

Does landscape composition alter the spatiotemporal distribution of the pine processionary moth in a pine plantation forest?

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Abstract Landscape composition and physiognomy affect community structure and species distribution across space and time. The pine processionary moth (PPM) (*Thaumetopoea pityocampa* Den. & Schiff., Lepidoptera, Notodontidae) is a common pine defoliator throughout southern Europe and Mediterranean countries. We surveyed the spatiotemporal distribution of the PPM in a pine plantation forest in southwestern France and used the density of the winter nests as a proxy for population density. The study spanned 4 years (2005–2008) and showed a high temporal variability in nest density. We found a strong edge effect with nest densities at stand edges more than twice as large as within-stand densities. At the landscape scale, the spatial distribution of the moth exhibited a significant spatial autocorrelation in 3 out of 4 years of our study. The spatial scales of the autocorrelation ranged from ca. 2 km to more than 22 km. We found a positive correlation between spatial distributions corresponding to certain sampling years,

but the relationship was not systematic. Landscape configuration appeared to be an important driver of the PPM spatial pattern. Bivariate Moran's *I* correlograms showed that patch richness density as well as the percentage of local landscape covered by various land uses were correlated with population density. The study showed that accounting for landscape characteristics may be important in order to understand forest insect pest distribution, even in cases where the host species is abundant and homogeneously distributed throughout the study area, e.g., pure plantation forests.

Keywords Forest insect · Landscape composition · Pine plantation forest · Pine processionary moth · Spatial distribution · *Thaumetopoea pityocampa*

Introduction

Landscape composition and physiognomy affect community structure, species richness, and distribution (Tscharntke et al. 2005; Ritchie et al. 2009). The effects of landscape configuration encompass a variety of processes, including dispersal, source–sink dynamics, neighborhood effects, and metapopulation dynamics (Dunning et al. 1992). Likewise, population dynamics are largely dependent on the spatial arrangement of habitat patches, the interaction between landscape structure and individual behavior (Goodwin and Fahrig 2002), and indirect effects of landscape via the distribution and dynamics of natural enemies (Kruess and Tscharntke 1994; Cappuccino et al. 1998). Many forest insects display complex dynamics with outbreaks (Berryman 1996) and sometimes spatial synchrony (Liebhold and Kamata 2000). Various factors interplay, such as specialist and generalist natural enemies (Bjørnstad and Bascompte

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2001; Klemola et al. 2002; Dwyer et al. 2004), landscape structure (Johnson et al. 2006, 2004), and interaction between these factors (Bjørnstad et al. 2002). One consequence of such a system is that forest insects often exhibit complex spatial distributions with a substantial amount of temporal variability (Liebhold et al. 1993).

The subject species, the pine processionary moth (PPM) (*Thaumetopoea pityocampa* Den. & Schiff., Lepidoptera, Notodontidae), is a common pine defoliator occurring on various pine species throughout southern Europe and Mediterranean countries, where it is the most important pine defoliator. PPM distribution range is controlled by the minimum winter temperatures (Battisti et al. 2005). Recent studies revealed that PPM distribution is expanding both in altitude (Battisti et al. 2006) and latitude (north), probably in relation to climate changes (Battisti et al. 2005; Robinet et al. 2007). The PPM is also a pest of public concern because of the larvae urticating hairs that cause severe allergic reactions in people and animals (Vega et al. 2004). Population dynamics of PPM is characterized by outbreaks of irregular frequency. It is a serious pest in the Massif des Landes de Gascogne, the largest monospecific plantation forest in Europe, with 1 million ha of maritime pines (*Pinus pinaster*, Aiton 1789). This plantation forest constitutes a somewhat simplified ecosystem where the host species strongly dominates and is rather homogeneously distributed throughout the region. The spatial heterogeneity of this landscape is therefore low, at least when considered from the insect viewpoint. Habitat is neither rare nor fragmented with regard to PPM dispersion ability, and this raises the question of whether or not landscape affects PPM spatial dynamics (Turner et al. 2001). PPM colonies may also display local spatial variability due to edge effects, as has been reported for other forest insects (e.g., bark beetles; see Peltonen 1999). Edge effects may be related to host finding by female moths or other factors and are poorly documented in the literature.

The aim of this study was to assess the relationships linking PPM distribution and landscape composition at spatial scales ranging between 2 and 16 km. There are many processes by which landscape may drive (at least partly) PPM spatial pattern, among which the role of predators, parasites, and/or pathogens that may be favored in some landscape configuration or by some type of land use, as well as more or less subtle impacts upon the male or female dispersal across space. Specifically, we addressed the questions of whether the spatial pattern of the PPM was spatially autocorrelated, to which extent the structure was repeated through time, and whether some relationships with the forest landscape could be identified and at what spatial scale(s). Additionally, we designed a sampling procedure to test the presence of an edge effect upon PPM spatial distribution.

Materials and methods

Background biology

Information given below corresponds to populations inhabiting southwestern Europe. Although governed by climatic conditions, moth emergence from soil generally occurs between mid June and mid August. Soon after emergence, adults mate and females select a host tree and lay one egg batch on the pine needles. Hatching occurs from August to September. Larvae are gregarious, feed on pine needles, and build a silk nest in which they develop until next spring [Fig. S1 in Electronic Supplementary Material (ESM)]. Colonies generally remain in the same host tree. Depending on weather conditions, the later instar occurs in February or March, and larvae migrate into soil where they pupate until emergence in the following summer (Démolin 1969; Géri et al. 1985). Nests inhabited by larvae are white and easy to count (Fig. S1 in ESM). Larvae maintain their nest, which quickly deteriorates after their migration into soil. Ageing, empty nests quickly turn brownish.

