Factors affecting pine processionary moth (*Thaumetopoea pityocampa*) incidence in Mediterranean pine stands: A multiscale approach

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ABSTRACT

The occurrence of the pine processionary moth (*Thaumetopoea pityocampa*, hereafter PPM) in Mediterranean pine forests and plantations is of increasing concern as processes such as global warming and forest cover expansion have amplified the frequency and virulence of outbreaks. This study attempts to provide as complete an overview as possible of the different factors involved in pine forest susceptibility to PPM in 98 pine stands in Central Spain. A large study area (~3,000 km^2) was considered, including three different spatial scales (<1 ha, 1 ha, 10 ha) and four different pine tree species (*Pinus pinaster*, *P. nigra*, *P. sylvestris*, *P. pinea*), monitored over a 4-year period. Models were fitted for each of the three spatial scales, as well as for a combination of them (multiscale model). Pine species had a strong influence on vulnerability to PPM, with higher incidences in stands dominated by *P. pinaster* and *P. nigra* and lower for those dominated by *P. sylvestris* and *P. pinea*. Grazing pressure, a factor thus far disregarded, was also determining, with a prominent role at both the multiscale and the stand-scale levels. Other variables were highly influential at some of the spatial scales, showing a greater resistance in pine forests or plantations with a higher diversity of pine sizes, greater tree density, and a larger cover of non-host tree species. Open habitats also played a role in PPM incidence: we detected that, both at the locality and the plot scale, the presence of clearings occupied by bushes or rocky outcrops reduced vulnerability to PPM, while the clearings with a more simplified structure produced the opposite effect. We conclude that PPM incidence is greater in structurally simple pine forests, with strong grazing pressure and abundant open spaces without woody vegetation that may favour PPM pupation. To reduce damage by PPM, pine forest and plantations should be managed to avoid oversimplified forest structures. Patches of non-host tree species should be promoted, as well as some presence of shrubs in open areas. This implies avoiding overgrazing and other management models leading to an excessive increase in bare soil. Nevertheless, it should be noted that the implementation of these recommendations should consider the remaining challenges that need to be addressed in the current context of global change, such as the increased risk of wildfires and the emergence of other pests and diseases.

1. Introduction

Thaumetopoea pityocampa (the pine processionary moth, hereafter PPM) is a well-known univoltine moth (Lepidoptera: Thaumetopoeidae) widely present in the Mediterranean region, whose caterpillars feed on the leaves of different *Pinus* (and *Cedrus*) species (Stastny et al., 2006), sometimes causing spectacular outbreaks (Masutti and Battisti, 1990). Although pines rarely die, and affected trees show a remarkable ability to overcome the growth reduction induced by processionary defoliation (Linares et al., 2014), outbreaks are considered a problem in forests and plantations, especially for services like timber production or carbon sequestration (Jacquet et al., 2012). Urticating caterpillar hairs can cause rashes and strong allergic reactions in humans, so strong episodes of processionary moths are also considered a major public health problem (Battisti et al., 2017). Concern about the effects of PPM has grown in recent years, due to the increase in its distribution area favoured by the expansion of pine plantations and global warming (Hódar and Zamora, 2004; Netherer and Schopf, 2010; Battisti et al., 2017, De Boer and Harvey, 2020).

Understanding the factors controlling vulnerability to PPM is of

paramount interest for the management of established forests and plantations and the elaboration of habitat restoration plans. Previous studies show that PPM is primarily driven by climate conditions, with both mild winters (Hódar and Zamora, 2004; Battisti et al., 2005; Barbaro et al., 2013) and hot summers (Battisti et al., 2006) favouring PPM population growth. There is also some consensus on the high vulnerability of the species *Pinus nigra* (Buxton, 1983; Masutti and Battisti, 1990; Hódar et al., 2002), and on the role played by plant species diversity in the mitigation of PPM infestations (Cayuela et al., 2011; Jactel et al., 2011, Poeydebat et al 2021). For other factors, however, evidence is less conclusive, if not contradictory. For example, *P. pinaster* is sometimes presented as a species somewhat resistant to PPM (Buxton, 1983; Hódar et al., 2002), but important outbreaks affecting it have also been reported (Jacquet et al., 2013). At the landscape scale, Samalens and Rossi (2011) conclude that a high patch richness reduces processionary density, while Dulaurent et al. (2011a) highlights the role of habitat complementarity between pine patches and open habitats favouring PPM populations. Castagneyrol et al. (2020) found, using an experimental approach, that pine density increased PPM density, while reducing PPM attack rate. Young trees are more vulnerable to PPM according to Buxton (1983), but Régolini et al. (2014) reports higher infestation rates in old ones. These findings, not always in agreement with one another, suggest that we do not yet have a comprehensive understanding of the interactions between PPMs and their host plants,

making it difficult to take corrective management measures.

It should be noted that most PPM studies consider only one or very few factors, and only one or very few pine species. Moreover, studies usually focus on a single spatial scale, despite the strong scale-dependency of many ecological effects (Samalens and Rossi, 2011). In addition, most studies take little account of the management of pine forests, except for measures directly aimed at controlling the processionary (Buxton, 1983; Cayuela et al., 2011). In the specific case of the Iberian Peninsula, many pine forests and plantations complement logging and resin exploitation with grazing by domestic livestock, which has notable effects on the structure of the pine stands. Despite this, to our knowledge the effect of grazing management on PPM incidence has not yet been explored.

