Remote-sensing and tree-ring based characterization of forest
defoliation and growth loss due to the Mediterranean pine
processionary moth

Gabriel Sangüesa-Barreda¹, J. Julio Camarero^{2,3*}, Alberto García-Martín^{4,5}, Rodolfo
Hernández⁶ and Juan De la Riva^{5,7}

¹Instituto Pirenaico de Ecología (CSIC). Avda. Montañana 1005, Apdo. 202, 50192 Zaragoza,
Spain.

²Dept. d'Ecologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, España.

³ARAID, Instituto Pirenaico de Ecología (CSIC). Avda. Montañana 1005, Apdo. 202, 50192
Zaragoza, Spain.

⁴Centro Universitario de la Defensa de Zaragoza. Academia General Militar. Ctra. de Huesca,
s/n. 50090 Zaragoza, Spain.

⁵Grupo GEOFOREST- Instituto Universitario de Ciencias Ambientales (IUCA), Universidad
de Zaragoza.

⁶Laboratorio de Sanidad Forestal. Servicio Provincial de Agricultura, Ganadería y Medio
Ambiente de Teruel. Dpto. Agricultura, Ganadería y Medio Ambiente, Gob. Aragón,
C/Agustín Planas Sancho 10, 44400 Mora de Rubielos, Teruel, Spain.

⁷Departamento de Geografía y Ordenación del Territorio, Universidad de Zaragoza, C/Pedro
Cerbuna, 12, 50009 Zaragoza, Spain

*Corresponding author:

Dr. J. Julio Camarero

ARAID-Instituto Pirenaico de Ecología, CSIC.

Avenida Montañana 1005, Zaragoza E-50192, Spain.

E-mail: jjcamarero@ipe.csic.es

Tel. 0034-976-716031, Fax: 0034-976-716019

Abstract

Outbreak insects are among the major biotic disturbances affecting Mediterranean forests by reducing their growth and vitality through severe defoliations. Despite their relevance for the management of these drought-prone areas, we lack information on their long-term spatio-temporal dynamics. We combine remote sensing (vegetation indexes) and dendrochronological information (basal area increment, BAI) to assess the effects of pine processionary moth (*Thaumetopoea pityocampa*, PPM) defoliations on growth and cover changes of several pine species, mainly *Pinus nigra*. We compared both datasets with a long-term field survey of PPM stand defoliations carried out in eastern Spain during the period 1970-2012. Lastly, we fitted linear-mixed models of BAI using as predictors climatic variables and a multi-scalar drought index to distinguish drought-related growth reductions from those attributed to PPM outbreaks. PPM severe defoliations mainly affected edge or low-density stands. Several vegetation indices (Moisture Stress Index, Normalized Burn Ratio and Normalized Difference Infrared Index) reflected the cover decrease corresponding to severe PPM defoliations. We found that trees affected by severe PPM defoliations took two to four years to recover BAI values similar to those observed before the outbreak. The combined use of remote sensing and dendrochronology allows monitoring the impact of outbreak insects at ample spatial and temporal scales. We consider both powerful tools to further assess the interacting effects of climate warming and PPM dynamics on drought-prone forests.

Keywords: basal area increment; dendroecology; Landsat images; *Thaumetopoea pityocampa*; vegetation indices.

1. Introduction

Outbreaks of defoliating insects represent one of the major biotic disturbances of Mediterranean forests negatively influencing the growth and persistence of damaged trees (Jacquet et al., 2012). Outbreaks may affect extended areas and represent a major stressor of these drought-prone forests (Dajoz, 2000; Barbosa et al., 2012). Despite their relevance, there is a lack of information considering large spatio-temporal scales (50-150 km², 10-50 years) on how outbreak species modify the structure and dynamics of affected stands. The few available datasets are field observations of stand defoliation which usually lack precise data on the loss in vigour and the growth reduction of affected areas (but see Montoya and Hernández, 1998). Thus, we need more reliable information on how outbreaks of defoliating insects disturb Mediterranean forests to ascertain if some stands or periods are more prone to experience outbreaks than others. These data should allow determining if outbreaks are increasing or decreasing in severity, frequency and extent as related to climate warming (Raffa et al., 2008) or due to changes in land-use (Lockwood and DeBrey, 1990).

