# Tree damage and population density relationships for the pine processionary moth: Prospects for ecological research and pest management

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## ABSTRACT

The pine processionary moth (*Thaumetopoea pityocampa*, PPM) is one of the most destructive pests in Mediterranean woodlands. Assessment of PPM impact involves the quantification of pest damage at the stand level from visual evaluations by forestry technicians, using different infestation indices. One such index, widely used in national and regional forest monitoring programmes, is an ordinal index that ranges from no infestation (0) to massive defoliation (5). This index now offers an outstanding opportunity to investigate patterns and processes in PPM population dynamics. Its use as a proxy for insect population density requires, however, knowledge on the relationship between stand defoliation and population density-related measures, which is something that has not been explored to date. In this study, we investigated the relationship between the infestation index, quantifying damage at the stand level by the PPM, and fined-grained measures of PPM population size (number of egg batches, number of hatched caterpillars, number of winter tents) within and between generations. We used data from a long-term monitoring programme conducted in three pine woodland stands at Mora de Rubielos, Spain, for a 19-year period. Generalized linear models (GLM) were fitted in order to test the following hypotheses: (1) high values of population density-related variables, on a log basis, will cause high defoliation in the coming winter (within generation); and (2) high defoliation rates will be associated with high stocks of population size at the next generation of PPM (between generations). Our results indicate that, within the same generation, there was a poor relationship between the infestation index and all three fine-grained measures of population size (maximum $R^2 = 0.442$), possibly as a result of post-sampling larval survival over winter due to climatic factors. Goodness of fit was higher for PPM population density-related measures in the next generation and the infestation index (maximum $R^2 = 0.735$). Overall, the results suggest that visual evaluation of pest damage by PPM at the stand level provides an accurate proxy for population size at the next generation, and therefore opens the potential to the use of this index to investigate PPM population dynamics where no direct measures of population size exist.

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## 1. Introduction

Quantitative assessment of forest pest impact is a key element in designing forest management programmes. Rapid assessments can involve the quantification of tree defoliation and/or mortality at the stand level from in-the-field visual evaluations by forestry technicians (Innes, 1988; Redfern and Boswell, 2004; Cayuela et al., 2011; Hódar et al., 2012; Eickenscheidt and Wellbrock, 2014) or, more typically, from interpretation of remote sensing data or aerial photographs or surveys (Wulder et al., 2006; Eklundh et al., 2009; Mozgeris and Augustaitis, 2013; see Rullan-Silva et al., 2013 for a review). These measures, though typically used to aid forest managers in assessing the damage across large areas, have been also used as a proxy for insect population density in order to investigate the spatio-temporal dynamics of the pest and to forecast potential outbreaks (e.g. Aukema et al., 2006,

2008; Foster et al., 2012; Sambaraju et al., 2012; Allstadt et al., 2013). The latter process requires knowledge of the relationship between tree damage and population density-related measures (Sutherland, 1996), which can occur only if a number of populations has been studied while simultaneously measuring both tree damage and the actual number of insects. Studies that attempt to relate insect density to individual tree or stand damage within forested systems often compare natural egg or larval densities to defoliation (e.g. Gansner et al., 1985; Lysyk, 1990; Williams et al., 1991; Carroll and Quiring, 1993; Parsons et al., 2005). Unfortunately, investigations of such relationships are scarce in the scientific literature, due mostly to lack of fine-grained population density-related data available, especially when pest management programs are conducted across large areas. Thus, in the absence of proper calibration, this relationship may be held as true when it is not, leading to erroneous conclusions about the dynamics of the target species.

This study investigates the relationship between an ordinal index widely used in Mediterranean woodlands to quantify tree damage at the stand level by the pine processionary moth (*Thaumetopoea pityocampa*, Lepidoptera: Thaumetopoeidae; henceforth PPM), and fined-grained measures of population size, using data from a long-term monitoring programme conducted in Mora de Rubielos, Spain, for a 19-year period. PPM is one of the most damaging pests in Mediterranean pine woodlands. Their larvae (caterpillars) feed on the needles of pine trees over winter and, in large numbers, they can severely defoliate trees, reducing tree growth, weakening trees and making them more susceptible to attack by other pests or diseases, or to environmental stress caused by drought (Hódar et al., 2003; Arnaldo et al., 2010; Erkan, 2011; Jacquet et al., 2012, 2013). In the last few decades, the area affected by PPM outbreaks in Europe has expanded northwards and upwards in the mountains, and the pest is now affecting higher altitude and latitude areas where it used to be absent (Hódar and Zamora, 2004; Battisti et al., 2005; Robinet and Roques, 2010). This has resulted in high attack rates in areas hardly affected by this insect in the past (Battisti et al., 2005).

