2 with two degrees of freedom.

We measured the synchrony between time series of two regions by the proportion of concurrent peaks (local maxima) and troughs (local minima) between pairs of time series. This synchrony measure is called *concurrency* by Gouhier and Guichard (2014). We used the function *peaks* (with randomization of type 2) of the R-package *synchrony* to compute concurrency and associated *P* values.

2.4. Covariates

In order to interpret the significance of periodic patterns and the value of periods we documented a series of explanatory variables at the cluster level. We recorded the number of plots (mean: 10, range: 2–28), the mean longitude (1.8°, −6.2–10.7), latitude (62.9°, 60.1–65.7), elevation (325 m, 4–1493) and area of the clusters (587 km^2, 1–3528).

Then using National Forest Inventory maps derived from aerial photographs we retrieved the percentage cover of pines (18%, 0–92), other conifers (4%, 0–21), broadleaved (25%, 0–76) and open habitats (53%, 6–96) in buffers of 2 km radius around each of the sampled plots and calculated their mean value per cluster (1986–2006 period, http://inventaire-forestier.ign.fr/spip/spip.php?rubrique180).

The relationship between each covariate and the significance of PPM periodicity (based on Kolmogorov Smirnov tests) for the 129 clusters was assessed using two *anova* models. The covariate was the response variable and the factors were the significance of PPM periodicity (significant or not significant) and the regions. The first *anova* model contained only the significance factor which allowed computing the within and across regions relationship between the covariate and the significance status. The second *anova* model contained two factors, significance status and region, which allowed testing the relationship between the covariate and the significance status within regions. The analyses were made with the *R*-package lm.

The effects of covariates on the period length were analyzed using multiple linear regressions. The response variable was the period length and the regressors were the covariates. At this step, no GRECO region effect has been included in the model. A best subset method was used to obtain the best subset with one, two, three and four covariates. The *R*-package *leaps* (http://cran.r-project.org/web/packages/leaps/leaps.pdf) was used for the best subset of covariates procedure and the *R*-Package *lm* for the regressions. Then at a second step, a random effect of GRECO region was added to the simple regression with the best regressor in order to test whether the relationship between the covariate and the period length could be due to a region effect. The *R*-package *lme4* with the option (*REML* = *FALSE*) was used and the likelihood-ratio test of the regression coefficient was done using the *R*-package *anova* for comparing models with and without the covariate.

3. Results

3.1. Test of outbreak periodicity with spectral analyses, at different spatial scales

At the regional scale, spectral analyses showed that PPM outbreaks were significantly periodic in all but one region (the region Centre) *i.e.* in 89% of the studied regions (P values < 0.001 for Kolmogorov–Smirnov tests). The period length varied between 7 and 9 years (Table 1).

Each region was composed of 9–19 clusters of plots (Table 1, Fig. 1). At this spatial scale, on average 70% of the clusters showed a significantly periodic pattern of PPM outbreaks (Table 1, Fig. 1). The mean period length varied between 7 and 11 years (range: 3–15 years).

The cluster area and the number of plots per cluster, which were highly correlated ($r = 0.62$), showed a consistent pattern of significant difference between periodic and non periodic clusters within and across regions ($P = 0.00074$ and 0.00254 respectively) and within regions ($P = 0.000035$ and 0.000166 respectively).

In the nine regions (Fig. 2), clusters showing significantly periodic PPM outbreaks were always of smaller area (mean ± standard error = 476 ± 41 km^2) than the others (840 ± 129 km^2).

Only one explanatory variable was significantly correlated with the period length at the cluster level. In the clusters showing a significantly periodic pattern of PPM dynamics, the length of the period significantly decreased with increasing proportion of pine cover in the landscape surrounding monitoring plots ($n = 89$, $F = 11.8$, $P = 0.00091$, Fig. 3). The test remained significant ($P = 0.0079$) when a random effect of region was included in the model. The best regression with two and three covariates added the mean longitude and altitude of clusters but were no longer significant ($P = 0.071$ and 0.117 respectively).

