Climate change and the incidence of a forest pest in Mediterranean ecosystems: can the North Atlantic Oscillation be used as a predictor?

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Abstract Many forest pest species strongly depend on temperature in their population dynamics, so that rising temperatures worldwide as a consequence of climatic change are leading to increased frequencies and intensities of insect-pest outbreaks. In the Mediterranean area, the climatic conditions are strongly linked to the effects of the North Atlantic Oscillation (NAO). The aim of this work is to analyze the dynamics of the pine processionary moth (*Thaumetopoea pityocampa*), a severe pest of *Pinus* species in the Circunmediterranean, throughout a region of southern Spain, in relation to NAO indices. We related the percentage of forest plots with high defoliation by pine processionary moth each year with NAO values for the present and the three previous winters, using generalized linear models with a binomial error distribution. The time series is 16-year long, and we performed analyses for the whole database and for the five main pine species separately. We found a consistent relationship between the response variable and the NAO index. The relationship is stronger with pine species living at medium-high altitudes, such as Aleppo (*P. halepensis*), black (*P. nigra*), and Scots (*Pinus sylvestris*) pine, which show the higher defoliation intensities up to 3 years after a negative NAO phase. The results highlight, for the first time, the usefulness of using global drivers in order to understand the dynamics of pest outbreaks at a regional scale, and they open the window to the development of NAO-based predictive models as an early-warning signal of severe pest outbreaks.

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1 Introduction

Insect pests are a major threat to many forests worldwide, from boreal to tropical forest ecosystems (Ayres and Lombardero 1998; Volney and Fleming 2000). Rising temperatures around the world as a consequence of climatic change are increasing the frequency and intensity of pest outbreaks accompanied by range shifts of pests poleward or to higher altitudes (Bale et al. 2002; Gitai et al. 2002; Jepsen et al. 2008). The pattern is consistent in many parts of the globe and with very different pest species (Gitai et al. 2002; Netherer and Schopf 2010). Many forest pest species strongly depend on temperature in their population dynamics, and several field and laboratory studies demonstrate the importance of temperature as a physiological driver for insect growth and development (Hodkinson 1999; Bale et al. 2002; Netherer and Schopf 2010, and references therein). It is well known that the effect of temperature (mainly the minimum values) determine the eruptive phases of outbreaking species in forest pests, such as the winter moth *Epirrita autumnata* (Jepsen et al. 2008), the spruce budworm *Choristoneura fumiferana* (Gray 2008), and the pine processionary moth *Thaumetopoea pityocampa* (Démolin 1969a; Hódar and Zamora 2004; Battisti et al. 2005, 2006), among others (Volney and Fleming 2000; Bale et al. 2002; Netherer and Schopf 2010).

Models for climatic change predict rising temperatures for the Mediterranean basin (Moreno 2005), and in fact the Iberian Peninsula has shown a steady temperature rise over the past century (Esteban-Parra et al. 1995; Moreno 2005; Brunet et al. 2007), mainly in the form of higher minimum temperatures. In particular, winter temperatures are currently warming, reducing the number of days with frost. As a consequence, many studies have shown alterations in distribution, phenology, and abundance of different plant and animal species in Spain (Peñuelas et al. 2002; Menzel et al. 2006; Gordo and Sanz 2010). Nevertheless, despite the recognized importance of temperature, organisms are affected by more than one feature of climate, making the weather component of climate important (Hallett et al. 2004; Stenseth and Mysterud 2005). This is why a single meteorological factor at a local scale, such as temperature, contains less information than weather packages such as the North Atlantic Oscillation (NAO), which is a better predictor of ecological processes (Hallett et al. 2004; Stenseth and Mysterud 2005).