In Spain, forest monitoring programmes from the 1970s onwards have consistently evaluated damage by PPM at the stand level by means of an ordinal index (henceforth infestation index), with value ranges from no infestation (0) to massive defoliation (5). This index has been typically used to evaluate tree damage and determine threshold values above which to recommend the application of treatments – mostly biological insecticides – to control PPM outbreaks. To date, the relationship between the infestation index and population density-related measures are unknown for the PPM. Thus, this is the first study to investigate the relationship between defoliation at the stand level and different measures of PPM population density, namely number of egg batches, number of hatched caterpillars, and number of winter tents. In particular, we tested the following non-mutually exclusive hypotheses: (1) high stocks of population size at the beginning of the cycle will cause high defoliation (H₁); and (2) high defoliation rates will be associated with high stocks of population size in the next generation of PPM (H₂; Fig. 1). The reason for testing such relationships is twofold. From a research perspective, this opens the possibility of using this index to investigate patterns and processes in PPM population dynamics where no direct fine-grained measures of population density exist. This can be particularly useful since the collection of such data is indeed a hard and time-consuming task, and time series are typically short, making it difficult to analyse spatio-temporal population dynamics. From a management perspective, it might support current protocols of action (e.g. application of insecticides) when threshold values are reached (i.e. infestation index ⩾3). Since tree damage in late winter is evaluated at the end of larvae development, and PPM insecticides target early larval stages, the application of insecticides must be applied at the beginning of the next PPM cycle, by late summer or early autumn (Cayuela et al., 2011). Thus, it is implicitly assumed that there is a positive relationship between tree damage caused by PPM and population density in the next generation, but this has not been demonstrated to date.

In the case of PPM, damage is measured at the end of larval development, whereas population density is often measured through male captures in pheromone traps, counts of the number of egg batches or caterpillars that hatch at the beginning of the cycle, or number of winter tents later in winter, and therefore closer in time to the estimation of tree damage at the stand level. A number of biotic and abiotic factors might thus affect post-sampling survival (Wainhouse, 2005), weakening the relationship between population density-related measures and the infestation index. Post-sampling survival would imply mortality of late larval instars, pupae, and moths, which together with possible fluctuation in fecundity, can introduce considerable variation into the relationship between defoliation and larvae density at the next generation (Lysyk, 1990). Likewise, winter climatic conditions have been shown to influence PPM outbreaks (Démolin, 1969; Hódar and Zamora, 2004; Battisti et al., 2005, 2006; Hódar et al., 2012), and therefore it is not clear whether fine-grained measures of population density will relate to tree damage at the stand level within the same cycle. As for the relationship between the infestation index and population density-related measures at the next generation, this might be likewise affected by factors acting on the survival of pupae after their burial, such as soil moisture (Markalas, 1989).

Overall, our study is meant to help elucidate the potential of the infestation index in ecological research, as there are many long-term databases held by public administrations that might be used to investigate different issues related to PPM population dynamics, provided that it accurately reflects measures of population density. In addition, given that the application of control methods for aggressive pests, such as PPM, is a key issue in Mediterranean forestry, we aim to provide a practical evaluation of the utility of the infestation index for decision making in current PPM control protocols.

## 2. Material and methods

### 2.1. Study area

The area of study is located in Mora de Rubielos, in Teruel province, north-eastern Spain (Fig. 2a). It was established in the 1970, in response to a call from an international meeting held in Teruel, sponsored by the International Organization for Biological Control (IOBC). As a result of this meeting, the Working Group on "Integrated Pest Management in Mediterranean Woodlands" of the IOBC was created, as part of a joint effort to investigate the ecology of the PPM and develop proposals for integrated management of forest insect pests (Démolin, 1970). No insecticides have been applied in the area at least since the early 1970s. The area is managed by the Forest Lab of Mora de Rubielos, a research centre currently under the administration of the Forest Health Lab of the Aragón Regional Government.