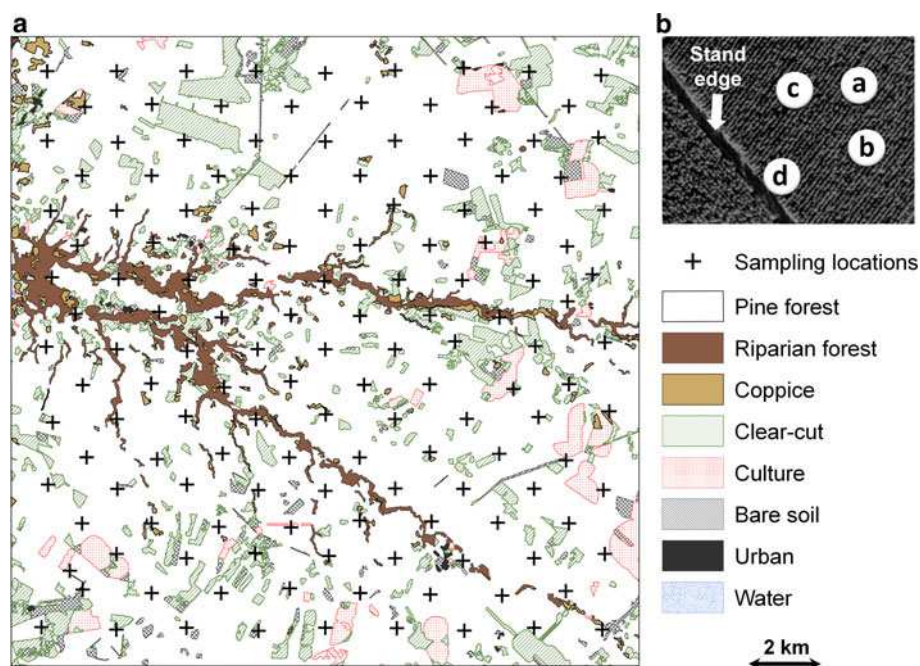
Study site and sampling procedure

We studied the dynamics of PPM in a pure maritime pine plantation forest (*P. pinaster*) in southwestern France (Fig. 1a). We estimated the average winter nest density in 145 sampling locations scattered on a 16×16 km area (sampling window = 25600 ha) with a grid size of $\sqrt{2} \approx 1.4$ km (Fig. 1a). An initial sampling grid was designed, and some sampling locations had to be slightly displaced when they were located on an area where the vegetation consisted of nonhost species.

We defined four subsamples (SS) at each sampling location, referred to as *a*, *b*, *c* and *d* hereafter (Fig. 1b). Three SSs (*a*, *b*, and *c* in Fig. 1b) were separated by a distance of 25 m and consisted of a group of 20 pine trees. We investigated possible differences in nest densities at the stand edges by setting up a fourth, complimentary, SS (*d* in Fig. 1b) on the closest stand edge and separated from other SSs by a distance ≤ 200 m.

Overall, $4 \times 20 = 80$ trees were sampled at each sampling location. The number of winter nests was recorded visually for each tree. Because the mean tree density and tree size changed markedly from one location to another as a result of different stand age, we estimated the average tree density and expressed the density of winter nests as the number of nests per hectare. Tree density of each stand was estimated on the basis of the relascope estimates within each subsample. We additionally expressed PPM densities as the number of colonies per tree, but we believe that this unit is not adapted

Fig. 1 Sampling site and protocol. **a** Satellite-based map of the study site. The study site consists of a maritime pine forest (*Pinus pinaster*) with a central elongated riparian forest patch. Sampling localities are distributed along a regular grid and are represented by black crosses centered on small red dots. **b** Subsamples. The number of pine processionary moth (PPM) (*Thaumetopoea pityocampa*) winter nests was assessed in three subsamples located within pine stands (*a*, *b*, *c*) and one additional subsample located at the stand edge (*d*)



to the context of our plantation forest where stands are pure and comprise trees of similar age class. Host-tree density is highly correlated with age and hence to tree density, and this may lead to overestimating the PPM density in plots planted with old (large) pines where tree density is low as a consequence of their age (size). All statistical analyses were performed using both units of measurement and yielded similar conclusions.

PPM nest density was monitored every year from 2005 to 2008. In 2005, we sampled the 145 locations shown in Fig. 1a. The sample intensity was decreased in 2006 and the following years but the surveyed area remained unchanged. As a consequence, the mesh size of the sampling grid was extended to 2 km in 2006. The number of sampled points is given in Table 1 and ranged from 145 to 78 according to the sampling year. Some plots were logged during the course of the study, and we had to replace them by new plots that were chosen as close as possible to the initial locations. The number of sampling plots common to the 4 years of our study was 78. Plots represented different age classes, excluding young pine plantations (≤ 4 years) where PPM populations are generally low (Piou, personal observation).

Landscape mapping

Landscape description was based on a high-resolution and multispectral satellite image (SPOT 5 XS, 10 m) covering the study area (© CNES, distribution Spot Image SA, 13 July 2005). Land cover of the study site was categorized into eight main land uses by supervised classification

(Fig. 1a; urban areas, water, pine plantations, riparian forest (RF), cultures, coppices, clear cuts, and bare soil).

Data analysis

Landscape analysis

Landscape around each sampling point was described using a circular area of radius = 1000 m, hereafter referred to as buffers. Rossi and van Halder (2010) recently showed the importance of buffer size upon our perception of landscape features (hence on the ability to identify landscape–species relationships) in a study of butterfly species richness. For this reason, we tested three buffer sizes (radius = 250, 500, and 1000 m), which led to very similar results. As a consequence, we only report the results of the spatial analyses for a single buffer size (radius = 1000 m). We used different landscape metrics (Table 2) to describe the “local” landscape corresponding to the buffers. The mean proportion of landscape covered by water and urban development was, respectively, 0 and 0.16% of the buffer area, and therefore, these classes were ignored.