The present study seeks to obtain an overview as complete as possible of the different factors that influence the vulnerability of pine forests to PPM, integrating a number of environmental descriptors and considering three different spatial scales. The study is based on a database of almost 100 pine stands and covers a large area in Central Spain. Data on PPM incidence were collected over a 4-year period to smooth over the interannual fluctuations in PPM populations. We start from the hypothesis that PPM is mainly controlled by abiotic factors (especially climatic) and that there are differences in vulnerability associated with pine species. On this basis, our study will investigate the role of a suite of compositional, habitat, structural and functional factors that operate
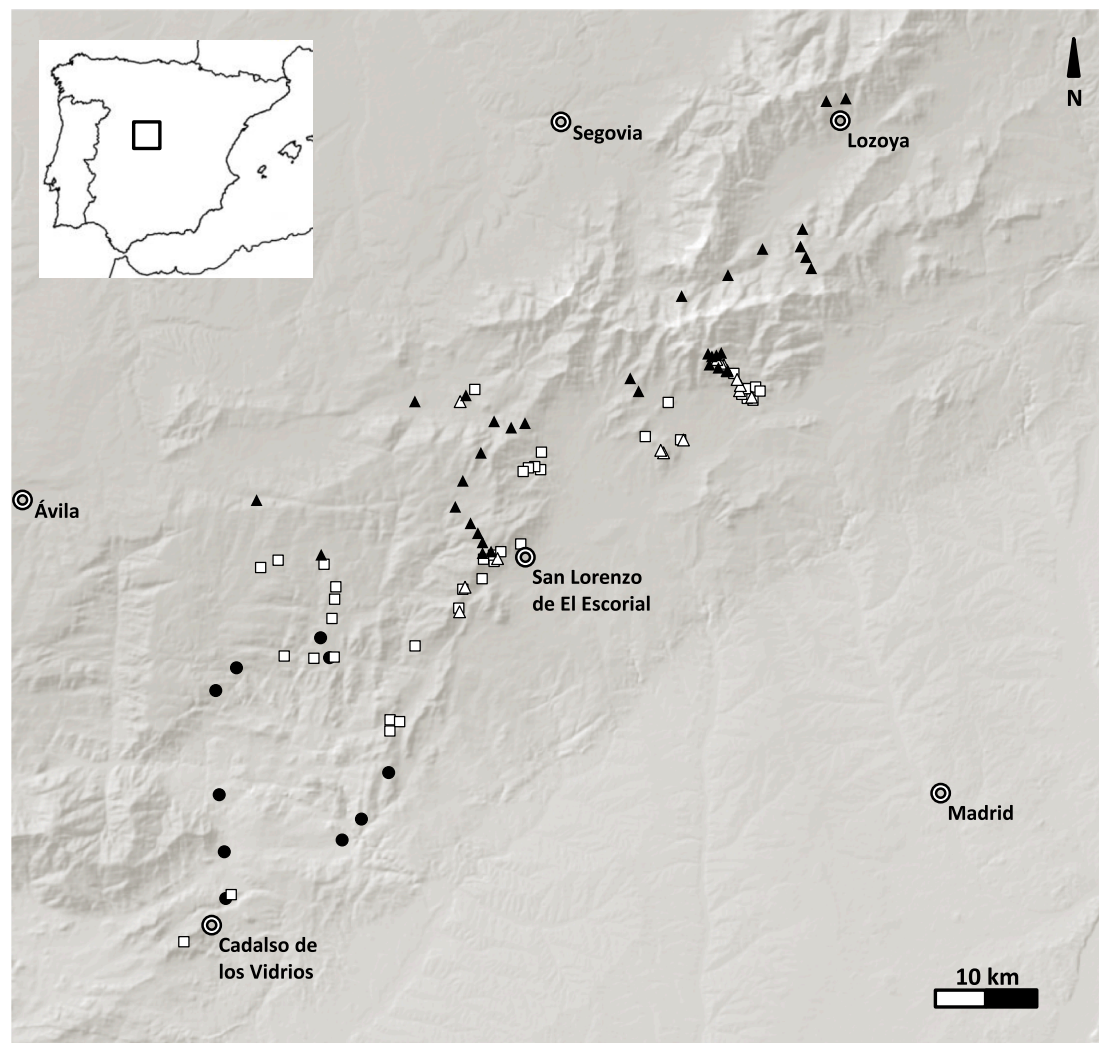

Fig. 1. Map showing the position of the 98 sampling units and the dominant pine species in each of them. Black circles: *Pinus pinea*; white quadrats: *P. pinaster*; white triangles: *P. nigra*; black triangles: *P. sylvestris*. Points are overlaid on a hillshade and major cities and towns are given as reference.

across scales and that, unlike abiotic factors and species, are clearly manageable. To achieve this goal, we will use a set of 24 variables, described at increasing detail as we reduce the spatial scale, and we will analyze PPM incidence separately for different spatial scales, and through a global multiscale approach.

2. Methods

2.1. Study area and pine species

This study was carried out in the Guadarrama and Malagón mountains, a hilly area northwest of Madrid (Spain), showing an elongated shape of more than 100 km in length from southwest to northeast, and covering about 3000 km^2 (Fig. 1). The area is dominated by rocky siliceous substrata (mainly granite and gneiss), and has a Mediterranean climate, with mean annual temperatures ranging from 14 °C at the lowest altitudes (750 m) to 4 °C at summits (Peñalara peak, 2430 m), and mean annual rainfall ranging from 550 to 1500 mm (Ninyerola et al., 2005), with a severe summer drought. The vegetation includes Mediterranean grassland, shrubland, open woodland, sclerophyllous forests, deciduous forests and pine forests. Present and past human land uses, combined with primary ecological factors, are responsible for the current distribution of these vegetation types.