The site has a northern Mediterranean climate, with cold, wet winters and hot, dry summers. Average annual rainfall between 1971 and 2012 was 487 mm, with a maximum yearly precipitation of 733 mm and a minimum of 323 mm. The average temperature was 10.4 °C, with mean monthly summer temperatures of 21.5 °C and mean monthly winter temperatures of 5.7 °C. The area covers approximately 13,000 ha of naturalized pine woodlands, dominated mostly by *Pinus nigra salzmanii*, *P. sylvestris,* and *P. pinaster*.
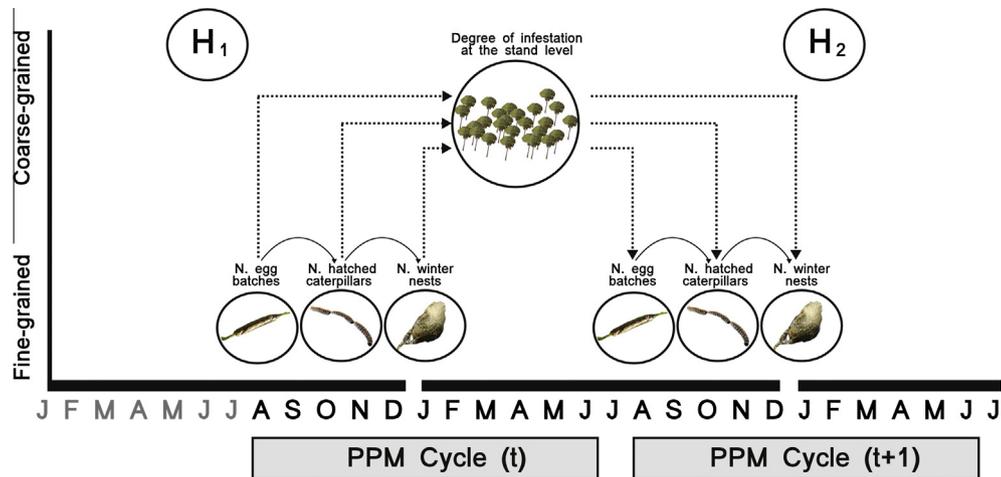
**Fig. 1.** Schematic representation of the potential relationships between three population density-related measures (number of egg batches, number of hatched caterpillars, number of winter tents) and the infestation index. The x-axis represent time in a monthly basis (from January, J, to December, D), whereas the y-axis represent the resolution at which the variables were measured (i.e. coarseness). Two non-mutually exclusive hypotheses were tested in this study: (H$_1$) high stocks of population size at the beginning of the cycle will cause high defoliation; and (H$_2$) high defoliation rates will cause high stocks of population size in the next generation of PPM. The direction of the arrows therefore indicate causality. Prolonged pupal diapause is not considered here (see text).
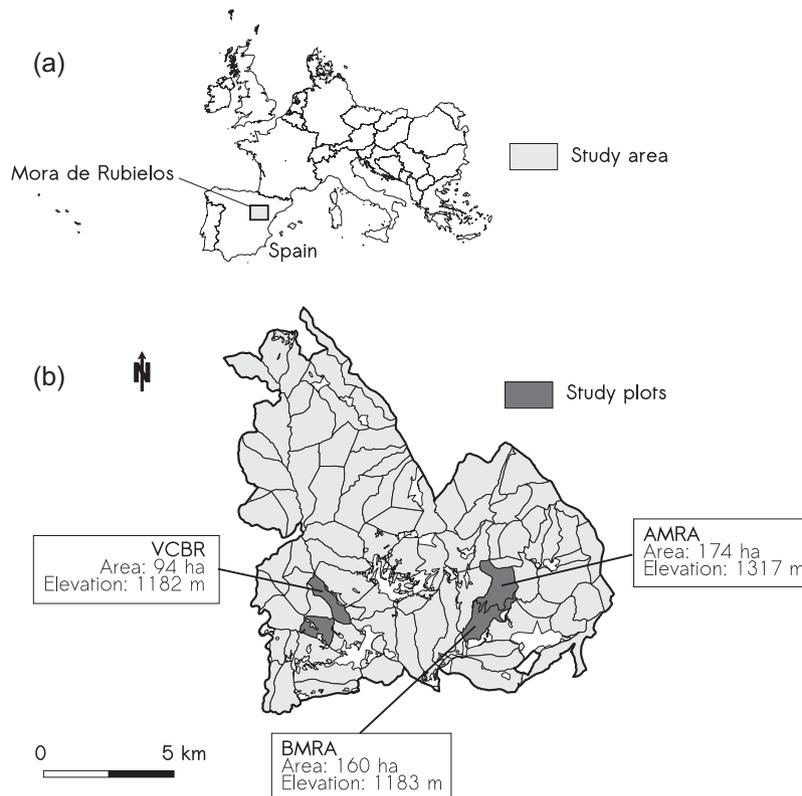