The pine processionary moth (*Thaumetopoea pityocampa*, Lepidoptera: Notodontidae; hereafter PPM) is a severe pest of *Pinus* species in the Circunmediterranean (Dajoz 1998). Long ago, temperature, namely the winter minimum, was recognized as the main limitation for the development of the PPM, and that outbreaks were preceded by mild winters. This is a key factor determining the outbreak capacity of PPM, as low winter temperatures heavily determine the larval survival of this insect (e.g. Breuer et al. 1989; Battisti et al. 2005; Buffo et al. 2007). Several studies have found, as a consequence of the general rise in temperatures, a progression in latitude and/or altitude with respect to the previous distribution of the pest, as well as an increase in outbreak severity (Hódar et al. 2003; Hódar and Zamora 2004; Battisti et al. 2005, 2006; Robinet et al. 2007). These works suggest that mild winters promote larval survival and higher numbers of adults, resulting in heavier defoliation in the next generation of larvae. Nevertheless, some other works have suggested also a role of biotic factors in shaping the PPM cycle, either predators-parasitoids, food quality-quantity, or both (Battisti 1988; Robinet 2006; Hódar and Zamora 2009). Thus, whithin the neverending debate concerning whether the dynamics of wild animal populations are mainly regulated by abiotic (climate) or by biotic, endogenous density-dependent, processes, PPM seems to fit both possibilities, in agreement with modern thinking, considering endogenous and exogenous factors in a more unified way, operating together on any population (Bjørnstad and Grenfell 2001).

Due to the general pattern of extension and intensified virulence of the PPM, implementation of tools that predict the behavior of the pest on a broad scale are invaluable for forest management. Different pine species inhabit the Circunmediterranean and have been used massively in afforestation, and thus methods for controlling aggressive pests such as PPM constitute key issues in Mediterranean forestry. However, although records and studies at different sites suggest a general spreading pattern for the PPM by using temperature as the key factor (Hódar and Zamora 2004; Battisti et al. 2005, 2006; Robinet et al. 2007), there has been no attempt to date to explain the population dynamics of the plague at a regional scale.

The aim of this work is to analyze the dynamics of the PPM over an entire region of Spain using a global driver. The approach is based on the relationship between the rising temperature in Spain and a parallel increase in the North Atlantic Oscillation (NAO) index (Moreno 2005; Stephenson et al. 2006; Brunet et al. 2007). The NAO index, in particular the winter NAO of Hurrell (Hurrell 1995), has been used to model and predict the effect of climate change in many plant and animal species (Briers et al. 2004; Vähätalo et al. 2004; Gordo and Sanz 2010). In recent times, the winter NAO has been invoked as a large-scale climatic index useful to relate to broad areas, since its influence is broad in scale, both spatially and temporally (Hallett et al. 2004; Stenseth and Mysterud 2005). Specifically, the questions we address are:

1) Is there a relationship between the PPM outbreaks, on a regional scale, and a large-scale climatic index such as the NAO?
2) Are there differences in the response of pine species thriving at different altitudinal ranges?
3) Can be the NAO used as an early warning signal of severe outbreaks?

2 Materials and methods

The area of study is the region of Andalusia (southern Spain). This area covers around 87,300 km^2, and includes a wide variety of habitats, from lowlands and meadows on the western side to high mountains (well above 3,000 m a.s.l. in Sierra Nevada) on the eastern side. Climate also shows a sharp contrast: while western Andalusia has a temperate climate characterized by dry and hot summers (Csa, according to the Köppen climatic classification), the more montainous eastern side can be classified as a cold steppe (Bsk), while mountains above 1,500 m in altitude have cooler climate types (AEMET 2011). Around 44,000 km^2 are considered forested, and 19% of them are covered by pine woodlands (Junta de Andalucía 2003), both natural (around 5%) and afforested. Five main species, stone (*Pinus pinea*), cluster (*P. pinaster*), Aleppo (*P. halepensis*), black (*P. nigra*), and Scots (*P. sylvestris*) pines, represent the bulk of the pine woodlands, while some exotic species (mainly *P. canariensis* and *P. uncinata*) are scarce.

