



Periodicity and synchrony of pine processionary moth outbreaks in France



S. Li ^{a,b}, J.J. Daudin ^{c,d}, D. Piou ^e, C. Robinet ^f, H. Jactel ^{g,h,*}

^a Université de Bordeaux, ISVV, UMR1065 Santé et Agroécologie du Vignoble, Bordeaux Sciences Agro, F-33175 Gradignan, France

^b INRA, ISVV, UMR1065, F-33140 Villenave d Ornon, France

^c INRA, UMR 518 MIA, Paris, France

^d AgroParisTech, UMR 518 MIA, Paris, France

^e Ministère de l'Agriculture, de l'Agroalimentaire et de la Forêt, DGAL-SDQPV, Département de la Santé des Forêts, 252 rue de Vaugirard, F-75732 Paris, France

^f INRA, UR633 URZF, F-45075 Orléans, France

^g INRA, UMR1202 BIOGECO, F-33610 Cestas, France

^h Univ. Bordeaux, BIOGECO, UMR 1202, F-33600 Pessac, 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 cyclicality 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 cyclicality of *T. pityocampa* outbreaks while the Moran effect, here the role of low temperatures, is likely to explain synchrony.

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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).

* Corresponding author at: INRA, UMR1202 BIOGECO, F-33610 Cestas, France.

E-mail address: herve.jactel@pierroton.inra.fr (H. Jactel).

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 km²) 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

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