**Fig. 2.** (a) Location of the study area in Mora de Rubielos, in Teruel province, north-eastern Spain, and (b) geographical distribution and main characteristics of the three pine woodland stands analysed in this study: Alto de Mora (AMRA), Bajo de Mora (BMRA), and Valle de Cabra (VCBR).

The elevation ranges from 1000 to 1800 m.a.s.l. For management purposes, the woodlands were distributed in plots of different sizes according to tree age and density (Fig. 2b). Of a total of 92 pine woodland stands, only three were used in the present study: Alto de Mora (AMRA), Bajo de Mora (BMRA), and Valle de Cabra (VCBR) (Fig. 2b). The mean elevation in these stands ranged between 1182 and 1317 m.a.s.l., and the area covered ranged from 94 to 174 ha. *P. nigra salzmanii* was the dominant species in AMRA and BMRA, whereas both *P. nigra* and *P. pinaster* were dominant at VCBR.

Although AMRA and BMRA were close to each other (Fig. 2b), these two plots differed in elevation, stand characteristics, and soil organic matter. AMRA was located at the highest elevation (1317 m on average) and had an average tree density of 390 trees/ha. The trees, averaging 6.6 m high, come from natural pine woodlands and grow on soils with higher organic-matter content. Meanwhile, BMRA was located at a lower elevation (1183 m in average), had an average tree density of 355 trees/ha, with trees averaging 4.5 m. Part of the stand come from natural pine

woodlands but some areas were planted in the early 1950s, and had soils with lower contents in organic matter. However, to account for potential spatial autocorrelation between these two plots, we propose alternative statistical models where AMRA and BMRA were considered either separate or together as if they were the same plot (see Section 2.3).

## 2.2. Sampling protocols and data

Since 1973, forestry technicians have evaluated the degree of infestation by PPM in all pine stands at the end of the winter season (February–April), according to six categories: 0 = no infestation, 1 = scattered tents, scant defoliation, 2 = defoliation and tents visible from the stand border, 3 = strong defoliation and numerous tents at the stand border, some defoliation in the centre of the stand, 4 = very heavy defoliation both at the border and centre of stands, and 5 = massive defoliation, almost no foliage remaining (Montoya and Hernández, 1991). Henceforth this variable will be referred to as the infestation index.

From 1973 to 1991, a monitoring programme of PPM populations was conducted in the three above-mentioned stands at the Forest Lab of Mora de Rubielos. To estimate population density, three fine-grained measures were recorded yearly: number of egg batches, number of hatched caterpillars, and number of winter tents. At the beginning of the study period, an area of approximately 0.25 ha was selected within each stand, representing the most common environmental conditions, and 40 trees of *P. nigra salzmanii* were chosen within this area, separated at a minimum distance of 5 m from each other. At the beginning of the study period, trees were 2.7 m height in average, and the same trees reached an average height of 3.2 m by 1981. The pines selected were all of similar heights for two reasons: (1) to avoid differences in pine vulnerability to attack, as pine height has been suggested a critical factor determining the likelihood of attack by PPM (Dulaurent et al., 2012); and (2) to facilitate sampling of egg batches by forestry technicians.