Table 1
Summary of spectral analyses testing the periodicity of pine processionary moth outbreaks at two spatial resolutions: in the 9 regions and then in the clusters per region. Periods were given in bold when significant ($P < 0.05$).

GRECO region	Number sampled plots	Period of outbreak (years)	Number clusters	Number periodic clusters (%)	Mean (±SE) period of outbreak (years)
Bretagne	109	**7**	13	8 (62%)	11 (±1)
Centre	203	10	19	14 (74%)	10 (±1)
Bourgogne	62	**8**	9	7 (78%)	8 (±1)
Massif Central	166	**9**	16	12 (75%)	10 (±1)
Aquitaine	270	**9**	17	10 (59%)	9 (±1)
Landes	234	**7**	15	12 (80%)	7 (±1)
Pyrénées	81	**7**	11	9 (82%)	11 (±1)
Alpes	97	**8**	10	5 (50%)	8 (±1)
Méditerranée	131	**8**	18	12 (67%)	8 (±1)
Total	1353	8 (89%)	128	89 (70%)	

3.2. Synchrony of PPM outbreaks across regions

The test of synchrony between temporal variation of PPM infestations in the 9 regions showed that the peaks of PPM infestations (*i.e.* outbreaks) were not synchronous at the largest spatial scale (*i.e.* country level, Table 2). However some neighbouring regions exhibited synchronous PPM infestation dynamics: the four central north-western regions (Bretagne, Centre, Massif Central, Bourgogne) had three synchronous PPM outbreaks, the two south eastern regions (Méditerranée and Alpes) had four common peaks of infestation whereas the three south-western regions (Aquitaine, Landes, Pyrénées) showed five synchronous outbreaks (Fig. 4).

3.3. Modelling periodic outbreaks of the pine processionary moth

We fitted the time series of each region by the sinusoidal model with the period length corresponding to the highest R^2 between observed and predicted temporal data. Although PPM dynamics did not show a significantly periodic behaviour in one region (according to the spectral analysis) the periodic term was significant in the model.

In all regions we could successfully fit the temporal pattern of PPM infestation with the sinusoidal model (all P values < 0.01, Fig. 4). However the model could only account for 21–50% of the variance of observed data.

4. Discussion

Based on a large collection of long time series, this study provides the first formal evidence of cyclicity in *T. pityocampa* population dynamics. We showed that in the vast majority of French regions where the insect is present outbreaks occur on a regular temporal pattern with peak defoliations every 7–11 years on average. These values are close to those suggested by Geri and Millier (1985) and Robinet (2006), which varied between 6 and 10 years. Hódar et al. (2012) observed oscillatory patterns in the percentage of pine stands with strong PPM defoliations but they did not test for cyclicity. Tamburini et al. (2013) reported peaks of PPM attacks every 4 to 10 years but did not find regular cycles, maybe because they used the area of attacked forest as a proxy of population density, a less accurate measure than percentage of attacked trees per plot, and they did not apply spectral analysis.

Delayed density-dependent processes are the most often cited drivers of cyclicity in forest defoliator population dynamics (Myers and Cory, 2013) and several are known to affect PPM populations. The first is the mortality induced by natural enemies such as predators (Dwyer et al., 2004; Elkinton et al., 1996), parasitoids (Berryman, 1996; Baltensweiler and Rubli, 1999; Ruohomäki et al., 2000; Turchin et al., 2003) and pathogens (Anderson and May, 1980; Myers, 1993; Liebhold et al., 2013; Elderd et al., 2013). At least 18 parasitoid, 15 predator and 10 pathogen species have been recorded on the different stages of *T. pityocampa* (Battisti et al., 2015). No clear information is available on the density dependence of parasitoids but it is likely to occur since several parasitoid species are highly specialized on PPM and cause large mortality, such as *Baryscapus servadeii* (Hymenoptera, Eulophidae) and *Villa brunea* (Diptera, Bombyliidae) (Battisti et al., 2015). Due to the gregarious behaviour of the larvae, viral diseases are also more often observed in high population density (Battisti et al., 2015). Several