The outbreak effects on forest growth and vigour at large spatio-temporal scales may be inferred by using remote sensing or aerial survey datasets (Goodwin et al., 2008; Dennison et al., 2009; Eklundh et al., 2009), and dendrochronological reconstructions of past outbreaks (Esper et al., 2007). To our knowledge, no study has attempted to combine both sources of information to assess the occurrence of insect outbreaks across Mediterranean drought-prone forests (but see examples from boreal and subalpine forests in Babst et al., 2010; De Rose et al., 2011; Magnussen and Alfaro, 2012). If successful, the combination of both approaches would allow: (i) determining if outbreaks are related to specific climatic or site conditions, and (ii) reducing the costs of

field surveys by focusing on specific periods or areas. Finally, these assessments of defoliations must necessarily be calibrated with field data.

The pine processionary moth (*Thaumetopoea pityocampa* Dennis & Schiff., hereafter abbreviated as PPM) is one of the most important defoliator insects in the Circum Mediterranean area, mainly affecting evergreen conifers such as *Pinus* and *Cedrus* species (Masutti and Battisti, 1990; Montoya and Hernández, 1998). Therefore, the PPM constitutes a good model species to analyze the effects of outbreaks on forest cover and growth changes at large scales. PPM larvae usually feed on young needles during autumn and winter (Démolin 1969). Defoliations negatively affect the height and radial growth, increase the mortality rate of saplings and reduce the reproductive ability of trees (Hódar et al., 2003; Carus, 2004; Hernández et al., 2005; Kanat et al., 2005; Palacio et al., 2012). Some authors describe PPM outbreaks occurring every six years on average (Battisti, 1988; Hódar and Zamora, 2004), while others suggest no cyclic behaviour of the PPM populations (Gery and Miller, 1985).

Here, we perform a multi-proxy assessment of the effects of PPM outbreaks on defoliation and growth of Mediterranean pine forests by comparing fine-resolution remotely sensed vegetation indices and dendrochronological reconstructions of wood production. The remote-sensing assessment of defoliations is related to spatially derived information (topography, forest features, and soil types) to define areas prone to PPM outbreaks. Further, the tree-ring reconstructions of PPM outbreaks are compared with local climate data to infer the effects of climatic stressors (e.g., drought) on growth. We aim: (i) to determine the vegetation indices which better reflect the effects of PPM outbreaks on defoliation intensity, and (ii) to perform dendrochronological reconstructions of severe PPM defoliations. In both objectives we compare our inferences with a 43-year long field survey of stand defoliations (period 1970-2012).

2. Materials and methods

2.1. Study area, defoliation degree and analysis.

The study area is located in eastern Spain (Sierra de Gúdar, Teruel, Aragón; Figure 1). It includes forests of several pine species, namely: *Pinus sylvestris* L., *Pinus nigra* Arn. subsp. *salzmannii* (Dunal), *Pinus pinaster* Ait. and *Pinus halepensis* Mill. This area covers 128 km² and it was selected because it encompasses a wide altitudinal gradient from 1000 to 1800 m.a.s.l. where all the aforementioned pine species are naturally distributed (Montoya 1970). The understory vegetation is dominated by junipers (*Juniperus sabina* L., *J. communis* L.) and shrubs (*Berberis vulgaris* L., *Genista scorpius* L.). The soils are basics and calcareous. The climate is Mediterranean with continental influence. The mean annual temperature is 10.2 °C and the total annual precipitation is 519 mm (see Supplementary Information, FigureS1 and TableS1).

PPM defoliations were annually recorded in late winter by the Aragón Forest Health Laboratory located at Mora de Rubielos (Teruel, Spain) from 1970 up to 2012. They carried out field surveys by following the existing forest demarcation according to silviculture and topographical features, and using a PPM damage visual scale recorded at the stand level considering six levels (see Montoya and Hernández, 1998). To simplify further analyses, we re-classified the PPM damage scale into three stand defoliation degrees (hereafter abbreviated as DD): undamaged trees with some PPM nests but no defoliation in the crown (DD = 1, class DD1), partial to moderate defoliation, mostly affecting stand edges and isolated trees (DD =2, class DD2), and severe defoliation affecting the whole stand (DD = 3, class DD3; Figure 2).