The six remaining land-use classes were described using the proportion of the landscape they occupied within the buffers [the corresponding landscape metric is referred to as PLAND (proportion of landscape) sensu McGarigal et al. (2002)]. In addition, we computed a metric that reflected the landscape diversity, the patch richness density (PRD), which expresses the density of patches corresponding to different landscape classes. Computations were done using the software Fragstats (McGarigal et al. 2002).

Spatial statistics

We investigated the presence of spatial autocorrelation by means of the Moran's I (1950) spatial autocorrelation statistic; I is computed for different distance classes d as:

Table 1 Descriptive statistics for the winter nest density (nest · ha⁻¹) of the pine processionary moth (PPM) *Thaumetopoea pityocampa* in a 25600 ha study area in southwestern France on four consecutive sampling occasions (2005–2008)

Year	Mean	SD	Minimum	Maximum	Sampling points (n)
2005					
<i>a</i>	70	98.6	0	526.1	145
<i>b</i>	77.5	103.8	0	601.3	145
<i>c</i>	79.6	103.4	0	569.6	145
<i>d</i>	199	232.2	0	1172.7	145
<i>a–d</i>	106.5	112.4	0	573.8	145
2006					
<i>a</i>	9.2	23.2	0	126.7	80
<i>b</i>	11.8	20.4	0	70.7	80
<i>c</i>	9.9	21.1	0	99.9	80
<i>d</i>	24.8	37.2	0	133.8	80
<i>a–d</i>	13.9	17.3	0	66.9	80
2007					
<i>a</i>	4.4	14.6	0	82.5	78
<i>b</i>	6.6	18.1	0	99.2	78
<i>c</i>	5.5	16.9	0	99.2	78
<i>d</i>	13	33.3	0	177.1	78
<i>a–d</i>	7.4	15.8	0	89.7	78
2008					
<i>a</i>	14.8	33.6	0	198.3	78
<i>b</i>	15.5	38.9	0	187.2	78
<i>c</i>	17.1	52.6	0	361.1	78
<i>d</i>	48.3	88.8	0	423.1	78
<i>a–d</i>	23.9	43.7	0	231.4	78

Four subsamples (*a*, *b*, *c*, and *d*) were surveyed at each sampling point. *a*, *b*, and *c* were located inside the stand, whereas *d* was located near the stand edge. *a–d* indicates the mean value for the four subsamples. *SD* standard deviation

Table 2 Descriptive statistics for two landscape metrics computed for various land-use types within circular areas (buffers) centered on the sampling points ($n = 145$)

	PRD	PLAND					
		Pine (%)	Clear-cut (%)	Riparian forest (%)	Culture (%)	Bare soil (%)	Coppice (%)
Mean	1.42	79.98	8.97	4.04	3.18	2.10	1.50
SD	0.37	13.93	8.73	8.52	6.65	3.09	2.17
Minimum	0.64	30.47	0	0	0	0	0
Maximum	2.23	99.42	54.35	55.10	31.91	19.40	12.12

PRD patch richness density, *PLAND* proportion of landscape (see McGarigal et al. 2002, for a complete description of each metric), *SD* standard deviation

$$I(d) = \frac{\frac{1}{W} \sum_{h=1}^n \sum_{i=1}^n w_{hi} (y_h - \bar{y})(y_i - \bar{y})}{\frac{1}{n} \sum_{i=1}^n (y_i - \bar{y})^2} \quad \text{for } h \neq i$$

where y_h and y_i are the values of the observed variable at sites h and i , d is the distance class, and w_{hi} is the Kronecker weight. A pair of observations h and i takes the value $w_{hi} = 1$ if it belongs to the distance class d and $w_{hi} = 0$ otherwise. In this way, only the pairs of sites (h , i) within the distance class d were taken into account in the calculation of $I(d)$. W is the sum of the w_{hi} for a given distance class d . Moran's I is usually comprised in the interval $[-1, +1]$, and positive (negative) autocorrelation leads to positive (negative) values of I (Legendre and Legendre 1998). The significance of each individual value of $I(d)$ was tested using a randomization test based on 2000 randomizations (Fortin and Dale 2005, p. 126). However, testing the overall significance of the correlogram is more difficult because $I(d)$ values lack statistical independence and multiple testing is necessary (Legendre and Legendre 1998). We used Holm's corrected probability level, which is fully described in Legendre and Legendre (1998, p. 18, 721).

The presence of a general spatial structure of landscape composition was assessed by means of the Mantel correlogram (Oden and Sokal 1986; Fortin and Dale 2005). The sampling points were described by means of a multivariate distance derived from the landscape metrics. The geographical distance matrix that contains the distance separating the sampling points was then altered as follows: for each distance class d , points separated by a distance that belongs to d were linked by 1s and 0 otherwise, and the Mantel statistic was computed. The plot of the resulting set of Mantel statistics against d is referred to as the Mantel correlogram. The significance of each coefficient was tested using a Monte Carlo method (2000 permutations), whereas the global significance was assessed using the Holm's correction, as described above. The spatial relationships between PPM winter nest density estimated at different dates and various landscape continuous descriptors were assessed using a modified Moran's I statistic (Fortin and Dale 2005).