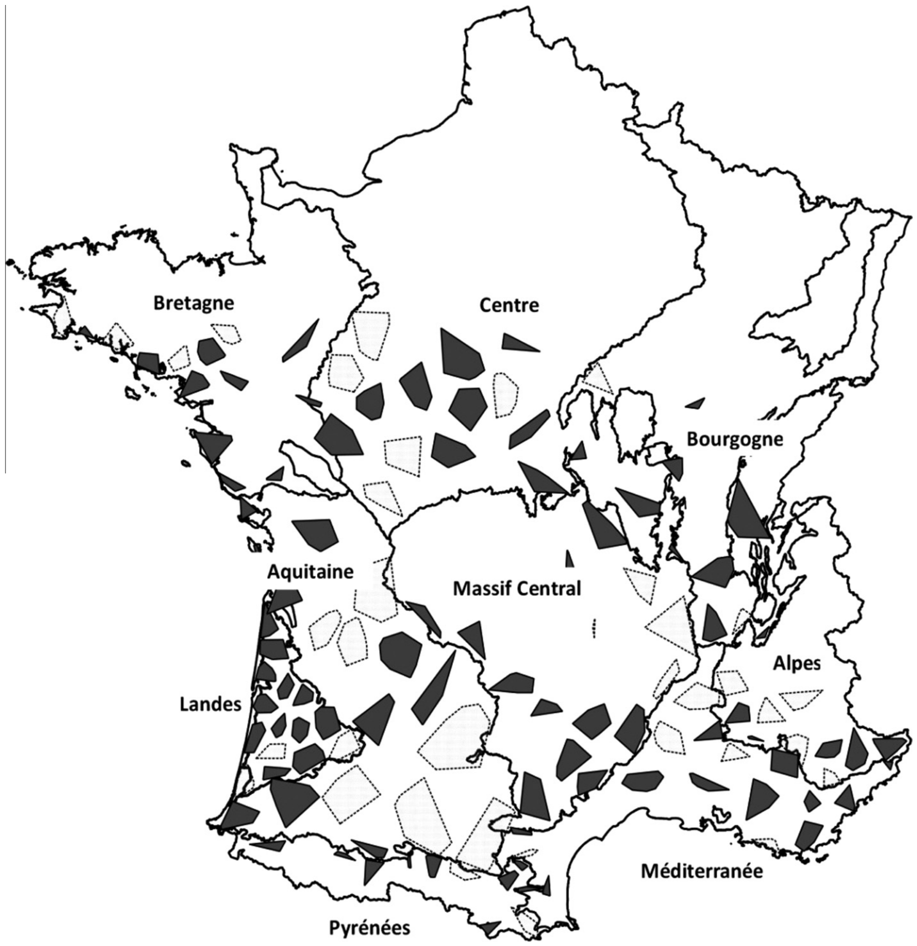

Fig. 1. Clusters of plots for the long term monitoring of the pine processionary moth (PPM) dynamics in the 9 GRECO regions of France. In dark grey are the clusters showing significantly periodic patterns of PPM outbreaks, in light grey are the clusters without periodic patterns.