2.2. Climate data

To obtain a regional climatic series characterizing the study area, local data from six meteorological stations were combined into a regional mean from the period 1970-2012 (Supplementary Information, Figure S1 and TableS1). To estimate the missing data for each station and to combine them, we used the MET program from the Dendrochronology Program Library (Holmes, 1994). For each station, monthly variables (temperature and total precipitation) were transformed into normalized standard deviations to give each station the same weight in calculating the average monthly values for each year.

To estimate the drought intensity experienced by the study forests we used the Standardised Precipitation-Evapotranspiration Index (SPEI). This drought index shows the cumulative water stress for several months on different time scales with negative and positive values corresponding to dry and wet periods, respectively (Vicente-Serrano et al., 2010). The SPEI values for the period 1971-2010 and the 0.5° grid including the study area were obtained from the website <http://sac.csic.es/spei/index.html>. According to that index, the driest years of the area for the study period were: 1979, 1983, 1999, 2005 and 2009.

2.3. *Remote sensing images and derived vegetation indices*

To perform remote-sensing analyses we selected Landsat images because they show an adequate temporal, spectral and spatial resolution for both regional and local scales. Landsat images have been used in numerous studies on forest defoliation induced by insects (Royle and Lathrop, 1997; Heikkilä et al., 2002; Franklin et al., 2008; Thayn, 2013). Besides, the Landsat program currently offers the longest and more consistent historical archive of satellite images (Hantson and Chuvieco, 2011).

Images were taken in 15 different years (path 199, row 32) from 1987 to 2011 (Table 1). We selected images without clouds or with a minimum cloud coverage. Images were always captured between March and May, when the maximum period of PPM defoliation occurs (Montoya and Hernández, 1998). These images were obtained from three different datasets: (i) the U.S. Geological Survey (USGS, <http://earthexplorer.usgs.gov/>), (ii) the European Space Agency (ESA), and (iii) the Spanish Remote Sensing Program (PNT, <http://www.ign.es/PNT/>).

To better identify true changes, multi-temporal studies require a previous geometric and radiometric homogenization of input images (Hantson and Chuvieco, 2011). As a result, these two pre-processing techniques were applied to obtain radiometric variables suitable to be compared with field PPM defoliation data.

The geometric rectification was only applied to images obtained from PNT, since USGS and ESA images were acquired geometrically corrected with an estimated Root Mean Squared Error (RMSE) lower than 1 pixel. A similar error were found for the PNT images using a second-order polynomial model and ground control points taken from high-resolution ortho-photographs (pixel size equal to 1m^2). Finally, the geometric quality of all imagery dataset was evaluated by comparing ten characteristic points in the scenes with the same points in high-resolution ortho-photographs.

The radiometric correction addresses atmospheric and topographic effects in the surface reflectivity registered in Landsat images. In this process, the relative data on surface reflectivity given in digital numbers is transformed into an absolute form in reflectance values. In areas of rough terrain, as the study area, a good topographic normalization is required to compensate for the varying solar illumination associated with the irregular shape of the terrain (Riaño et al., 2003). Most authors agree that independently of the topographic correction method selected, the critical fact is to

estimate specific correction parameters for the different land-covers present in the study area (McDonald et al., 2000; Hantson and Chuvieco, 2011). As a result, we used the empiric-statistic topographic normalization method proposed in the PNT for Landsat images (Hantson et al., 2011). We applied the method estimating its specific parameters independently for areas with a low-medium or high Normalized Difference Vegetation Index (NDVI) values ($NDVI < 0.4$ or $NDVI > 0.4$). The performance of topographic shade removal was validated in all the images taking into account the decrease in the correlation coefficient between the local incidence angle and the spectral bands after the application of the topographic normalization. All this procedure was done with the digital image processing software ERDAS IMAGINE 2010 (ERDAS, USA). Lastly, we calculated several vegetation indices widely used in similar studies on forest insect defoliation using remote sensing data (see their definitions and acronyms in the Supplementary Information, Table S2).