By the end of the summer, once the eggs hatched, forestry technicians systematically searched for and collected egg batches in the selected trees. Despite predation of egg batches by birds (Barbaro and Battisti, 2011), we assume this variable could be a good indicator of the number of adults, which are otherwise very difficult to measure given the short lifespan of this phase. A total of 4925 egg batches were sampled throughout the study period (Table 1). The total number of eggs and number of hatched eggs (i.e. hatched caterpillars) were measured in each egg batch, though we only used the latter as a measure of population stock at the beginning of the larval phase (Table 1). The number of winter tents in a random subgroup of eight trees were counted at the end of the winter and used as a measure of population density at the end of the larval phase. It should be noted that PPM shows prolonged pupal diapause – that is, some of the larvae pupating in the soil can emerge as moths several seasons after burial. However, according to data compiled at the study site, the percentage of pupae in prolonged diapause was not so high (8.70–16.91% on average; Hernández, unpublished results), and thus for this analysis, we did not take into account the possible effects of this feature of the life cycle.

## Table 1
Mean (range in brackets) number of egg batches, hatched caterpillars, and winter tents in each pine woodland stand and all stands together.

|  | N. egg batches | N. hatched caterpillars | N. winter tents |
|---|---|---|---|
| AMRA | 127.05 [5, 640] | 21196.05 [610, 132,587] | 4.47 [0, 18] |
| BMRA | 96.73 [5, 415] | 14898.53 [435, 59,002] | 4.84 [0, 11] |
| VCBR | 35.42 [4, 163] | 5721 [694, 30,302] | 1.68 [0, 12] |
| All stands | 86.40 [4, 640] | 13,938 [435, 132,587] | 3.66 [0, 18] |

## 2.3. Data analysis

We used generalized linear models (GLM) to test our two hypothesis, $H_1$ and $H_2$ (see Fig. 1). For each hypothesis, we explored the specific relationship between the infestation index and each of the three population density-related variables on a log basis. For each response variable, we examined eight alternative models: (1) a null model ($y \sim \beta_0$), where the dependent variable $y$ was estimated as the average of all observed values; (2) a site-specific model ($y \sim \beta_{0[Site]}$), where the dependent variable $y$ was estimated as the average observed value at each stand; (3) a general response model ($y \sim \beta_0 + \beta_1 \cdot x$), where the dependent variable $y$ was a linear function of the explanatory variable $x$; (4) a site-specific general response model ($y_t \sim \beta_{0[Site]} + \beta_1 \cdot x$), where the dependent variable $y$ was a linear function of the explanatory variable $x$, while accounting for average differences in the dependent variable among sites; and (5) a response conditioned by the site model ($y \sim \beta_{0[Site]} + \beta_{1[Site]} \cdot x$), where the relationship between the dependent and the explanatory variables was specific to each site. To account for similar responses in AMRA and BMRA as a result of spatial autocorrelation, we further examined extensions of models 2, 4, and 5, where AMRA and BMRA were considered as a single site, so models with site-specificity included differences between AMRA/BMRA and VCBR. GLMs were fitted using a Gaussian distribution error when the infestation index was the dependent variable, and a Poisson error distribution for any of the population density-related measures as dependent variables.

Alternative models were compared using the Akaike Information Criterion corrected for small sample size (AIC$_c$, Burnham and Anderson, 2002). Models with a difference in AIC$_c$ > 2 indicate that the worst model has virtually no support and can be omitted from further consideration. The $R^2$ of the model fit [1 – SSE/SST, sum of squares error (SSE) sum of squares total (SST)] of observed vs. predicted was used as a measure of goodness-of-fit. All analyses were performed using the R environment (R Development Core Team, 2013).

## 3. Results

There was a positive relationship between all three measures of population density and the infestation index within the same PPM cycle (Fig. 3a–c). The best models in all cases indicated that this relationship was the same in all three stands (i.e. same slope), although the average intensity of infestation was higher in AMRA/BMRA as compared to VCBR (i.e. different intercepts) (Table 2). $R^2$ ranged from 0.387 for number of egg batches to 0.436 for number of hatched caterpillars (Table 2).