$$I_{xy}(d) = \frac{\frac{1}{W} \sum_{h=1}^n \sum_{i=1}^n w_{hi}(x_h - \bar{x})(y_i - \bar{y})}{\left(\frac{1}{n} \sqrt{\sum_{h=1}^n (x_h - \bar{x})^2} \right) \left(\frac{1}{n} \sqrt{\sum_{h=1}^n (y_h - \bar{y})^2} \right)}$$

for $h \neq i$

where x_h , y_h , x_i , and y_i are the values of the observed variables x and y at sites h and i , d is the distance class, and w_{hi} is the Kronecker weight. Two distance increments were used for correlogram computation. An increment of 1000 m was used for analysis of the landscape–PPM relationships based on the 2005 data set. The reduced number of sampling points ($n = 78$) in 2006–2008 led to a higher minimum intersample distance, and a larger distance increment of 2000 m was therefore used in correlogram computation. We also computed the correlogram for the 2005 data set with the simplified sampling scheme used in 2006–2008. Both correlograms were similar, thus indicating that the sampling scheme used in the 2006–2008 period captured similar spatial patterns. All correlograms were interpreted for distances ≤ 15000 m. The uni- and bivariate Moran's I and Mantel correlograms were computed using the software R (R Development Core Team 2008) and the associated package *ncf* written by Bjørnstad (2009).

Results

We report results obtained using data expressed as number of nests per hectare.

PPM density

PPM nest density changed markedly during the course of the study. It was highest in 2005, sharply decreased in 2006 and 2007, and increased in 2008 (Table 1). This pattern corresponded to the outbreak dynamics of the species, which was recorded throughout southwestern France (Pauly 2007). The different SSs yielded very contrasted density estimates (Table 1). The nest density at the stand edges (SS d) was roughly twice that observed within the stands (SSs a , b , and c) (Table 1).

PPM spatial autocorrelation

PPM nest density spatial distribution exhibited a significant autocorrelation in 2005, 2006, and 2008 but not in 2007, when the average density was at its lowest level (Table 3 diagonal; Fig. 2). Moran's I correlograms for PPM density between 2005 and 2008 are shown in Fig. 3a. The first autocorrelation coefficient was negative in 2005 and 2008, which reflected the existence of an important local variability, i.e., variance between closest sampling points. This

Table 3 Significance of the uni- and bivariate Moran's I correlograms of pine processionary moth (PPM) density (nest \cdot ha $^{-1}$) between 2005 and 2008

	2005	2006	2007	2008
2005	<i>0.047</i>	0.319	0.095	<i>0.015</i>
2006	–	<i>0.003</i>	0.083	<i>0.019</i>
2007	–	–	0.099	<i>0.003</i>
2008	–	–	–	<i>0.003</i>

Probability thresholds derived from Holm's probability adjustment procedure (see “Material and methods” for details). Values ≤ 0.05 are deemed significant (in italic). On diagonal univariate Moran's I . Above diagonal bivariate Moran's I

short-range variability sharply decreased in 2006, as indicated by a positive and somewhat high value of Moran's I coefficient. This may be due to very low levels of PPM density recorded that year.

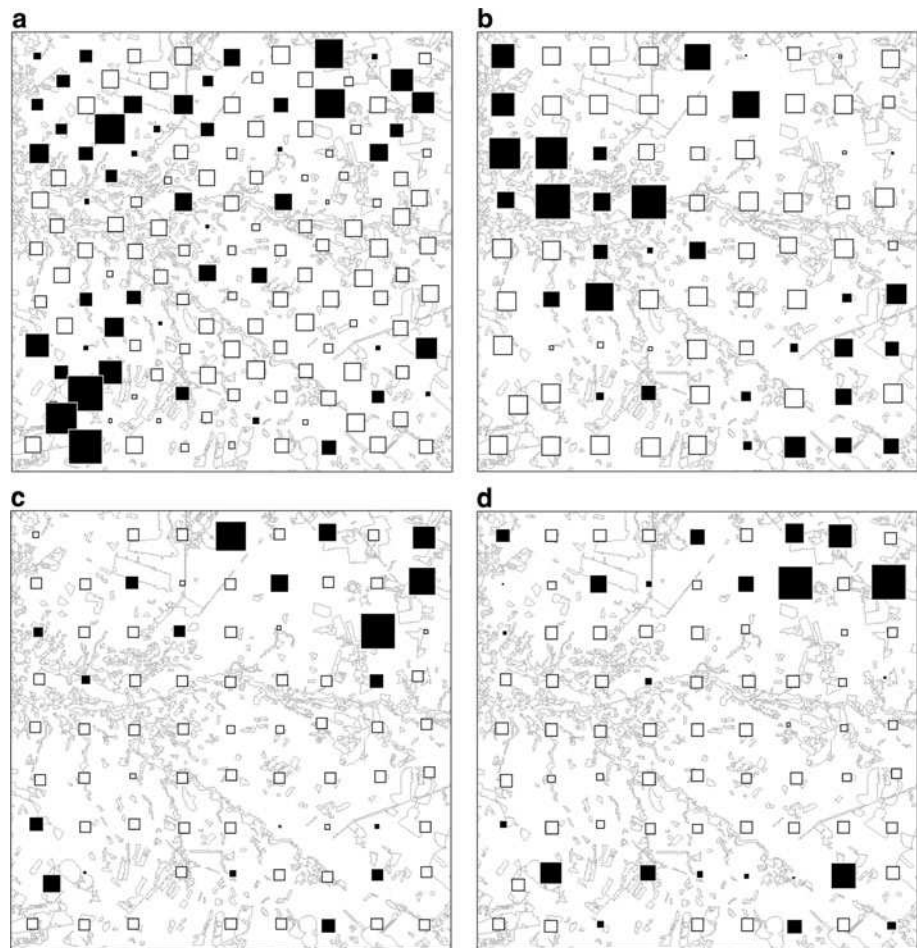
Temporal variability of PPM spatial distribution

Bivariate Moran's I of the PPM nest density, computed on the basis of the sampling points that were common to all dates, revealed a lack of correlation between the patterns observed in 2005, 2006, and 2007 (Table 3, above diagonal). On the contrary, a significant and positive relationship was observed between 2005 and 2008 samples.