2.4. *Linking PPM defoliations data to radiometric data*

Since forest edges and isolated trees are prone to severe PPM defoliations (Montoya and Hernández, 1998), we delimited the major forests in the study area with a high-resolution ortho-photographs. In these delimited areas we applied an internal 200-m wide buffer and then we extracted their spectral information. This was done using the software ARCGIS 10.0 (ESRI, USA).

To test the responsiveness of changes in vegetation indices to PPM defoliations, we compared 30 forests with different defoliation degrees (10 forests per DD) for the year 1992, which was the one with most severe PPM defoliations recorded in the study area. These forests were dominated by *P. nigra*, and presented similar values of density, aspect and slope. We compared the observed DD and the vegetation indices values

using ANOVAs followed by post-hoc T2 Tamhane tests. The values of the different vegetation indexes showed normal distributions. We also checked the presence of spatial autocorrelation of the vegetation indexes by using Moran correlograms, which indicated the absence of significant spatial patterns (*results not presented*). The same forests were used for the study of the temporal variability of remote-sensing derived vegetation indexes. Finally, we spatially compared according to the stand DD one year with high DD (1992) and one without defoliations (2000).

2.5. Dendrochronological methods

Remote sensing data were supplemented with a dendrochronological sampling on six forests with recent PPM defoliations and dominated by *P. nigra* (Table 2). This pine species is the most susceptible to PPM defoliations (Montoya and Hernández, 1998). Field sampling was done in autumn 2012 using standard dendrochronological methods and selecting isolated trees or those located near forest edges (Fritts, 2001). Two cores were taken at 1.3 m using a Pressler increment borer. Sixty seven trees were cored twice to give a total sample size of 134 radii. The wood samples were air-dried and visually cross-dated. A minimum of 10 to 12 individuals (20-24 radii) were processed for each site. Tree rings were measured to the nearest 0.01 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was checked using the program COFECHA (Holmes, 1983).

To eliminate the decreasing tendency of tree-ring widths as the tree ages and the stem enlarges we calculated the basal area increment (hereafter abbreviated as BAI), which is a more biological meaningful variable to quantify growth changes than tree-ring width. The BAI was calculated from tree-ring widths as the difference between consecutive cross-sectional basal areas (BA) estimated for years $t + 1$ and t as:

$$BAI_{t+1} = BA_{t+1} - BA_t = \pi((CL_t + TRW_{t+1})^2 - (CL_t)^2) \quad (1)$$

where CL is the core length measured for dated tree-rings formed in years $t+1$ and t and TRW is the tree-ring width.

2.6. Linear mixed-effects models of basal area increment

Past insects outbreaks can be reconstructed using several dendrochronological procedures such as: comparing growth series of host vs. non host tree species, using a regional “climate-driven” host chronology (instead of the non-host chronology), establishing pointer years (extremely narrow rings caused by the defoliation) or identifying morphological or anatomical signatures of the defoliation (Swetnam et al. 1985, Rolland et al. 2001, Sutton and Tardif 2005, Paritsis et al. 2009). Here, we use a method similar to the second one aforementioned, given that all pine species in the study area are potential PPM hosts, and applied it to BAI data. To determine which climatic variables best describe BAI and to establish lower growth periods attributable to PPM defoliations, we adjusted the following linear mixed-effects models of the BAI:

$$Y_i = X_i\beta + Z_ib_i + \varepsilon_i \quad (2)$$

where Y_i represents BAI, and β is the vector of fixed effects (climate variables or drought indices), b_i is the vector of random effects (tree identify and tree age), X_i and Z_i , are fixed and random effects regressor matrices, and ε_i is the within group error vector.