The relationship between the infestation index in a given cycle and the measures of population density at the next cycle was also positive in all cases (Fig. 3d–f). Best models differed for different dependent population density-related variables. For number of egg batches and number of hatched caterpillars, the best model indicated that the relationship of these variables with the infestation index was particular to each site (i.e. different slope and intercept in all three sites) (Table 3). For the number of winter tents, the best model was a general response model (i.e. same intercept and slope at all sites), where the relationship between the number of winter tents on a log scale and the infestation index was the same in all three stands (Table 3). $R^2$ ranged from 0.388 for number of winter tents to 0.735 for number of egg batches (Table 3).

## 4. Discussion

The estimation of pest population size is of great importance in a variety of biological problems, which may be related to
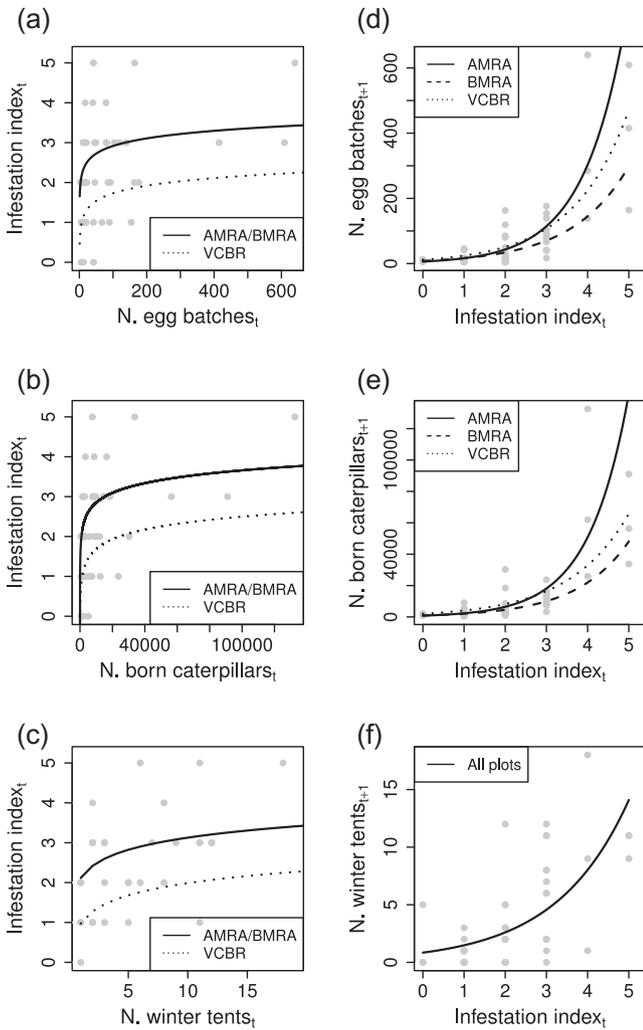
**Fig. 3.** Predictions of best-fit models for the relationship between number of egg batches (a), number of hatched caterpillars (b), and number of winter tents (c), with the infestation index within the same PPM cycle; and the infestation index with any of these three population density-related measures at the next PPM generation (d–f, respectively).

population growth, ecological adaptation, genetic constitution, natural selection, evolution, and so on. Stages such as pupae, eggs or larvae are typically used to monitor long-term changes in insect density (Wainhouse, 2005). Collecting fine-grained measures of pest population size over time is a hard and time-consuming task.

Measures made from forest monitoring programs, whose aim of sampling populations is only to classify the population as being above or below a critical threshold rather than to estimate population density (Wainhouse, 2005), can be used as surrogates of population density, provided that a relationship does exist. Finding good surrogates of population density that are easy to measure is thus a key step in forest pest management programmes.

Different studies have demonstrated a strong correlation between population density at the beginning of the pest cycle and defoliation (Gansner et al., 1985; Lysyk, 1990; Williams et al., 1991; Carroll and Quiring, 1993; Parsons et al., 2005). Such relationships enable forecasts of tree damage and are thus critical to guide forest pest management. Our results, however, revealed a poor relationship between fine-grained population density and the infestation index within the same generation. That is, when there is a low number of insects at the beginning of the PPM cycle, we would expect low defoliation by the end of the winter; however, when this number is high, the outcome is uncertain in terms of defoliation, this depending mostly on winter climatic conditions, which ultimately governs larval survival. The relationship was similar in AMRA and BMRA, which might indicate that the PPM populations are not differentiated here, and similarly affect both stands. Overall, low correlations can be attributed mostly to climatic factors determining post-sampling larvae survival over winter (Démolin, 1969; Battisti et al., 2005; Buffo et al., 2007; Robinet et al., 2007; Pimentel et al., 2011; Hódar et al., 2012).