Relationships between PPM nest density in 2005 and landscape features

The landscape was dominated by pine plantations with scattered patches of culture or clear cuts and featured a long central RF (comprising deciduous tree species and mostly *Quercus spp.* and *Alnus glutinosa*). The average landscape composition of 1000 m circular buffers centered on each sampling location is given in Table 2. The landscape descriptors (i.e., metrics) computed for these buffers exhibited a clear spatial pattern as expressed by the Mantel correlogram (Fig. 3b), which was significant ($P < 0.05$, Holm's correction). This indicated that buffers of 1000 m provided a sensible assessment of the landscape characteristics and also rendered its large-scale spatial variability. Landscape was surveyed only in 2005, and therefore, its relationships with the PPM distribution could only be investigated for that year. The bivariate correlograms between PPM density and landscape metrics were significant in all cases but for clear cuts ($P \geq 0.05$, Holm's correction), thus reflecting the correlation between the insect spatial distribution and landscape characteristics. However, correlograms yielded contrasting results according to the spatial scale considered. A negative relationship between PPM nest density and the RF percentage

Fig. 2 Maps of the pine processionary moth (PPM) winter nest density in **a** 2005, **b** 2006, **c** 2007, and **d** 2008. Data are centered, and the size of the symbols is proportional to the observed values. *Black squares* positive-centered values (corresponding to original values > mean). *White squares* negative-centered values (corresponding to original values < mean)



of landscape cover was observed for distances ≤ 4000 m (Fig. 3c). Similar relationships were observed with the percentage of landscape covered by coppices as well as with the PRD. Interestingly, a positive relationship between the percentage of land covered by culture and PPM nest density emerged for distances ≤ 4000 m (Fig. 3c). The relationships between PPM and landscape metrics [e.g., PLAND RF and coppices) changed with the distance lags considered. For example, it was positive for PLAND RF and coppices at scales of ≥ 5000 m. These features mostly reflected the position and sizes of both landscape and population patches with regard to sampling window limits.

Discussion

Population spatial variability

Stand edge effect

As with many insects, *T. pityocampa* displayed a spatially aggregated distribution, and this appeared to be the case at

different spatial scales (Taylor 1984). The density was always higher at the stand edges (subsample *d*), and this was true every year of the study. This intrastand variability might be linked to the mechanisms implied in host selection by moth females for egg laying. It has been shown that the tree outline is an important factor that drives female choice for oviposition, with more visible trees being more easily spotted and used as a resource (Démolin 1969). This may be the reason for larger nest densities being observed in the edge subsamples (*d*). In addition, climatic conditions along edges (e.g., temperature and sunshine) may also be more favorable compared with within-stand conditions. Interestingly, Einhorn et al. (1983) reported a higher number of PPM males (captured in pheromone-baited traps) at edges of pine stands.

Large-scale spatial distribution and temporal variation

A strong variability was also apparent when comparing the density of winter nests between neighboring sampling locations at scales < 2000 m (i.e., the smallest distance lag of the correlograms in Fig. 3a). Various sources of heterogeneity could be invoked to explain such discrepancies.