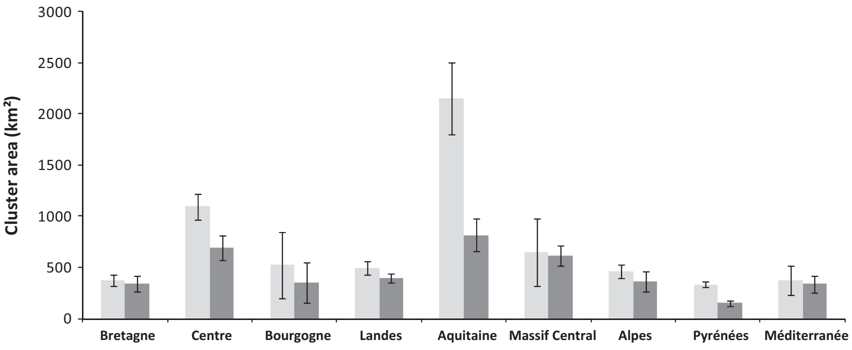

Fig. 2. Mean (±SE) area (km^2) of clusters showing significantly periodic patterns of PPM outbreaks (dark grey) and clusters without periodic patterns (light grey) in the 9 regions.

insectivorous birds are known to specifically prey on *T. pityocampa* (Barbaro and Battisti, 2011) and at least two have been reported to exhibit numerical response to the density of the prey, *i.e.* a density dependent feedback, the Eurasian hoopoe *Upupa epops* (Barbaro et al., 2008) and the great tit *Parus major* (Barbaro et al., 2013). Recently forest bats have been recognized as key predators of PPM and two species, the Kuhl's pipistrelle *Pipistrellus kuhlii* and the serotine *Eptesicus serotinus* have also shown numerical response to *T. pityocampa* density (Charbonnier et al., 2014).

The second main mechanism involved in defoliator cyclicity is the role of induced defenses from the host tree (Baltensweiler and Fischlin, 1988; Nykänen and Koricheva, 2004; Kapeller et al., 2011). Delayed inducible resistance (DIR) has been observed in several tree species where insect defoliations resulted in poor foliage quality for the subsequent moth generations (Haukioja, 1991). This is critical for capital breeders for which resources for reproduction are obtained through feeding as larvae (Myers and Cory, 2013), which is the case of *T. pityocampa*. Ruohomäki et al., 2000 also showed lower egg production capacity in *E. autumnata* fed on defoliated birches and Elderd et al. (2013) demonstrated that induced defense tannins lead to greater sensitivity of *L. dispar* to virus infection. Similarly, Battisti (1988) showed that a complete

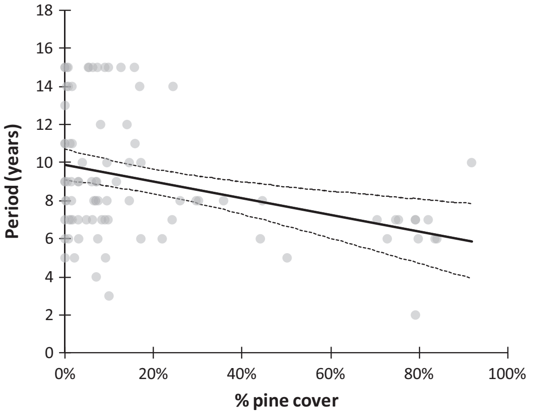

Fig. 3. Relationship between the length of the period of pine processionary moth outbreaks and the percentage cover of pine forests in the landscape surrounding monitoring plots within clusters showing significantly periodic patterns of infestation dynamics.

PPM defoliation resulted in a significant decrease in food quantity (smaller shoot and needle sizes) and quality (lower nitrogen content) in the following two years which could explain higher subsequent mortality of larvae. Later Hódar et al. (2004) also observed higher larval mortality on defoliated pine trees. According to the delayed density dependence theory, the time lag between change in population density and feedback from adverse density-dependent processes would equal a quarter of the cycle period (Klemola et al., 2014). This suggests a 2- to 3-year feedback delay for the pine processionary moth. Measuring the effect of PPM defoliations on the physiology of pine trees, Jacquet et al. (2013) found that defoliated trees needed at least three years to resume normal functioning which is consistent with Battisti’s (1988) observations. An additional mechanism compatible with this timeframe is the prolonged diapause of *T. pityocampa* pupae which can last 1–4 years (Roques, 2015). This process has been interpreted as a way to escape in time adverse life conditions, here a lack of feeding resources following intense defoliation (Tamburini et al., 2013). However the effects of population density on the frequency and duration of prolonged diapause have not been studied yet in *T. pityocampa*.