The pine forests of this region have been intensely managed since ancient times. Although there is consensus on the native status of the main pine species (Franco Mugica et al., 1998), it is very difficult to know which forests are of natural origin, which were planted, and which were simply favoured, with the only exception being the 20th century afforested areas, which are adequately documented. *Pinus pinea*, the stone pine, occupies the lower elevations, normally below 1000 m asl, and is almost always mixed to some extent with the holm oak, *Quercus ilex*. Cluster pine, *Pinus pinaster* is abundant between 900 and 1300 m asl, and plays an essential pioneering role, preferring poor, sandy or stony soils. Black pine (*Pinus nigra*) occupies higher altitudes, roughly between 1200 m and 1600 m asl. This species is the least common (Regato Pajares et al., 1992), although some recent plantations have expanded its range. Scots pine (*Pinus sylvestris*) is the most widespread in the region. It is common from 1300 m asl, where it competes with the broad-leaved *Quercus pyrenaica*, and dominates the oromediterranean forests, between 1600 m asl and the treeline, which in the study area is located at about 1900–2200 m asl. Most of these pine forests and plantations are strongly managed, both for extractive purposes (logging, resin or pine nuts) and for livestock grazing, which is in some cases intense. A few are included in one of the four protected areas existing in the region, and therefore have a lower human pressure.

The pine processionary moth is widely present in the study area. The butterflies emerge in July to August, and immediately copulation takes place, so that the females lay their eggs on the pine needles after less than 48 h of life outside. The first instar larvae emerge in September and remain on the trees feeding on pine needles until they descend to the ground in spring and enter the soil to pupate. Integrated control based on pheromone traps (G-traps) and nest boxes for birds is common in the Guadarrama and Malagón mountains, although there is no clear published evidence of the efficiency of this type of treatments. Notwithstanding, we found these are widely applied throughout the entire study area, including the pine forests most affected by PPM.

2.2. Sampling design and measurement of variables

We set 98 sampling points in the study area (Fig. 1), either in pine forests or plantations, to try to sample as diverse a set of observations as possible. Thus, within the limitations imposed by the availability and physical accessibility to pine forests or plantations, we tried to collect the widest possible range of abiotic factors, habitat types, structural configurations, community compositions and intensity of human use, especially with regard to livestock pressure. We then defined three

spatial scales to inspect each sampling point: *stand*, *plot* and *locality*. We considered the stand scale the area covered by pine trees within a 1 ha circle (56.4 radius) centred in sampling points (that is, disregarding the cover of other tree and shrub species). These areas ranged from 0.25 ha to 0.99 ha (average 0.75 ha). We considered the plot scale the whole 1-ha circle, including vegetation other than the pine stands. The locality scale comprised an entire 10 ha-circle (179 m radius) centred in the sampling points.

All stands were visited to record the prevalence and intensity of PPM infestation for four consecutive years (2016–2019) in February-March. We followed the 6-category scale commonly used in Spain for PPM monitoring programs (proposed by Montoya and Hernández, 1991, and followed, among others, in Hódar and Zamora, 2004; Cayuela et al., 2011; Cayuela et al., 2014): 0 = no infestation, 1 = scattered nests, scant defoliation, 2 = defoliation and nests visible, mainly from the stand border, 3 = strong defoliation and numerous nests at the stand border, and 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. The data from the four years were then pooled, with the aim of having, for each stand, an estimate of its vulnerability to the PPM that is more precise and independent from the interannual variability (PPM incidence, hereafter).

Sampling units were described by 16 independent variables measured at the three different spatial scales. These were related to their abiotic conditions, habitat types, species composition, and forest structure and use. The variables were selected among those that have been reported to be related to the incidence of PPM or, for grazing pressure, for constituting a major determinant of the structure and functioning of the forest (supplementary material I). Since some variables were measured at more than one spatial scale, the total number of predictors of PPM effects was 24 environmental descriptors plus the identity of the pine tree species (Table 1). These variables were obtained by field surveys, interpretation of aerial photographs and extracting climatic data from a high resolution (200 m) climatic atlas (Ninyerola et al., 2005). Specific details for each variable are given in supplementary material I.

2.3. Data analysis

Prior to the analysis with the complete set of variables, we conducted an analysis restricted to PPM incidence, 'pine species' and 'elevation', using linear models (LM). This preliminary analysis was carried out in order to have a clear idea of the association between 'elevation' and 'pine species', and also of the relative effect of both variables on PPM incidence in the study region, including the possibility of an interaction between the two.

With the whole set of variables, PPM incidence was modelled using GLMs, model averaging, and following two approaches. First, we built a multiscale model using predictors from the three spatial scales. Second, we built models for each scale separately using the particular predictors measured at each of the three single spatial scales. In all, therefore, four models were built. 'Pine species' was the only predictor common to the four models.

Prior to the GLMs, some predictors were ln (x + 1) or x^2 transformed to reduce their asymmetry (Table 1), and all of them were z-standardised. We avoided simultaneously including in the same model variables with $|r| > 0.5$, always preferring those with higher correlation with PPM incidence (see supplementary material II for the Pearson correlation matrix). Then, for each scale we used all possible combinations of predictors, only including main effects, to fit a complete set of models. Next, to minimise the dependence of the resulting patterns on the selection of single models and to strive for generalisation we identified the strongest set of models and performed model averaging with them (Burnham and Anderson, 2002; Claeskens and Hjort, 2012). We retained those models whose accumulated Akaike weights were ≤ 0.95. We visually checked the residual plots of these models to make sure that the normality and homoscedasticity requirements of the GLMs were met.