Since 1992, the Andalusian Environmental Council established a network including plots of pine woodland stands scattered throughout the region (Junta de Andalucía 2006), in which the incidence of defoliation by the PPM at the stand level is evaluated by trained rangers every winter, according to six categories: 0 = no infestation, 1 = scattered nests, scant defoliation, 2 = defoliation and nests visible at the stand borders, 3 = strong defoliation and numerous nests at the stand borders, some defoliation in the centre, 4 = very heavy defoliation both at the borders and the centre of stands, and 5 = massive defoliation, almost no foliage remaining (Montoya and Hernández 1991). Although the sampling

intensity varies between years, the high number of stands (over 4000) and the surface area covered (around 700,000 ha, scattered throughout the Andalusian region) ensures representative results every year. In this work, we used the entire database of the Andalusian Environmental Council (4158 stands) for the period 1992–2009. We did not attempt to separate in this study stands that had been subjected to aerial fumigation of insecticides to control PPM and untreated stands, as a previous study showed that the degree of infestation by PPM decreases substantially after an outbreak both in fumigated and untreated woodlands (Cayuela et al. 2011). This suggests that, at the stand level, the PPM cycle may be at least partially under natural biological control (predators-parasitoids, host plant, or both; see also Hódar and Zamora 2009).

We used Hurrell's winter NAO (Hurrell 1995, DJFM) as a global predictor of the incidence of PPM in pine woodland stands. In an earlier work (Hódar and Zamora 2004), we have shown that the defoliation by the PPM can be explained, on a local scale, by the local climatic conditions. However, for the extension of the area covered in this work, we used a remote predictor common to the overall area. In this sense, the NAO index has been repeatedly tested as a straightforward indicator of the climate in several parts of Europe (Hallett et al. 2004; Stenseth and Mysterud 2005). For the present study, we used not only the winter NAO, but also NAO values for the three previous winters as explanatory variables, in order to seek for delayed effects. There was no collinearity in the set of explanatory variables used (maximum Pearson's correlation $r=0.174$, $P=0.498$).

To investigate the temporal connection between the winter NAO and the incidence of PPM, we calculated for every winter and pine species the percentage of plots with defoliation equal to or above level 3 (high defoliation level) (Table 1). In this way, a high percentage indicated a winter of extensive defoliation for the species, and a low percentage a winter with the pest at latent levels. We first calculated Pearson's correlations to explore the relationships between the percentage of pine woodland stands affected by PPM every year and the winter NAO for the present and the three previous winters. We then used generalized linear models with a binomial error distribution and a logit link function to account for the effects of winter NAO values for the present and the three previous winters on the percentage of pine woodland stands affected by PPM every year. To determinate the set of explanatory variables that constitute the best model fit, we performed a backward stepwise model selection based on the Akaike Information Criterion (AIC) (Akaike 1973). With this model, we tested the extent to which the winter NAO can be used as a straightforward predictor of the defoliation intensity, and the potential time lag of this response in all pine woodlands. We repeated the analysis separately for the main five pine species, which followed an altitudinal gradient, with stone pine occupying the lowest elevations (Avg. alt.=340 m), followed by cluster and Aleppo pines at intermediate elevations (Avg. alt.=870 and 950 m respectively), and black and Scots pines at the highest elevations (Avg. alt.=1490 and 1810 m respectively). The elevation at which pines are found is also a reflect of the geographical distribution of the pine species, stone and cluster pine being common in the lowlands of western Andalusia, Scots and black pine in the mountains of the eastern side, and Aleppo more frequent at the eastern side but with a wide altitudinal range. Since the altitude of the stands correlated with the dominant pine species, our aim with these models was to test whether the relationship between the winter NAO and the response variable was mediated by the local effect of elevation.

All the analyses were performed with the bulk of data and with the subset of stands that had the whole time series between 1994 and 2009 (Table 1), since only a small percentage of woodland stands had data for the years 1992 and 1993. All the statistical analyses were performed with the R environment (R Development Core Team 2009).