As pointed out by Myers and Cory (2013) a high fecundity is required in cyclic species to allow fast population growth in order to recover after the end of the decline. *T. pityocampa* has several biological attributes which can help to quickly build up populations: a sex pheromone is released by female moths to improve mating success, they can lay about ca. 150–350 eggs in egg masses. These are covered with scales from female wings offering a protection again parasitoids. Larvae are gregarious, living in large colonies within silky nests offering a protection against adverse climatic conditions. In addition caterpillars are mainly active by night and covered with urticating setae, which represent passive and active defenses against natural enemies (Battisti et al., 2015).

Although cyclicity appears like a common pattern in PPM population dynamics we detected some variability in both the occurrence of cyclic outbreaks and the length of cyclic periods. Only one region (Centre) did not show significant cyclicity. This region corresponds to the expansion area of *T. pityocampa* (Robinet et al., 2007) where driving factors of population dynamics can be different than those operating in the core area. For example the natural enemies of the pine processionary moth may have not yet followed their prey in the new colonized range (Auger-Rozenberg et al., 2015). The spectral analysis also failed to detect regular cycles in about 30% of the clusters of plots. These particular clusters with irregular dynamics were of larger area than those showing cyclic patterns, whereas no other characteristics could explain the differences. We can hypothesize that plots being more distant from each other in these clusters, they were in more different environmental conditions, leading to greater heterogeneity within cluster, thus eventually preventing coherent fluctuations among PPM populations.

The mean length of the period was also variable between clusters and regions, varying from 7 to 11 years. Interestingly the period length was significantly shorter in clusters with higher land cover with pines, the host species of *T. pityocampa*. In a study on the forest tent caterpillar Cooke et al. (2012) also found variation in the cyclic pattern of disparate populations and suggested that populations inhabiting more complex landscapes are less likely to be synchronized due to barriers to dispersal. We can also assume that PPM populations living in forest landscapes with a more continuous pine cover are more able to exchange individuals, either favouring contagion by diseases during the decline phase or mating during the recovering phase, leading to an overall acceleration of the cycles.

The PPM outbreaks are not synchronous across the entire country, which is consistent with the variability in period length across regions. This also means that external periodic drivers operating a very large scale such as sun spots (Nilssen et al., 2007) or North Atlantic Oscillation (Hódar et al., 2012) cannot be involved in PPM outbreaks cyclicity. However we found significant synchrony among regions and those regions which showed synchronous PPM population dynamics were contiguous to each other. Three main groups of regions with similar temporal PPM dynamics could be defined, corresponding to the southeast, southwest and central west part of the country. Spatial synchrony of forest defoliator outbreaks is expected to result from three main processes: exchange of individuals through repeated dispersal events, dispersal of their natural enemies or the influence of common environmental factors that also exhibit spatially synchronous fluctuations, i.e. the “Moran effect” (Liebhold et al., 2004; Hajek et al., 2014). It is unlikely that PPM populations can exchange a lot of individuals across such a large geographical extent (i.e. several hundreds of km) since the flight capacity of female moths is quite low. They can fly on average 5 km on flight mills (Robinet et al., 2012) which is consistent with the annual range expansion of the species (Battisti et al., 2005). Similarly predators and parasitoids are probably not able or inclined to disperse across entire regions.

Table 2
Proportion of synchronous peaks of observed pine processionary infestations (outbreaks) between pairs of regions (in bold, P values < 0.05).