Table 1
Descriptive variables taken for the 98 sample units, classified according to their type and the scale at which they were recorded (L, Locality scale; P: Plot scale; S: Stand scale). A brief definition is given, as well as the observed range and, where appropriate, the transformation applied for including them in the models. All variables were z-standardised previous to modelling. More information on the method of measurement of each variable is given in supplementary material I.

| Variable	Type	Scale	Definition	Range	Transformed
Sept – March Temperature (°C)	Abiotic	L	Mean annual temperature of the period from September to March (Ninyerola et al. 2005)	3.5–11.6	
Elevation (m)	Abiotic	L	Elevation of the center of the 10 ha circle	600–1805	
Aspect (radians)	Abiotic	L, P	Angular difference between the aspect of the 10 Ha (L scale) or the 1Ha (P scale) circle and the north.	L: 0.12–3.14 P: 0–3.13	
Slope (%)	Abiotic	L, P	Obtained from the maximum difference in altitude within the 10 Ha (L scale) or the 1 Ha (P scale) circle divided by the diameter	L: 2.8 %-56.1 % P: 0.9 %-70.9 %	
Diversity of habitat types	Habitat	L, P, S	Shannon diversity index obtained from the relative cover of the different habitats recorded within the 10 Ha circle (L scale), 1 Ha circle (P scale) or stand (S scale)	L: 0.11–1.72 P: 0.05–1.60 S: 0.50–2.15	
Pine cover (%)	Habitat	L, P	Cover of pine stands in the 10 Ha (L scale) or the 1 Ha (P scale) circle.	L: 0.25–0.98 P: 0.24–0.99	x^2
Open favourable habitats (%)	Habitat	L, P	Sum of the relative covers of open habitats lacking woody vegetation or rocks, considered to be favourable for pupation, for each of the scales	L: 0–0.45 P: 0–0.65	$Ln(x+1)$
Open unfavourable habitats (%)	Habitat	L, P	Sum of the relative covers of open habitats covered with rocks or woody vegetation apart from pines, considered to be unfavourable for pupation, for each of the scales	L: 0–0.72 P: 0–0.75	$Ln(x+1)$
Clear forest floor (%)	Habitat	S	Sum of the relative covers of bare ground, grassland and moss within the pine stand	0–0.87	$Ln(x+1)$
Number of tree species	Composition	P	Number of tree species	1–8	
Number of woody species	Composition	P	Number of woody species taller than 50 cm	2–14	
Non-host tree cover (%)	Composition	P	Cover of tree species other than *Pinus* spp. and *Cedrus* spp.	0–0.32	$Ln(x+1)$
Pine density (Ha⁻¹)	Structure	S	Density of pine trees taller than 3 m	63–1217	
Canopy cover (%)	Structure	S	Cover of pine tree canopies within the stands	0.05–0.76	
Maturity	Structure	S	Average size class of the stand pine trees	1.33–5.50	
Diversity of pine sizes	Structure	S	Shannon diversity index obtained from the size classes of the pine trees occurring in the stand	0–1.75	
Grazing pressure	Functional	S	Index based on visual evidence of grazer actions on herbaceous vegetation, woody vegetations, soil, and excrement density	0.16–2.83	
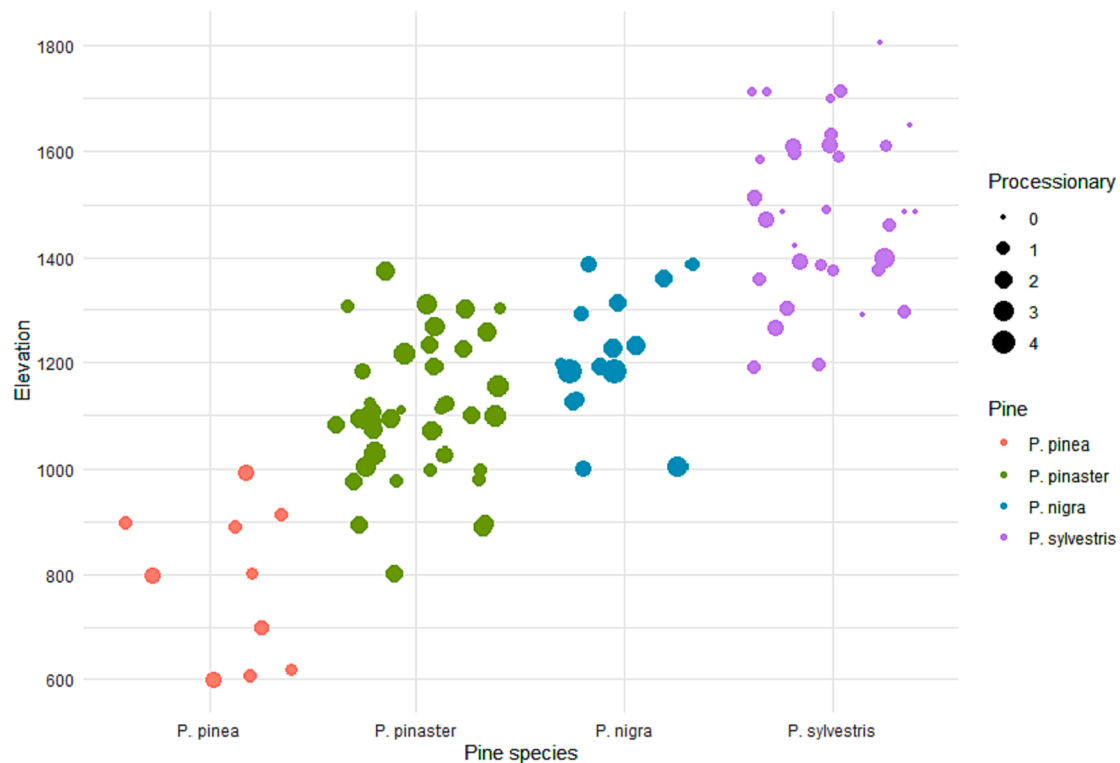
Fig. 2. Plot of the relationship between PPM incidence, pine species and elevation. Each point represents one observation, and circle size represents PPM incidence. Random horizontal jittering added for ease of visualization.