We used as predictors seasonal climatic variables (mean temperature, total precipitation and mean SPEI) by considering the climatic variables most related with *P. nigra* growth according to previous studies (Camarero et al., 2013). We used the following seasons: autumn (previous September to November) and winter (December to

February) prior to the growth year, spring (March to May) and summer (June to August) of the growth year. The May SPEI calculated at a timescale of 9 months was also selected following a previous work (Pasho et al., 2011; Vicente-Serrano et al., 2012).

Linear mixed-effects models were fitted to BAI data of the six study sites (MP, AM, RO, FU, LR and AC). BAI of the previous year was also introduced into the model as an additional fixed effect to account for the first-order temporal autocorrelation of growth, and tree age was introduced as a random factor. Residuals of the models were checked for normality, homoscedasticity and autocorrelation. The effects of climate and drought indices on BAI were tested and compared with a null model considering BAI as a constant. We also evaluated the existence of multicollinearity among fixed effects (climate variables and SPEI) by calculating the Variance Inflation Factor which was always lower than 3 suggesting no redundancy problems (Zuur et al., 2009). The models were fitted using the restricted maximum likelihood method. We used an information-theoretic approach for multi-model selection based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). We also calculated the difference in AICc between each model and the best one (Δi), and the relative probability that the model i was the best one for the observed data (W_i). We considered models with a substantial support those in which the $\Delta AICc$ between models was less than 2 (Zuur et al., 2009). Finally, the BAI residuals of the models were related to site levels of PPM defoliation. We fitted linear mixed-effects models using the *nlme* library (Pinheiro and Bates, 2010) of the R statistical suite version 3.0.0 (R Development Core Team 2013).

3. Results

3.1. Spatio-temporal relationships between PPM defoliations and vegetation indices

As expected, we found a higher number of years with severe defoliations (DD3) in *P.nigra* forests than elsewhere (Figs. 1 and 2). The vegetation indices most strongly related to PPM defoliation degrees were the Moisture Stress Index (MSI), the Normalized Difference Infrared Index (NDII) and the Normalized Burn Ratio (NBR)(Fig. 3). MSI values were positively associated to the PPM defoliation degree, whereas NBR and NDII were negatively related to it (Fig. 4). We observed high MSI values and low NBR and NDII ones in years with severe PPM defoliations such as 1992 and 1995 or even after moderate defoliations (2010). On the contrary, we found low MSI values and high NBR and NDII ones during periods without PPM defoliations (2000, 2003 and 2007).

In a spatial context, the MSI showed different patterns in two contrasting years characterised by high (1992) or absent (2000) PPM defoliations (Fig. 5). Further, these different patterns in the vegetation index were more noticeable when considering sites defined as PPM-prone areas. The areas recognised as severely defoliated by the PPM (high MSI values) in 1992 coincided with the most defoliated forest demarcations found in the field survey. Similar results were found in the case of other vegetation indices suitable for detecting PPM defoliations (Supplementary Information, Figure S2).

3.2. *Effects of PPM defoliations on basal area increment*

The linear-mixed models of basal area increment (BAI) for *P. nigra* showed that the most significant climate drivers of BAI were the positive effect of May SPEI (MP, AM and RO sites) and winter maximum temperature (FU and LR sites) (Table 3; see also Supplementary Information, Table S3). Besides, BAI was also negatively affected by the maximum temperatures of the previous autumn and the current summer. On the contrary, warmer spring maximum temperatures enhanced BAI.

We observed a BAI decrease after years with severe PPM defoliation (Fig. 6). We found growth reductions in periods with consecutive moderate (DD2) or strong PPM defoliations (DD3; Supplementary Information, Fig. S3). On average, defoliated trees took from two to four years to recover BAI values similar to those observed before the PPM outbreak. The growth reductions appeared in all study sites, corresponding to negative residuals of the climate-modelled BAI values, and coincided with periods of PPM defoliations affecting the whole study area (1978-1985, 1990-1992, 1995-1996). Years with negative BAI residuals and severe PPM defoliations usually did not coincide with dry years, suggesting that those growth declines can be attributed to PPM-induced canopy defoliations.