On the contrary, there was a good relationship between the infestation index and population density-related measures at the next PPM generation, particularly for the number of egg batches and hatched caterpillars. These results indicate that, despite that biotic as well as abiotic factors can influence survival in late-instar larvae and pupae (Markalas, 1989; Battisti et al., 2000; López-Sebastián et al., 2007), their effects are quite limited in terms of numeric changes in the PPM population. Thus, we conclude that the infestation index acts as a good surrogate of population density-related variables for early stages of the next PPM generation. Remarkably, there were differences in such relationships in AMRA and BMRA. This might be linked to differences in tree height, as higher trees have been shown to be more vulnerable to PPM attack (Dulaurent et al., 2012). The fact that AMRA had higher trees on average than did BMRA might explain why it had higher population densities but similar levels of defoliation (see Fig. 3). Although high correlations between the infestation index and population-density-related measures in the next generation might be taken as empirical evidence to justify the use of insecticides at the beginning of the next PPM cycle once an outbreak occurs (infestation index $\geqslant 3$), it should be noted that, as shown earlier, a high number of insects at the beginning of next cycle will not necessarily lead to high defoliation rates. In other words, while the infestation index

**Table 2**
Comparison of alternative models for the PPM infestation index ($y_t$) as a function of each of the three population size-related explanatory variables (number of egg batches, number of hatched caterpillars, number of winter tents). Site-specific models included either the three original sites (AMRA, BMRA, VCBR) or just two sites (AMRA and BMRA merged into one single plot). Best models (lowest AICc) are indicated in boldface type. The number of parameters ($k$) and $R^2$ refer to the best model.

| Model | Formulation | AICc | | |
|---|---|---|---|---|
| | | N. egg batches | N. hatched caterpillars | N. winter tents |
| Null | $y_t \sim \beta_0$ | 159.89 | 159.89 | 159.89 |
| Site-specific (3 sites) | $y_t \sim \beta_{0[Site3]}$ | 146.86 | 146.87 | 146.87 |
| Site-specific (2 sites) | $y_t \sim \beta_{0[Site2]}$ | 144.60 | 144.60 | 144.60 |
| General response | $y_t \sim \beta_0 + \beta_1 \cdot x_t$ | 151.43 | 148.25 | 148.90 |
| Site-specific general response (3 sites) | $y_t \sim \beta_{0[Site3]} + \beta_1 \cdot x_t$ | 143.19 | 139.05 | 141.25 |
| Site-specific general response (2 sites) | $y_t \sim \beta_{0[Site2]} + \beta_1 \cdot x_t$ | **141.05** | **137.05** | **138.94** |
| Response conditioned by site (3 sites) | $y_t \sim \beta_{0[Site3]} + \beta_{1[Site3]} \cdot x_t$ | 147.44 | 143.50 | 143.58 |
| Response conditioned by site (2 sites) | $y_t \sim \beta_{0[Site2]} + \beta_{1[Site2]} \cdot x_t$ | 143.44 | 139.50 | 141.29 |
| $R^2$ | | 0.387 | 0.436 | 0.413 |
| $k$ | | 3 | 3 | 3 |

**Table 3**
Comparison of alternative models for each of the three population size-related variables (number of egg batches, number of hatched caterpillars, number of winter tents) at time $t + 1 (y_{t+1})$ as a function of PPM infestation index in the previous period $(x_t)$. Site-specific models included either the three original sites (AMRA, BMRA, VCBR) or just two sites (AMRA and BMRA merged into one single plot). The best model (lowest AICc) is indicated in boldface type. The number of parameters $(k)$ and $R^2$ refer to the best model.