Table 1 Yearly number of pine stands with defoliation (Inf) equal to or above the level 3 and below 3 when using all stands and with the subset that had the entire time series between 1994 and 2009. Winter NAO values are also shown for the whole series and the three previous winters

Year	All stands		Stands with full time series		NAO
	Inf ≥ 3	Inf < 3	Inf ≥ 3	Inf < 3	
1989	-	-	-	-	5.08
1990	-	-	-	-	3.96
1991	-	-	-	-	1.03
1992	144	795	-	-	3.28
1993	179	716	-	-	2.67
1994	243	2607	147	1575	3.03
1995	173	3072	111	1611	3.96
1996	138	2958	75	1647	−3.78
1997	278	2555	161	1561	−0.17
1998	616	2696	275	1447	0.72
1999	371	2922	155	1567	1.70
2000	282	2948	161	1561	2.80
2001	85	3356	46	1676	−1.90
2002	317	3019	175	1547	0.76
2003	393	3190	152	1570	0.20
2004	422	3201	145	1577	−0.07
2005	215	3424	77	1645	0.12
2006	182	3599	94	1628	−1.09
2007	252	3692	86	1636	2.80
2008	362	3727	104	1618	2.11
2009	431	3646	111	1611	−0.40

3 Results

Pearson's correlations revealed a positive relationship between the percentage of defoliated stands and the winter NAO, a negative relationship with the winter NAO with one and two-year delays, and a positive relationship with the winter NAO with three-year delay (Fig. 1). Statistical significance of these correlations was not assessed because of the inflated probability of committing type II error. At the regional scale, both for the total database and the database with only woodland stands having the whole temporal series, the generalized linear models showed that the winter NAO index was important in determining the percentage of defoliated stands between 1992 and 2009 (Table 2, Appendix S1). When the analysis was repeated separately for the five pine species (Table 2), the results revealed similar trends, but, notably, the explained deviance values remained low for the pine species living at low altitudes and/or more resistant to the PPM (stone and cluster pine), while it increased in pine species living at medium-high altitudes (Aleppo, black and Scots pine). This indicates that the climatic conditions rendered markedly different consequences for the five pine species considered. In most cases, the winter NAO was positively related to the percentage of defoliated stands, whereas the relationship was inverse with one- and two-year delays (Table 2, Fig. 2) —that is, a
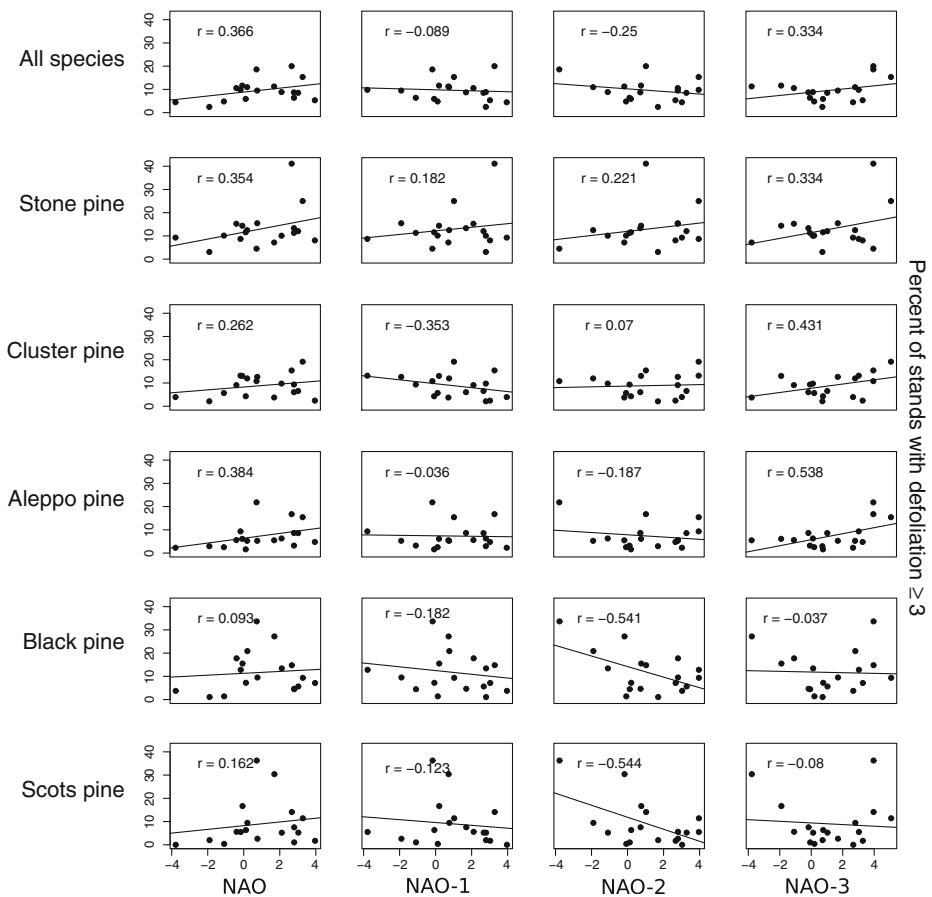
Fig. 1 Pearson's correlations between the percentage of pine woodland stands affected by PPM every year and the winter NAO for the present and the three previous winters (in columns) for all pine species and in stands dominated by stone(*Pinus pinea*), cluster (*P. pinaster*), Aleppo (*P. halepensis*), black (*P. nigra*) and Scots pine (*P. sylvestris*)