4. Discussion

We explored a multi-evidence detection methodology to assess the spatio-temporal scales of PPM outbreaks and related defoliation in Mediterranean pine forests. The study area constitutes an ideal framework for that purpose since: it contains several pine host species subjected to frequent PPM outbreaks across a wide environmental gradient (particularly *P. nigra*), and the history of PPM defoliations has been carefully described there for a 43-year long period. Our findings provide similar answers irrespective of the source, namely a reduction of tree radial growth and a decrease in tree cover reflected by changes in vegetation indices during periods with severe or moderate PPM defoliations. Further, our findings indicate that *P. nigra* trees take on average two to four years to recover growth levels similar to those observed before the outbreak. This recovery time seems to depend on the site characteristics of each forest. Further analyses could compare PPM-defoliation growth recovery and site characteristics in wide dendrochronological networks.

We found noticeable changes in some of the evaluated vegetation indices (NBR, NDII and MSI) in response to PPM canopy defoliations. The best spectral regions for PPM outbreak detection were near- and mid-infrared reflectance bands (bands 4, 5 and 7 in Landsat) which could capture a fast reduction of pine foliage and the consequent reduction in tree evapotranspiration (Chuvieco, 2010). In conifer forests the MSI was better than the NDVI for distinguishing forest damages because the former index showed significant relationships with decreases in canopy greenness (Vogelmann et al., 2009). NBR and NDII were also reliable indicators of insect outbreaks with different sensors and tree species (Beurs and Townsend, 2008; Wang et al., 2010; Meigs et al., 2011).

We also tried to collect and analyze satellite images obtained in different years to provide a long temporal perspective of PPM defoliation as has been done with other outbreak insects (Goodwin et al., 2008). We paid particular attention to periods of severe PPM defoliations (1991-1992, 1995), which allowed assessing the spectral variation during outbreaks, and also detecting the recovery process after the defoliations. In addition, Landsat images provided reliable results since the study pine forests were mainly monospecific and had high cover values. Lastly, we dedicated an additional effort to delimit PPM-prone areas using previous research (Montoya and Hernández, 1998) since Mediterranean forests are characterized for being highly heterogeneous due to topographical, climatic or land-use disturbances. Future studies should consider carefully this issue by focusing on PPM-prone vegetation patches at a landscape level.

The periods subjected to successive PPM defoliations were characterized by decreases in tree cover and a reduction on basal area increment of most *P. nigra* trees and forests. This growth decline loss was not solely explained by regional drought

stress, and could be attributed to PPM defoliations. However, we also noted that such radial-growth decrease was also contingent on local conditions since the relative importance of climatic drivers of growth differed among forests. These results are in agreement with a recent review showing a relative growth loss (in the 20-80% range) in trees affected by severe PPM defoliations (Jacquet et al., 2012). We found that the residuals of linear-mixed models of BAI based on climatic predictors allowed detecting growth reductions which may be attributed to PPM defoliations. It is unlikely that the effects of consecutive PPM defoliation on tree growth leading to the formation of 2-3 narrow annual rings could be confused with that of regional dry years, characterized by low SPEI values and a marked 1-year long growth depression (Granda et al. 2013). Therefore, we need long growth and PPM-defoliation series to disentangle the effects (and potential synergies) of climatic stress and outbreaks. Linear-mixed models allowed addressing individual- and stand-level growth data, which we consider important to better identify the effects of PPM defoliation on growth at several scales. To our knowledge, this is the first attempt to use these statistical techniques in the detection and assessment of the effects of insect outbreaks on tree growth.

Tree-ring information and remote sensing data indicated that the recovery of radial growth and cover of the PPM-affected forests were not immediate. We observed that it was necessary an average time of 2-4 years to recover growth and cover values similar to those observed before the outbreak. Our findings indicate that severe PPM defoliations induce mid-term losses in crown cover and stem wood production as has been observed in other conifers (Parsons et al., 2003). Nevertheless, PPM-defoliated trees are able to recover similar levels of stored carbohydrates soon after the outbreak remits (Palacio et al., 2012). This may be related with a higher photosynthetic activity of the new needles (Porté & Loustau, 1997), thus minimizing the short-term negative

effects of PPM defoliation on carbon storage. The growth decline induced by repeated and severe PPM defoliations could not be due to carbon (source) limitation, but respond to a reduced sink strength of growing meristems (cambium) due to defoliation (Palacio et al., 2012).