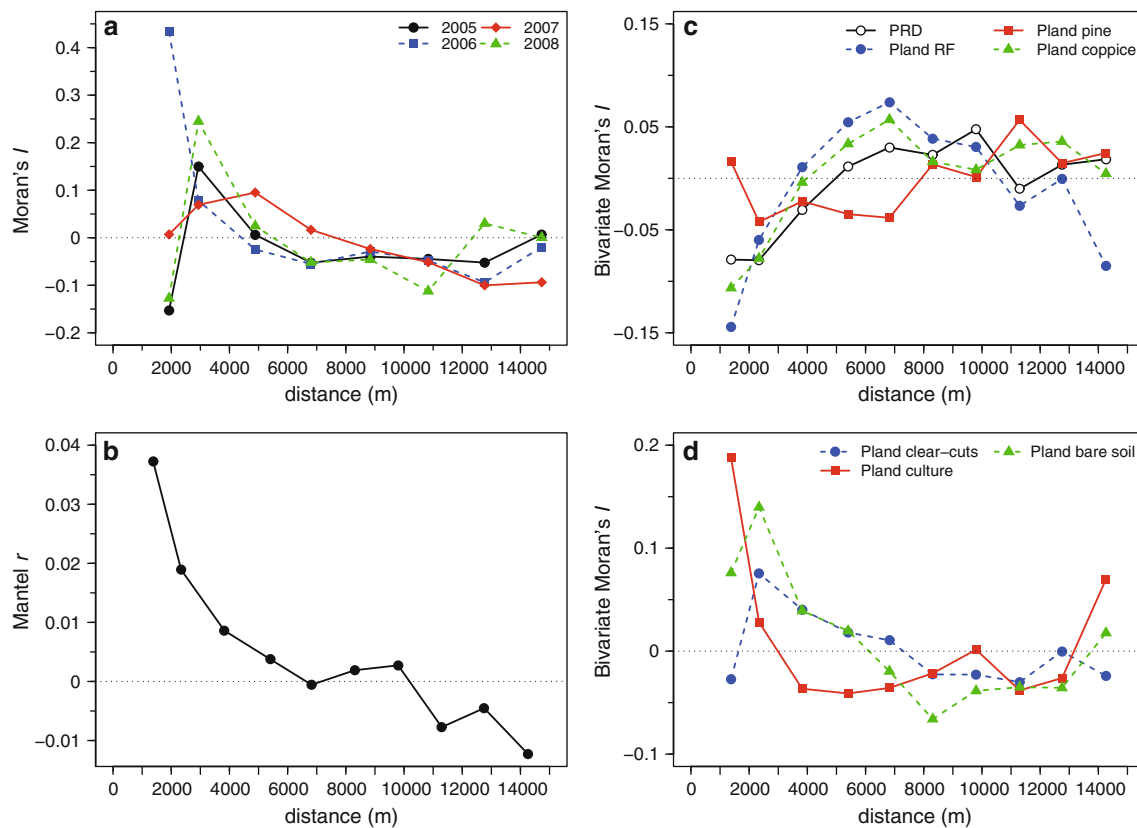


Fig. 3 Uni- and bivariate correlograms. **a** Univariate Moran's I correlogram for the winter nest density (nest \cdot ha $^{-1}$) of the pine processionary moth (PPM) (*Thaumetopoea pityocampa*) on 4 years of sampling (2005–2008). Spatial autocorrelation is significant in 2005, 2006, and 2008 (see Table 3). **b** Mantel correlogram computed with

the matrix of the multivariate distance derived from a set of landscape metrics (see text for details). **c, d.** Bivariate Moran's I correlograms computed for the PPM winter nest density (nest \cdot ha $^{-1}$) and various landscape metrics (all significant at $\alpha = 0.05$)

They include features such as differences in stand age, forest-track pattern (that create edges), or contrasted neighboring landscape configuration (see below). At the study site, the landscape features a central elongated RF and peripheral patches of clear cuts and cultures (Fig. 1). The areas corresponding to higher nest densities were distant from either side of the RF. Such large-scale patterns were clearly picked up by the correlograms when the PPM density was at its highest (2005, 2008). This survey started at the end of an outbreak phase in the study region. The density in 2006 and 2007 decreased sharply (decrease phase) and started to increase in 2008 (building phase). Patterns of distribution in 2005 and 2008 were positively correlated, which suggests that areas where the density was higher remained the same, at least at the scale of a few years, but could not be perceived during low-density periods. This observation is in agreement with the conclusions of Géri et al. (1985) in another region of France (Mont Ventoux). As a consequence, assessment of temporal patterns may preferably be based on comparison of observations made at similar phases of outbreak dynamics.

This remains to be explored with additional field work and over larger time scales.

Relationships with landscape

Our approach of landscape description based on 1000 m buffers revealed the presence of a strong autocorrelation of landscape composition. Most landscape metrics exhibited spatial correlation with PPM nest density in 2005. The percentage of landscape covered by pine was significantly correlated with PPM nest density. Because this land use was always highly dominant, we believe that such a relationship is meaningless and mostly conveyed correlations with other land-use types rather than a direct link with the host abundance (the average value of which is 80%). Interestingly, we found a negative relationship between PPM density and PRD. The latter metric renders the diversity of the landscape surrounding sampling locations. This is in accordance with the meta-analysis of Bianchi et al. (2006), who concluded that diversified landscapes harbored more biodiversity and had more potential for pest

control in agricultural landscapes. Various ecological mechanisms may explain such a negative relationship. Landscape composition and fragmentation can affect populations by altering survival rate according to neighborhood composition or by affecting dispersal success through fragmentation or composition. In our plantation forest site where stands are pure, this mechanism may act at spatial scales ranging from several juxtaposed patches of different land uses to the broad scale of our sampling window. On the other hand, the presence of nonhost species is known to lead to chemical barriers to host location through the disruption of olfactory host recognition. Such mechanisms have been described, for example, in the case of conifer-inhabiting bark beetles (Huber and Borden 2001) and might act similarly on PPM, as it is sensitive to various volatile terpenoids (Tiberi et al. 1999; Kanat and Alma 2003; Niccoli et al. 2008). More data are necessary to test these hypotheses in the case of PPM.

What influences the success of adult moths in locating a suitable habitat is the scale of movement relative to the scale of resource patchiness. In our case, the resource is near continuous, but landscape could affect the pattern of dispersal success through physical or chemical barriers. This is particularly plausible given the relatively poor dispersal abilities of *T. pityocampa*, whose female flying abilities barely exceed 2–3 km (Démolin 1969, in site with very low host density), whereas males can fly up to 20 km (A. Roques and J. Rousselet, personal communication). Besides the chemical hypothesis, landscape diversity or certain types of landscape components may also alter PPM spatial distribution by constituting physical barriers to dispersal and host location. This is the case in the RF, which strongly differs from pine plantations in terms of air temperature, humidity, and vertical movement. The PPM may have limited abilities to traverse such landscape units, with subsequent consequences upon movement behavior and resulting population spatial patterns. Another example is given by the positive relationship we found between the percentage of landscape covered by culture and the average number of winter nests.

We hypothesize that females will not traverse such large nonhabitat areas and thus tend to aggregate in the nearest host patches. Nevertheless, the fact that cultivated stands are open areas does not explain alone the positive relationship with PPM density, since no relationship was found when considering the percentage of landscape covered by clear cuts, which are open area as well. We still lack comprehensive data about female behavior and host selection to fully explain those differences.

Predators and parasitoids have direct effects upon insect herbivores, and it is recognized that these natural enemies are influenced by land-use patterns surrounding agricultural areas (Tscharntke et al. 2005; Gardiner et al. 2009). In the

case of the PPM, various birds and parasitoids constitute the pool of natural enemies. The hoopoe (*Upupa epops* L.) is an insectivorous bird often preying on larvae and pupae of the PPM (Battisti et al. 2000). This bird species is present in the study region, and its presence in pine plantations depends on the availability of suitable breeding sites (deciduous trees) in the neighborhood (Barbaro et al. 2008). Parasitoids also constitute important factors of regulation of PPM dynamics (Mirchev et al. 2004), and these species may be influenced by the presence of habitats other than pure pine stands (Dulaurent et al. 2010). It has been demonstrated on various occasions that the regulatory action of parasitoids may be promoted when additional sugar-rich food such as nectar or homopteran honeydew are available (Faria et al. 2008). These additional resources allow an increase of parasitoid longevity or fecundity and are possibly more available in a heterogeneous landscape (Dulaurent et al. 2010).