	Centre	Bourgogne	Massif central	Aquitaine	Landes	Pyrénées	Alpes	Méditerranée
Bretagne	**0.50**	0.29	0.16	0.38	0.29	0.31	0.21	0.25
Centre		**0.64**	**0.47**	0.25	0.36	0.25	0.36	**0.50**
Bourgogne			**0.58**	**0.44**	**0.43**	**0.44**	0.43	**0.43**
Massif central				0.26	0.32	0.42	0.32	0.37
Aquitaine					**0.63**	**0.63**	0.31	0.31
Landes						**0.50**	0.36	**0.43**
Pyrénées							**0.44**	**0.44**
Alpes								**0.71**

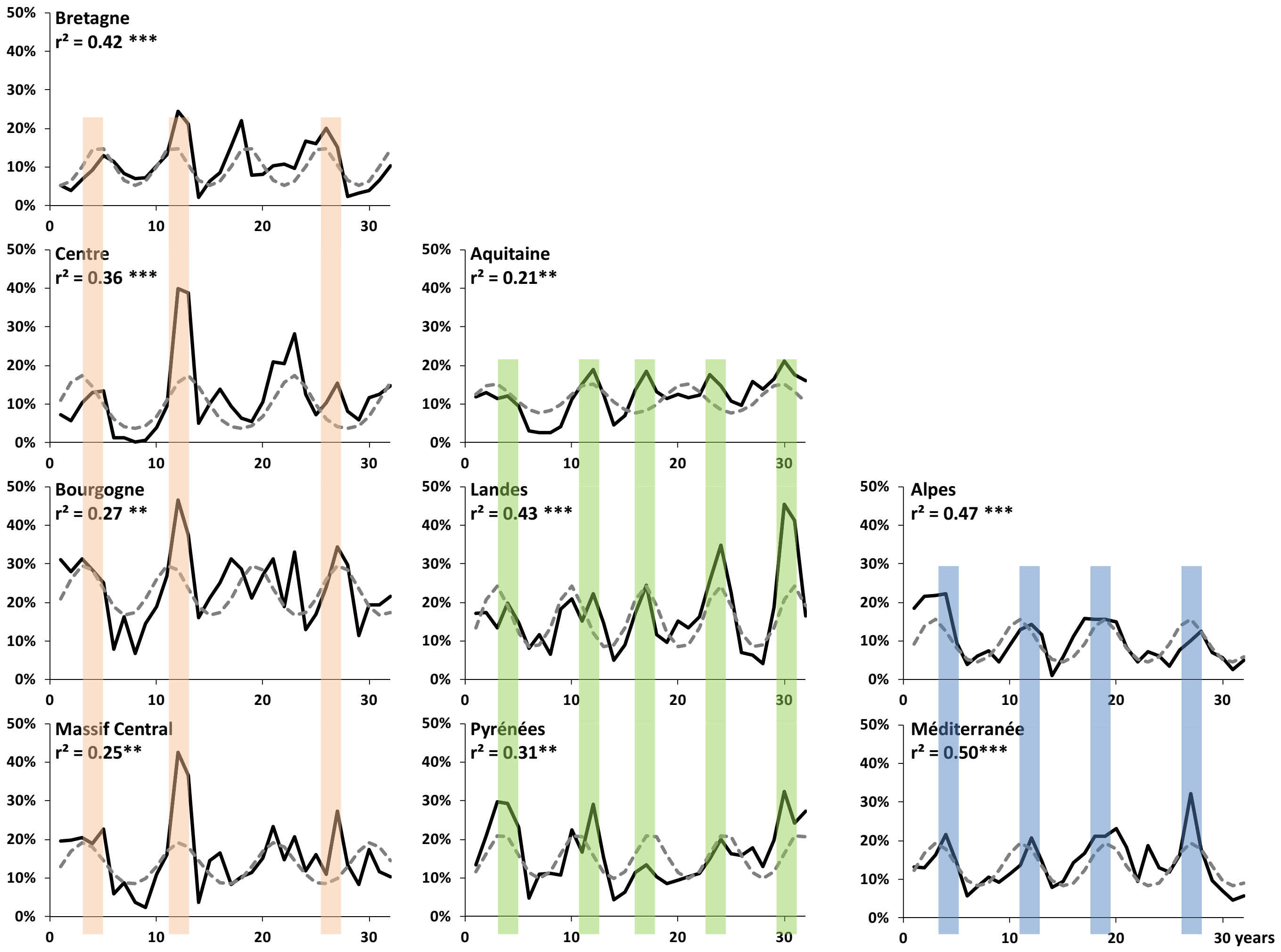

Fig. 4. Observed (black lines) and predicted (grey dashed lines) temporal patterns of pine processionary moth infestations in the 9 regions. The *x*-axis represents time (number of years) and the *y*-axis the mean percent of infested trees by cluster per year. Coloured strips were manually added to better show synchronous outbreaks among neighbouring regions. R^2 values indicate the sinusoidal model fit (***$P < 0.001$, **$P < 0.01$).

The most likely factors of synchronization over large distances that are observed with many forest defoliators are then the spatially correlated climatic factors, such as temperature (Peltonen et al., 2002) or precipitation (Haynes et al., 2013). *T. pityocampa* is well known to be particularly sensitive to temperature (Battisti et al., 2005; Buffo et al., 2007). Caterpillars are active in winter and they resist low temperatures by building a silky nest where they gather during the day. It has been shown that bigger nests accommodating larger colonies provide a better protection against low winter temperatures (Pérez-Contreras et al., 2003). Very low temperatures, which are lethal to PPM caterpillars at −16 °C, but also moderately low temperatures, which control feeding activities of larvae and thus their survival (Battisti et al., 2005), could be the main drivers of synchronous periodic outbreaks because they can occur simultaneously within neighbouring regions and their effect is density-dependent. However this "Moran effect" remains to be demonstrated with proper covariance analyses of weather data and spatial range of synchrony in *T. pityocampa* outbreaks (Peltonen et al., 2002).

It was possible to correctly fit the periodic fluctuations of mean PPM infestations in all nine regions using a sinusoidal model, which confirms the regularity of PPM dynamics. The estimated period was of ca. 8 years suggesting that the density-dependent factor inducing a decline in PPM populations and those allowing a recovery should occur over 3 to 4 years, which points out into the direction of slow processes such as the diapause of the PPM or the population dynamics of it predators.