Several studies have suggested an upward shift of the PPM defoliation in response to rising minimum temperatures (Battisti et al., 2006; Buffo et al., 2007). Moreover, some authors maintain that PPM is affecting high-elevation forests that were not previously defoliated by the insect (Goussard et al., 1999; Hódar et al., 2003; Hódar and Zamora, 2004). We consider that those assertions should be tested by considering ample spatio-temporal scales and complementary datasets as those analyzed here. The use of dendrochronology and remote sensing could provide an extensive database that would improve the management of the affected forests and help to answer important ecological questions. For instance, if the severity and frequency of PPM outbreaks increase in response to climate warming, affected forests would not have time to recover growth and cover levels. In this new scenario the effects of this biotic stressors and additional drought stress would likely induce growth decline, defoliation and intense mortality in Mediterranean pine forests, particularly in extensive reforestations. Many of these pine plantations are very susceptible to PPM defoliations like those dominated by *P.nigra* (Montoya and Hernández, 1998). Therefore, the economical and ecological relevance of the monitorization of these PPM-prone forests is evident.

In conclusion, remote sensing is a reliable tool to characterize severe PPM defoliations in Mediterranean pine forests using adequate vegetation indices. Multi-evidence based on remote sensing and dendrochronology allows detecting the negative effects of PPM outbreaks on tree cover and growth, and establishing the recovery time in the affected forests. These combined methods open new directions for assessing

insect outbreaks across wide spatio-temporal scales, which hold relevant information within the current global-change background.

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Figure captions

Figure 1. Study area in located in eastern Spain (Sierra de Gúdar, Teruel, Aragón) where the defoliations by the Mediterranean pine processionary moth were recorded from 1970 to 2012. The points indicate the location of the six sites where dendrochronological samplings were performed. Different colours indicate the forests dominated by *P. sylvestris* (dark blue), *P. nigra* (purple) or *P. pinaster* (soft blue). The upper right inset shows the Circum-Mediterranean countries where *T. pityocampa* has been reported (areas colored in orange).

Figure 2. Spatial patterns of defoliation by the pine processionary moth in the study area considering different forest demarcations (patches). The pie charts represent the frequency of years corresponding to one of the three defoliation degrees (DD1, no defoliation, green areas; DD2, moderate defoliation, yellow areas; DD3, severe defoliation, red areas) during the study period (1970-2012). The colored background represents the number of years of each forest demarcation with severe defoliation (DD3, colour scale).

Figure 3. Relationships observed between three defoliation degrees (see legend of Figure 2) and several vegetation indices (see their explanation in Supporting Information, Table S2) for a year with strong pine processionary moth defoliations (1992). Values are mean ($\pm$ SE) values considering 10 forest patches located within the study area for each defoliation degree. Statistics (F ratio and probability level) are displayed when significant ($P < 0.05$) differences among defoliation degrees were observed (indicated by different letters).

Figure 4. Temporal variation of several vegetation indices (MSI, Moisture Stress Index; NDII, Normalized Difference Infrared Index, NBR, Normalized Burn Ratio) showing tight relationships with pine processionary moth defoliation. The indices values are means $\pm$ SE for 30 *P. nigra* stands with similar density, aspect and slope values. The frequencies of defoliation degrees (see Fig. 2) for each year are also presented and correspond to different colors in the bars (DD1, white areas; DD2, yellow areas; DD3, red areas).

Figure 5. Values of the Moisture Stress Index (MSI) calculated for years with (1992) or without (2000) severe pine processionary moth defoliations. The upper right inset indicate the defoliation degrees recorded in the field survey using the codes explained in Fig. 2 (DD1, green areas, no defoliation; DD2, yellow areas, moderate defoliation; DD3, red-orange areas, severe defoliation). The lower most figures show the MSI values for sites delimited as PPM-prone areas, i.e. stand edges or isolated trees.