From this subset of models, we estimated the average coefficients (full averaging method) and assessed the relative importance (RIV) of the retained variables (the sum of the Akaike weights for the models in which each predictor appeared). We considered 50 % RIV as a cut-off threshold to differentiate important and unimportant predictors (Burnham and Anderson, 2002). Finally, we assessed pseudo-r^2 for each averaged model as the adjusted r^2-value of a linear model fitting the observed values against the values predicted by the averaged models (Jochum et al., 2017). This pseudo-r^2 value was used as a goodness-of-fit measure for the averaged models. Analyses were performed using R 4.0.3 (R Core Team, 2022) and the package MuMIn (Barton, 2020).

3. Results

PPM incidence ranged from 0 (no incidence in any of the 4 years) to 4.5 in a *P. nigra* stand (Fig. 2). As expected, 'elevation' conditioned belts shared by more than one species. Three pine species coexisted between 1200 m and 1400 m. Preliminary modelling of PPM against 'pine species' and 'elevation' found as best-fit model the one including only on 'pine species (AICc = 246.19; adjusted R^2 = 0.31; p-value = 2.2e^{-08}), with *P. pinaster* and *P. nigra* showing larger PPM incidences than *P. sylvestris* and *P. pinea*. A second model including 'pine species' and 'elevation' yielded a similar fit (AICc = 247.64; adjusted R^2 = 0.31; p-value = 7.6e^{-08}), with lower PPM incidences for upper positions, although this variable was not significant (p-value = 0.375). The model including the interaction showed a less satisfactory fit (AICc = 251.43), with no significant variables. Details of this preliminary modelling are given on supplementary material III.

The average multiscale model presented a pseudo-r^2 of 0.71 (Table 2), and included 11 variables, 7 of which had a RIV > 0.5 (Fig. 3, supplementary material III). Two variables ('pine species' and 'grazing pressure') were included in 100 % of the selected models and showed a strong effect on PPM incidence. *P. pinaster* and *P. nigra* were the most vulnerable species, and *P. pinea* the most resistant, while *P. sylvestris* (taken as the reference level parametrized as the intercept in the models) showed intermediate values. 'Grazing pressure', a variable measured at the stand scale, showed a strong positive effect on PPM incidence. Two other variables at the stand scale, 'diversity of pine sizes' and 'pine density', showed importance values higher than 0.9. PPM incidence was lower for stands with a higher diversity of tree sizes and a higher density of trees. 'Non-host tree cover' and 'open unfavourable habitats', at the plot scale, and 'elevation', at the locality scale, also exerted negative effects. The rest of the variables included in the model had importance values lower than 0.5 and negligible effects.

The models obtained separately for each of the three spatial scales (Fig. 4, supplementary material III) showed less predictive power than the multiscale model (Table 2). 'Pine species' held a RIV of 1 in all spatial scales (Fig. 4). Other variables specific of each spatial scale also showed a RIV of 1 in their respective averaged models: 'grazing pressure' for the stand-scale; and 'open favourable habitats' and 'open unfavourable habitats' both for the plot and the locality scale. It should be noted that 'open favourable habitats' at the locality scale and 'open

Table 2

General descriptors of the average models estimated for PPM incidence for each of the three spatial scales ("Stand", "Plot", "Locality") and for the "Multiscale" model, in which predictors from the three spatial scales were combined. Models were estimated for a sample of 98 observations. More details of each model are given in supplementary material III.

	Original n° variables	N° Variables after deleting correlated	Total set of models	Models used for model averaging	Pseudo-R2
Stand	8	6	64	9	0.65
Plot	10	7	128	13	0.58
Locality	9	7	64	6	0.65
Multiscale	25	11	2048	100	0.70

favourable habitats' at the plot scale had not been included in the multiscale model because of their high correlation with grazing pressure (r = 0.59 and r = 0.51 respectively, see supplementary material II).

4. Discussion

This study represents a major effort to include in a single survey many of the diverse factors previously claimed to influence PPM incidence on pine forests and plantations, along with some novel ones. We used a multiscale approach over a large region with a relatively high sample size, which allowed us to obtain a global view that is probably more generalisable than previous work focusing on a smaller number of environmental descriptors at more local scales. The multiscale model showed that PPM incidence was related to several structural and functional factors, some of them clearly manageable. Thus, it is possible to identify some interventions to reduce the vulnerability of forests and plantations to outbreaks. In addition, the models obtained for each scale were also able to detect some strong relationships, using a smaller set of variables.

Our observations coincide with previous work in recognizing *P. nigra* as a particularly sensitive species to lepidoptera infestation, and *P. pinea* as a very resistant one (Buxton, 1983; Masutti and Battisti, 1990; Stastny et al., 2006; Hódar et al., 2012a). However, our data also show high incidences in *P. pinaster*, a species sometimes considered as resistant in relation to *P. sylvestris* or *P. nigra* (Buxton, 1983; Hódar et al., 2002; Hódar et al., 2012a). Here we observed that incidence on *P. pinaster* stands was clearly greater than that of *P. sylvestris*, and similar to that of *P. nigra*. This result was consistently reached in all the estimated models, whatever the scale and the included variables. One possible explanation for the different vulnerability of *P. sylvestris*, *P. nigra* and *P. pinaster* is that they are a consequence of the elevation, since *P. sylvestris* occupies the higher altitudes, where PPM incidence is lower. Although we cannot rule out this possible interference, it should be noted that in all the models in which both variables were included, the effect of 'pine species' was stronger than that of 'elevation'. Moreover, the three species share an altitudinal range between 1200 m and 1400 m for which PPM incidences in *P. pinaster* and *P. nigra* stands were also higher than those observed in *P. sylvestris*. Our results, combined with other studies, point to a certain dependence of the vulnerability of pines to PPM on the geographical region. Thus, for example, *P. pinaster* populations in our study area would be more similar to those observed in western coastal populations of France and Portugal (Arnaldo et al., 2010 Jacquet et al., 2013) than to those observed in the southeastern mountains of the Iberian Peninsula (Hódar et al., 2002).