As shown by Fig. 4, whereas the sinusoidal models fit well the frequency of PPM outbreaks, they can produce large departure from observed amplitudes of PPM infestation, particularly during the highest peak of outbreak. This may explain why overall the sinusoidal models could only account for less than 50% of variance of PPM infestation. Because the magnitude of peak infestation appears to be more irregular than their frequency, a common feature in cyclically fluctuating forest insect, one might guess that other stochastic events, such as particular favourable weather conditions, could trigger higher infestation levels than predicted by the model. Here again, further investigations are needed to test this hypothesis.

Demonstrating the general cyclicity of *T. pityocampa* outbreaks and predicting the rhythm of fluctuations (i.e. period length) in large eco-regions of France is already a progress for forest managers because it will help to improve the surveillance and control of pest populations, focusing the means and tools on more exposed areas every given years.

However two main issues have to be addressed in order to develop a useful predictive model. The first is to better define the area (i.e. optimal size of plots cluster) at which PPM populations develop synchronous dynamics so as to be more accurate in the spatial resolution of the prediction. A combination of remote sensing information on PPM abundance at large scales (Bories et al., 2012) with estimates of spatial autocorrelation (Gilioli et al., 2013), could help to define this grain, *i.e.* the size of the smallest homogeneous landscape unit at which the predictive model should be developed. The second is to identify critical climate or weather drivers of survival rates of PPM, particularly just before and just after outbreak peaks, in order to better model the amplitude of infestations. In particular one could use lag-correlations between sinusoidal model deviances and mean monthly precipitations or temperatures observed in previous years, given that soil humidity is known to impact PPM pupae survival and diapause (Dulaurent et al., 2011) while temperatures affect both larvae survival and feeding activity (Robinet et al., 2007).

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