Figure 6. Pine processionary moth defoliations correspond to negative basal area increment (BAI) residuals of trees (lines) obtained after fitting linear mixed-effects models using climate and drought as predictors. Results are presented for each *P. nigra* study site (FU, LR, MP, RO, AM and AC). Lower yellow and red triangles indicate moderate (DD2) and severe (DD3) defoliation degrees, respectively. The right y-axis shows years with dry spring conditions characterized by low May Standardised Precipitation-Evapotranspiration Index (SPEI) values calculated at 9-month long scales (grey bars). The percentage in the lower left corner of each graph indicates the amount of variability in BAI accounted for by the climate-drought models.

Tables

Table 1. Characteristics of the images used in the remote-sensing analyses.

Acquisition date	Satellite-Sensor	Origin of images
9 th May 1987	Landsat 5-TM	USGS
17 th May 1990	Landsat 5-TM	ESA
18 th April 1991	Landsat 5-TM	ESA
20 th April 1992	Landsat 5-TM	USGS
20 th March 1994	Landsat 5-TM	ESA
28 th March 1995	Landsat 5-TM	ESA
1 st March 1997	Landsat 5-TM	ESA
1 st March 2000	Landsat 5-TM	USGS
19 th February 2002	Landsat 7-ETM+	USGS
10 th March 2003	Landsat 7-ETM+	USGS
13 th March 2007	Landsat 5-TM	USGS
2 nd May 2008	Landsat 5-TM	PNT
5 th May 2009	Landsat 5-TM	PNT
6 th April 2010	Landsat 5-TM	USGS
9 th April 2011	Landsat 5-TM	USGS

635

636 **Table 2.** Features of the six study sites where the dendrochronological sampling was

637 performed.

638

Site (code)	UTM (X)	UTM (Y)	Altitude (ma.s.l.)	Aspect (°)	Slope (°)	No. of trees / cores	Age ($\pm$ SE) (years)	Mean ($\pm$ SE) tree-ring width 1980-2012 (mm)
Fuennarices (FU)	693603	4465003	1098	47	12.8	12/24	54 $\pm$ 6	14.8 $\pm$ 0.9
Las Roquetas (LR)	695589	4466439	1414	68	19.3	10/20	126 $\pm$ 6	6.0 $\pm$ 0.4
MasíaPeñarroya (MP)	696212	4465673	1543	63	13.4	11/22	118 $\pm$ 3	4.8 $\pm$ 0.4
Las Roquetas (RO)	694833	4465555	1308	65	16.1	12/24	108 $\pm$ 13	10.0 $\pm$ 1.6
Alto de Mora (AM)	693991	4463069	1564	72	13.3	12/24	126 $\pm$ 7	3.9 $\pm$ 0.4
Alto de Cabra (AC)	685896	4467021	1256	55	14.0	10/20	113 $\pm$ 4	5.6 $\pm$ 0.5

639

Table 3. Basal area increment (BAI) variance (%) of *Pinus nigra* accounted for climate variables and by previous year BAI (BAI_{t-1}) according to selected linear mixed-effects models. The models were fitted considering the six *P. nigra* study sites (FU, LR, MP, RO, AM and AC). Positive (+) and negative (–) effects on BAI are indicated for the following variables: SPEI, May SPEI calculated at a time-scale of 9 months; TMSP, spring mean maximum temperature; TMSU, summer mean maximum temperature; TMWI, winter mean maximum temperature; and TMFAp, previous autumn mean maximum temperature. Bold values indicate the most important variable in each site.

Fixed factors (effect)	Sites					
	FU	LR	MP	RO	AM	AC
SPEI (+)	20.04	9.60	27.14	20.14	31.68	26.30
TMSP (+)	14.13	8.60	4.49	12.23		9.06
TMSU (–)	10.87	15.71	17.37	17.50		18.55
TMWI (+)	21.78	21.17	14.43	17.55	22.41	10.98
TMFAp (–)	0.47	4.70	11.45	2.40		6.15
BAI_{t-1} (+)	13.56	13.32	13.11	18.01	35.56	14.96

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6