After the pine species, grazing pressure showed the second highest effect size on PPM incidence, both in the multiscale and the stand-scale models. This is, to our knowledge, the first study reporting such a relationship. Cattle, the most common livestock type in the prospected pine stands, exerts important effects on the forest structure, especially on the understory, the herbaceous layer, and the soil. Grazed, and especially overgrazed, patches have less aboveground plant biomass, and are more exposed to sunlight, creating the appropriate warmer conditions in the upper soil layers for the pupation of caterpillars (Dulaurent et al., 2011a). Although grazing pressure could be measured only at the stand scale, it was indeed correlated with the surface of open habitats favourable for pupation both at the plot and the locality scale. Each of these three variables were the most predictive in their respective single-scale models, and the connection between them is immediate: landscapes with more surface of open patches lacking woody vegetation have the capacity to sustain larger grazer densities, and at the same time, a greater grazing pressure will keep these patches free of colonization of pine trees and other woody species. Interestingly, the amount of forest floor clear of woody vegetation ('clear forest floor') did not predict PPM incidence, even though it includes the open areas at the stand scale. We believe that the shading of the pines is determinant in excluding these spaces as suitable pupation sites.
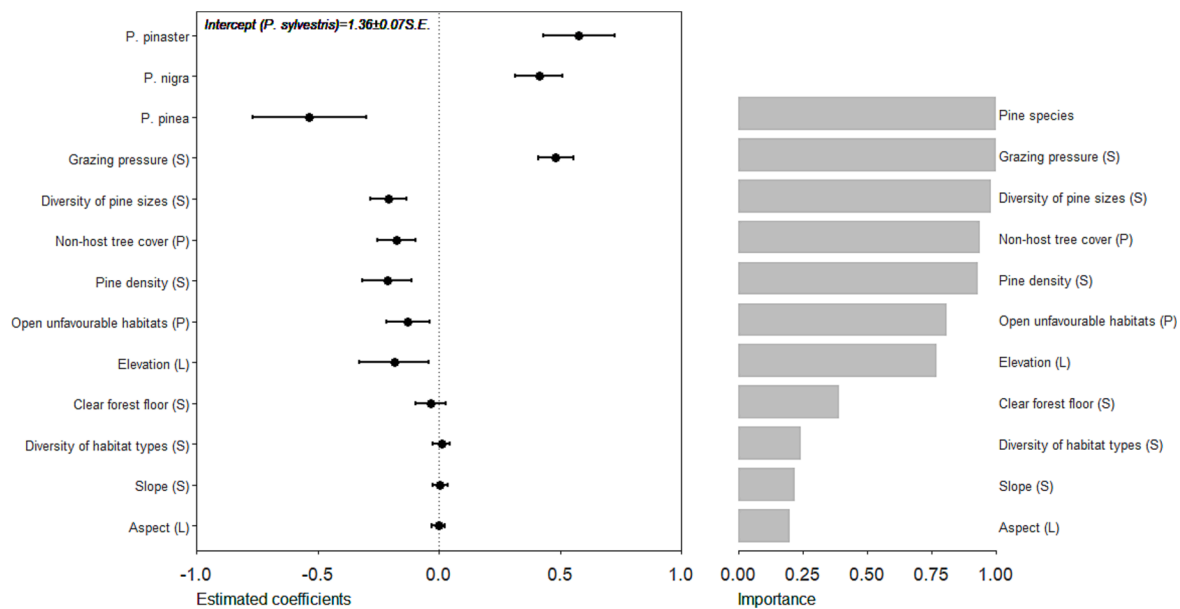
Fig. 3. Model averaging of the 100 models estimated for PPM incidence following the "Multiscale" approach. The average coefficients (±S.E) are presented on the left side and the relative importance values (RVI) of each predictor on the right. In brackets, the scale at each predictor was measured (L, Locality scale; P: Plot scale; S: Stand scale).

Habitat complementation between pine stands that provide leaves for the feeding of larvae and open patches that provide habitats for pupation has been previously underlined by Dulaurent et al., 2011a, and supports a higher abundance of PPM in the boundaries between the pine stands and the clearings (the 'edge effects' in Buxton, 1983; Samalens and Rossi, 2011; Dulaurent et al., 2012). Our data indicate that the ecological characteristics of the clearings are critical for this habitat complementarity effect. We detected that, both at the locality and the plot scale, the clearings defined as unfavourable for pupation reduced the incidence of PPM. These areas corresponded, essentially, to patches occupied by bushes (44 % at the locality scale, and 51 % at the plot scale) and, more secondarily, to rocky outcrops (15 % at the locality scale of, and 21 % at the plot scale). Torres-Muros et al. (2017) found that pupal survival was much lower in shrubland when compared with habitats with only herbaceous vegetation. This effect can be a consequence not only of the abiotic limitations of shrublands (e.g., lower temperatures under the bush canopy), but also by community-level effects, such as the better development of certain parasitoids in woody environments (Dulaurent et al. 2011b). The hypothesis that it is the characteristics of the clearings, and not the presence of the clearings themselves, that predicts PPM incidence is supported by some of the negative results obtained in our study. For example, the relative area occupied by pine patches showed no relationship with PPM at any scale, which implies that nor did the total surface occupied by the intervening clearings. In addition, none of the indices of habitat diversity were retained by the models at any of the scales. These indices are blind to the nature of the patches, and therefore may yield similar results for spatial compositions prone or adverse to pupation.