It is generally considered that accounting for the landscape spatial pattern is essential for understanding population functioning when habitat is rare or fragmented or if dispersal limits movement between habitat patches (Turner et al. 2001). The host species of *T. pityocampa* is clearly not a fragmented resource in our study site or at the scale of the Massif des Landes de Gascogne region. On the contrary, our survey is particular in that the habitat is dominant and virtually nonfragmented. Although our model species has modest dispersal abilities, host abundance and distribution prevents any strong impact of dispersal limitations. Interestingly, we nonetheless report effects of landscape composition upon the species spatial pattern possibly due to various nonhabitat patch effects, as discussed above. This result is important because it shows that even in a fairly homogeneous ecosystem mostly covered by host-tree species, landscape spatial information may be important for our understanding of the defoliator insect species distribution and dynamics.

Implications for sampling and monitoring PPM populations in plantation forests

Our data on PPM and, more generally, many forest pest species, often exhibit complex spatial autocorrelation. As a consequence, forest damage assessment and monitoring should ideally entail a multiscale spatially explicit approach (Samalens et al. 2007; Rossi et al. 2009), which requires considerable sampling effort. This task is complicated by autocorrelation (Fortin and Dale 2005), and various analytical solutions have been proposed (Webster and Oliver 1990). The presence of spatial autocorrelation has different consequences, among which those that regular sampling should be preferred over random sampling, in particular when mapping is one aim of the survey

(Webster and Oliver 1990). Another important aspect is the total number of points sampled. Our survey illustrated that local variance was very high, conveying the short-range aggregation of winter nest counts. Such information was used by Arnaldo and Torres (2005) to derive optimal PPM sampling. In our case, however, there is a clear spatial autocorrelation, and the methods used in the former paper are irrelevant (our data points lack statistical independence).

We emphasized the importance of noise in our data, and one possibility to reduce it would be to increase the sample support size, i.e., the number of trees sampled. The sample variance theoretically decreases linearly with the sampling unit size, but this decrease may be lower, however, in case of short-range autocorrelation (i.e., at scales \leq sample support) (Rossi and Nuutinen 2004). Given the higher PPM density at stand edges, alternate sampling strategies might be elaborated that account for this particular pattern of populations. Additional analyses are needed to evaluate whether these approaches could be used to optimize sampling intensity in PPM population monitoring in plantation forests.

Conclusions

1. PPM winter nest density appeared to be spatially structured at the scale of several kilometers and was correlated with certain landscape features. These relationships could be due to direct effects through the modalities of moth dispersal and a variety of indirect effects implying natural enemies.
2. These results showed that accounting for landscape characteristics may be important to understand forest insect pest distribution, even in cases where host species are very abundant and homogeneously distributed throughout the study area (e.g., plantation forests).
3. At the scale of 4 years, the density changed markedly due to the natural outbreak cycle of the species. Nest density was spatially structured in 3 out of 4 years of sampling. Population spatial pattern lacked clear temporal stability, but our ability to describe spatial pattern in years where density was at its lowest level is doubtful.
4. The presence of spatial autocorrelation indicated that sampling for monitoring PPM must be preferentially regular. Further analyses and field work are needed to design optimized sampling design for long-term monitoring, mapping, and control.
5. Our data revealed a strong stand edge effect that constituted a major driver of local PPM spatial variability.

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References

- Arnaldo PS, Torres LM (2005) Spatial distribution and sampling of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep. *Thaumetopoeidae*) populations on *Pinus pinaster* Ait. in Montesinho, N. Portugal. For Ecol Manage 210:1–7
- Barbaro L, Couzi L, Bretagnolle V, Nezan J, Vétillard F (2008) Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. Biodivers Conserv 17:1073–1087
- Battisti A, Bernardi M, Ghirardo C (2000) Predation by the hoopoe (*Upupa epops*) on pupae of *Thaumetopoea pityocampa* and the likely influence on other natural enemies. Biocontrol 45:311–323
- Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096
- Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Glob Chang Biol 12:662–671
- Berryman AA (1996) What causes population cycles of forest Lepidoptera? Trends Ecol Evol 11:28–32
- Bianchi FJJA, Booi CJH, Tscharnkte T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc R Soc B 273:1715–1727
- Bjørnstad ON (2009) ncf: spatial nonparametric covariance functions. R package version 1.1-3. <http://www.CRAN.R-project.org/>
- Bjørnstad ON, Bascompte J (2001) Synchrony and second-order spatial correlation in host–parasitoid systems. J Anim Ecol 70:924–933
- Bjørnstad ON, Peltonen M, Liebhold AM, Baltensweiler W (2002) Waves of larch budmoth outbreaks in the European Alps. Science 298:1020–1023
- Cappuccino N, Lavertu D, Bergeron Y, Regniere J (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia 114:236–242
- Démolin G (1969) Comportement des adultes de *Thaumetopoea pityocampa* Schiff.: dispersion spatiale, importance écologique. Ann Sci For 26:81–102 (in French)
- Dulaurent AM, Rossi JP, Deborde C, Moing A, Menassieu P, Jactel H (2010) Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth. J Appl Entomol. doi: 10.1111/j.1439-0418.2010.01547.x
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175