| Model | Formulation | AICc | | |
|---|---|---|---|---|
| | | N. egg batches | N. hatched caterpillars | N. winter tents |
| Null | $y_t \sim \beta_0$ | 7061.60 | 1216816.90 | 375.25 |
| Site-specific (3 sites) | $y_t \sim \beta_{0[Site3]}$ | 5954.19 | 1025040.40 | 352.19 |
| Site-specific (2 sites) | $y_t \sim \beta_{0[Site2]}$ | 6208.148 | 1082764.10 | 351.23 |
| General response | $y_t \sim \beta_0 + \beta_1 \cdot x_t$ | 2262.27 | 382278.30 | **273.20** |
| Site-specific general response (3 sites) | $y_t \sim \beta_{0[Site3]} + \beta_1 \cdot x_t$ | 1824.86 | 283333.80 | 276.09 |
| Site-specific general response (2 sites) | $y_t \sim \beta_{0[Site2]} + \beta_1 \cdot x_t$ | 2243.93 | 375143.30 | 275.67 |
| Response conditioned by site (3 sites) | $y_t \sim \beta_{0[Site3]} + \beta_{1[Site3]} \cdot x_t$ | **1750.05** | **269343.90** | 280.03 |
| Response conditioned by site (2 sites) | $y_t \sim \beta_{0[Site2]} + \beta_{1[Site2]} \cdot x_t$ | 2243.17 | 372863.60 | 277.99 |
| $R^2$ | | 0.735 | 0.617 | 0.388 |
| $k$ | | 6 | 6 | 3 |

gives a reliable forecast of population density-related measures in the next PPM generation, this is not necessarily so for the infestation index (defoliation) for the next generation. This contention is supported by the weaker relationship found for the infestation index and the number of winter tents in the next generation ($R^2$ = 0.388; see Table 3), as compared to the other two measures of population density. This can occur as a response to: (1) the effects of winter climate on larval survival (Démolin, 1969; Battisti et al., 2005; Buffo et al., 2007; Robinet et al., 2007; Pimentel et al., 2011; Hódar et al., 2012), as pointed out earlier; and (2) density-dependent mechanisms (Tamburini et al., 2013); when the defoliation is very high, more tents will appear the following year but, with very little foliage to consume, the population is likely to collapse. This could explain why aerial spraying of insecticides is not an effective measure in preventing future PPM defoliations (Cayuela et al., 2011). Global climatic indices, such as the winter North Atlantic Oscillation (NAO) index, seem a more promising option for early warning in order to conduct appropriate management programs to reduce or prevent the possibility of outbreaks, as PPM populations have been shown to be correlated with the climatic conditions for a given winter, but also for the previous ones (Hódar et al., 2012).

The results of the present study evidence that: (1) measures of PPM population density should not be used to forecast tree defoliation at the stand level due to the low correlations found between fine-grained measures of population size and the infestation index; and (2) the infestation index can be used to predict population stocks at the beginning of the next cycle, although this will not ultimately determine the fate of PPM populations throughout the winter. The high correlations found between this index and fine-grained measures of population density at the beginning of the next cycle open the potential to the use of this index to investigate PPM population dynamics where no direct measures of population size exist. In addition, these findings are important from a pest management perspective, since this index is still broadly used in Spain for forest management programmes to decide whether to apply aerial spraying of insecticides once a threshold value of the infestation index is reached (Cayuela et al., 2011).

Some caution is needed, however, since many of the best-fit models displayed site-dependent relationships between population density-related measures and the infestation index (Fig. 3a–e). This indicates, for instance, that the same number of egg batches might lead to different levels of defoliation and, likewise, similar defoliation levels will result in a varying number of egg batches in the next generation, depending on the characteristics of the stands. This may be related to the vulnerability of trees to insect attack, which might ultimately depend on features related to stand structure, including tree age (Jacquet et al. 2013), species composition and diversity (Arnaldo and Torres, 2006; Jactel and

Brockerhoff, 2007; Dulaurent et al., 2011a,b, 2012; Jactel et al., 2011), or microclimatic conditions (Démolin, 1969; Battisti et al., 2005; Hódar et al., 2012). These results might have implications when comparing similar levels of defoliation across an entire region to investigate population dynamics (e.g. Hódar et al., 2012), since these might not reflect equivalent values in terms of population density-related variables. Despite such limitations, these studies allow the analyses of broad-scale PPM population dynamics patterns, although complementary studies investigating the temporal dynamics of PPM within individual stands can provide further insights into the effects of climate and density-dependent factors on population dynamics while incorporating the effects of stand-level features.

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