The structure of pine stands was determinant of PPM incidence. The incidence decreased with pine tree density at the stand scale, a result in accordance with the negative relationship found by Régolini et al. (2014) between percentage of infested trees and stand density. Castagneyrol et al. (2020) found that a higher pine density increased the number of nests per plot but reduced the proportion of pines with at least one PPM nest. The reduction in PPM incidence at the stand scale observed in our study could be a consequence of a better survival of larvae on sun-exposed trees (Breuer et al., 1989), although Régolini et al. (2014) also discuss the possibility that such a pattern emerges from the way in which gravid females select trees. Another possible explanation is

that more dense stands increase the probability that a tree will avoid gravid moths (similarly to the 'dilution' of herbivores pointed out by Castagneyrol et al. 2020), which is particularly plausible if PPM populations are controlled by other factors, e.g. the availability of suitable sites for pupation.

The incidence of PPM was also dependent on the variability of tree sizes, with higher infestations in pine stands composed of pine trees more homogeneous in size. A greater diversity of sizes means that some crowns will provide shade to others, perhaps inhibiting the spread of the lepidoptera across the whole stand. Age-class diversity also implies a greater structural complexity, which is usually associated with a more diverse fauna and thus a higher likelihood of a top–down regulation of herbivores by predators and pathogens (Bouget and Duelli, 2004; Bereczki et al., 2014). A number of natural enemies, including birds (Barbaro and Battisti, 2011), parasitoid hymenoptera (Tiberi, 1990; Schmidt et al., 1999, Hódar et al., 2021), fungi (Er et al., 2007) and ants (Way et al., 1999) have been identified as regulators of PPM populations (De Boer and Harvey, 2020). While the conditions that maximise the joint effect of all of these have not been addressed, it is plausible that stands with more structural diversity harbour a greater diversity of these natural enemies. It is important to note that predation and other biotic factors not considered in this study may be mediating some of the observed responses, and therefore future research exploring the potential interactions between biotic and abiotic factors should be addressed. Forest longevity, on the other hand, did not result in a reduction in the incidence of PPM. This is consistent with findings by Régolini et al., 2014, showing that older and taller trees have higher infestation levels, perhaps because of their higher insolation. We certainly observed high infestation levels in some pine stands mainly composed of old trees, lacking intermediate age classes and with no regeneration.

Our data also confirmed a greater resistance to PPM of those pine forests or plantations that, at the plot scale, presented a greater coverage of non-host trees. In general, mixed forests are less prone to pest insect damage than monocultures (Guo et al., 2019), a pattern that has also been observed for pine forests affected by PPM (Dulaurent et al., 2011a; 2012; Castagneyrol et al., 2020, Poeydebat et al., 2021). As with structural diversity, explanations for the positive link between mixed forests and pest regulation are commonly based on the "natural enemy hypothesis" (Jäkel and Roth 2004; Jactel and Brockerhoff, 2007; Guyot
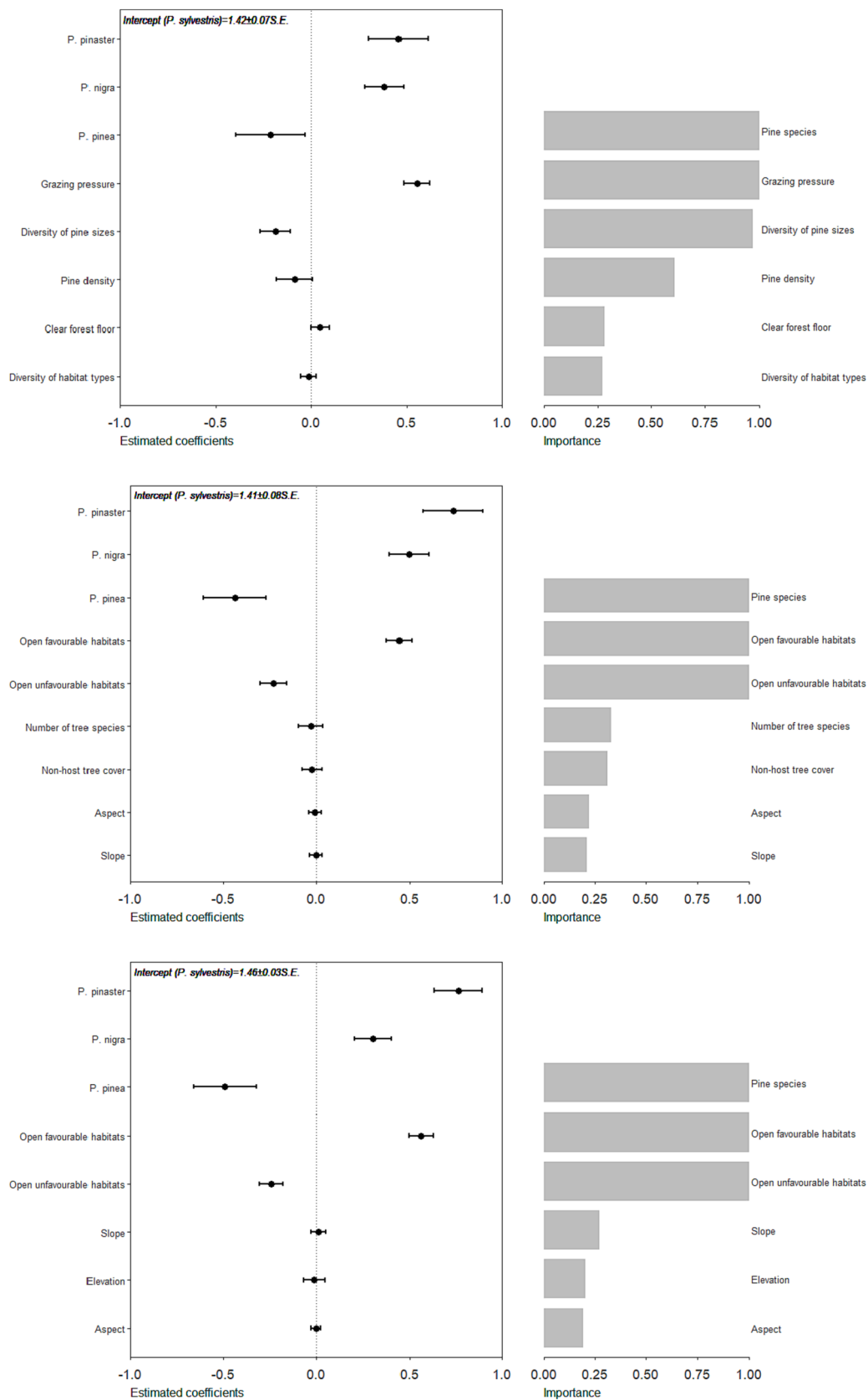
Fig. 4. Model averaging of the models estimated for PPM incidence at the scales of "stand" (a, 64 models), "plot" (b, 128 models) and "locality" (c, 64 models). The average coefficients (±S.E) are presented on the left side and the relative importance values (RVI) of each predictor on the right.