- Dwyer G, Dushoff J, Harrell Yee S (2004) The combined effects of pathogens and predators on insect outbreaks. *Nature* 430:341–345
- Einhorn J, Menassieu P, Michelot D, Riom J (1983) Piégeage sexuel de la processionnaire du pin, *Thaumetopoea pityocampa* Schiff. (Lep., *Notodontidae*) par des attractifs de synthèse. *Premiers essais dans le sud-ouest de la France*. *Agronomie* 3:499–505
- Faria CA, Wäckers FL, Turlings TCJ (2008) The nutritional value of aphid honeydew for non-aphid parasitoids. *Basic Appl Ecol* 9:286–297
- Fortin MJ, Dale MRT (2005) *Spatial analysis: a guide for ecologists*. Cambridge University Press, Cambridge
- Gardiner MM, Landis DA, Gratton C, DiFonzo CD, O'Neal M, Chacon JM, Wayo MT, Schmidt NP, Mueller EE, Heimpel GE (2009) Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol Appl* 19:143–154
- Géri C, Millier C, Xeuxet D (1985) Mesure des populations de processionnaire du pin (*Thaumetopoea pityocampa* Schiff—Lepidoptère *Thaumetopoeidae*) au Mont-Ventoux. *Ann Sci For* 42:143–184 (in French with English abstract)
- Goodwin BJ, Fahrig L (2002) Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Triphaxia borealis*. *Can J Zool* 80:24–35
- Huber DPW, Borden JH (2001) Angiosperm bark volatiles disrupt response of douglas-fir beetle, *Dendroctonus pseudotsugae*, to attractant-baited traps. *J Chem Ecol* 27:217–233
- Johnson DM, Bjørnstad ON, Liebhold AM (2004) Landscape geometry and travelling waves in the larch budmoth. *Ecol Lett* 7:967–974
- Johnson DM, Bjørnstad ON, Liebhold AM (2006) Landscape mosaic induces travelling waves of insect outbreaks. *Oecologia* 148:51–60
- Kanat M, Alma MH (2003) Insecticidal effects of essential oils from various plants against larvae of pine processionary moth (*Thaumetopoea pityocampa* Schiff) (Lepidoptera:Thaumetopoeidae). *Pest Manage Sci* 60:173–177
- Klemola T, Tanhuanpää M, Korpimäki E, Ruohomäki K (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99:83–94
- Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. *Science* 264:1581–1584
- Legendre P, Legendre L (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam
- Liebhold A, Kamata N (2000) Introduction—are population cycles and spatial synchrony a universal characteristic of forest insect populations? *Popul Ecol* 42:205–209
- Liebhold A, Rossi R, Kemp W (1993) Geostatistics and geographic information systems in applied insect ecology. *Ann Rev Entomol* 38:303–327
- McGarigal K, Cushman SA, Neel MC, Ene E (2002) *Fragstats: spatial pattern analysis program for categorical maps*. Computer software program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- Mirchev P, Schmidt GH, Tsankov G, Avci M (2004) Egg parasitoids of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) and their impact in SW Turkey. *J Appl Entomol* 128:533–542
- Moran P (1950) Notes on continuous stochastic phenomena. *Biometrika* 37:17–23
- Niccoli A, Panzavolta T, Marziali L, Sabbatini Peverieri G, Tellini Florenzano G, Tiberi R (2008) Further studies on the role of monoterpenes in pine host selection and oviposition of *Thaumetopoea pityocampa*. *Phytoparasitica* 36:313–321
- Oden N, Sokal R (1986) Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst Zool* 35:608–617
- Pauly H (2007) Remontée des populations de processionnaire du pin à la faveur de la douceur de l'hiver 2006–2007. La santé des forêts (France) en 2006. Tech. rep., Ministère de l'agriculture et de la pêche (in French)
- Peltonen M (1999) Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. *Scand J For Res* 14:505–511
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Ritchie L, Betts M, Forbes G, Vernes K (2009) Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *For Ecol Manage* 257:1920–1929
- Robinet C, Baier P, Pennerstorfer J, Schopf A, Roques A (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France. *Global Ecol Biogeogr* 16:460–471
- Rossi J-P, Nuutinen V (2004) The effect of sampling unit size on the perception of the spatial pattern of earthworm (*Lumbricus terrestris* L.) middens. *Appl Soil Ecol* 27:189–196
- Rossi J-P, van Halder I (2010) Towards indicators of butterfly biodiversity based on a multiscale landscape description. *Ecol Indic* 10:452–458
- Rossi J-P, Samalens J-C, Guyon D, van Halder I, Jactel H, Menassieu P, Piou D (2009) Multiscale spatial variation of the bark beetle *Ips sexdentatus* damage in a pine plantation forest (Landes de Gascogne, southwestern France). *For Ecol Manage* 257:1551–1557
- Samalens J-C, Rossi J-P, Guyon D, van Halder I, Menassieu P, Piou D, Jactel H (2007) Adaptive roadside sampling for bark beetle damage assessment. *For Ecol Manage* 253:177–187
- Taylor LR (1984) Assessing and interpreting the spatial distributions of insect populations. *Ann Rev Entomol* 29:321–357
- Tiberi R, Niccoli A, Curini M, Epifano F, Marcotullio M, Rosati O (1999) The role of the monoterpene composition in pinus spp. needles, in host selection by the pine processionary caterpillar, *Thaumetopoea pityocampa*. *Phytoparasitica* 27:263–272
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol Lett* 8:857–874
- Turner M, Gardner RH, O'Neill RV (2001) *Landscape ecology in theory and practice*. Springer, New York
- Vega J, Vega JM, Moneo I, Armentia A, Caballero ML, Miranda A (2004) Occupational immunologic contact urticaria from pine processionary caterpillar (*Thaumetopoea pityocampa*): experience in 30 cases. *Contact Dermatitis* 50:60–64
- Webster R, Oliver M (1990) *Statistical methods in soil and land resource survey*. Oxford University Press, Oxford