et al., 2015; Klapwijk et al., 2016). However, our data indicate that the reduction in PPM incidence would be a consequence of the increase in the coverage of non-host tree species, and not so much the species diversity (neither 'number of tree species' or 'number of woody species' showed any effect on PPM incidence), which suggests a density effect related to a lower host availability (Damien et al., 2016). Various mechanisms can explain this effect: for example, Hódar et al. (2002) propose that the unsuitable host trees could act as sinks for the gravid moths, given their limited capacity to locate and colonise the most suitable pines, while Castagneyrol et al. (2014) and Dulaurent et al., (2012) suggest that certain non-host trees (e.g. *Betula*) or structures (broadleaved hedgerows) reduce pine apparency, which disrupts visual cues used by female moths to select pine trees for oviposition. Finally, Poeydebat et al. (2021), who used an experimental approach, proposed that higher resistance in mixed pine-birch plots was possibly related to disrupting non-host volatiles, but also to a reduction in the amount of host pine resources due the presence of non-host trees.

Finally, we found very weak effects, if any, on abiotic factors on PPM incidence. Elevation showed, as expected, a negative coefficient in the models, but its importance and effect was low. This is somewhat surprising, since the role of elevation (highly correlated to temperature) in limiting regional distributions is well documented (Hódar and Zamora, 2004; Battisti et al., 2005; Battisti et al., 2006; Buffo et al., 2007; Barbaro et al., 2013). We believe that at the scales considered here the effects of other structural and functional factors are much stronger, thus blurring the role of temperature. Other geomorphological factors related to productivity (aspect and slope) did not show any clear relationship with PPM incidence.

5. Conclusions

Our study has shown that many of the factors that predict PPM incidence in pine forests and plantations are a consequence of human interventions or are at least clearly manageable, which supports and extend proposals made in previous works (e.g. Hódar et al., 2002, 2012b, 2015, Hódar, 2015, Doblas-Miranda et al., 2018). PPM vulnerability is greater in structurally simple pine forests (low cover of tree species other than pines, low tree size variability), with strong grazing pressure and abundant open spaces without woody vegetation. Thus, to reduce damage by PPM, pine forests and plantations should be managed to avoid oversimplified forest structures, like those consisting of just pines and open spaces as in parkland landscapes. Patches of non-host tree species should be promoted, as well as some presence of shrubs in open areas. This implies avoiding overly intensive uses, including overgrazing and overly aggressive silvicultural management techniques leading to an excessive increase in bare soil. Notably, some of the stands showing the highest levels of PPM were former pastureland areas, which were afforested in the twentieth century but still keep a substantial amount of livestock.

Forest management should not be restricted to a one-dimensional perspective. A simplistic interpretation of our results could lead to the misconception that grassland fragments and livestock grazing should be eradicated from pine forests to reduce PPM incidence. This type of management would produce, among other major problems, a strong increase in fire risk, which already shows a growing trend in the Western Mediterranean (Pausas and Fernández-Muñoz, 2012). We advocate a multifunctional management model, which integrates the prevention of fire risk, PPM incidence, and other threats that are currently spreading in Mediterranean pine forests, such as root disease caused by fungi of the genus *Armillaria* (Mesanza et al., 2017) or the pine wilt disease caused by wood nematodes (Abelleira et al., 2011). Regarding PPM, a certain incidence of PPM should be assumed as part of the natural functioning of the system, while minimizing the risk of severe outbreaks. Uses like logging or grazing are some of the ecosystem services provided by Mediterranean forests, and therefore they should be maintained in most cases, although regulated to guarantee their sustainability. An example

of such a management approach is seasonal grazing, which maintains a sustainable livestock load in forests during the peak months of productivity, but removes livestock during part of the year, thus avoiding intensive use that compromises the ecological functioning of the system (Carmona et al., 2013; Camarero et al., 2018).

CRediT authorship contribution statement

Francisco M. Azcárate: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **Javier Seoane:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing. **Mariola Silvestre:** Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data availability https://doi.org/10.6084/m9.figshare.21749369.v1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120728.

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