negative NAO promotes a higher defoliation one and two years later. In the case of black and Scots pine, this influence was also detected for NAO values with a three-year delay (Table 2, Fig. 2). Winter NAO values with one- and two-year delays accounted for most of the explained variance in the models (Table 2).

4 Discussion

Our results indicate, for the first time, a relationship between the damage by an insect pest on a regional scale and a large-scale climatic index, such as the NAO. The mean winter NAO has strong associations with mean winter temperature and precipitation in Europe (Hurrell 1995; Bojariu and Giorgi 2005). Positive NAO conditions are associated with increased precipitation over Northern Europe, decreased precipitation over Southern Europe and the Mediterranean region, and increased surface temperatures over Northern and

Table 2 Results of the generalized linear models accounting for the effects of winter NAO values for the present and the three previous winters on the percent of pine woodland stands affected by PPM for all species and for the main five pine species using all the forest stands (for a similar analysis using only the subset of stands that had the whole time series between 1994 and 2009 see the Appendix S1). Only the variables that constitute the best model fit based on the Akaike Information Criterion are shown

	Estimate	Std. Error	Resid. Dev.	Expl. Dev.	P(>|z|)
All					
Intercept	−2.310	0.019	1093.61		<0.001
NAO	0.069	0.008	1017.60	0.070	<0.001
NAO-1	−0.055	0.008	958.46	0.054	<0.001
NAO-2	−0.082	0.007	819.83	0.127	<0.001
NAO-3	0.034	0.007	797.27	0.021	<0.001
Stone					
Intercept	−2.196	0.032	329.45		<0.001
NAO	0.058	0.013	314.13	0.047	<0.001
NAO-2	0.064	0.013	290.72	0.071	<0.001
Cluster					
Intercept	−2.421	0.048	214.39		<0.001
NAO	0.0427	0.022	211.29	0.014	0.048
NAO-1	−0.131	0.019	159.95	0.239	<0.001
NAO-3	0.049	0.019	153.03	0.032	0.009
Aleppo					
Intercept	−2.867	0.042	567.41		<0.001
NAO	0.120	0.017	517.91	0.087	<0.001
NAO-1	−0.049	0.016	502.18	0.028	0.002
NAO-2	−0.104	0.013	431.25	0.125	<0.001
NAO-3	0.149	0.015	330.33	0.178	<0.001
Black					
Intercept	−1.870	0.044	666.01		<0.001
NAO	0.045	0.020	660.02	0.009	0.027
NAO-1	−0.054	0.021	640.04	0.030	0.011
NAO-2	−0.221	0.017	464.14	0.264	<0.001
NAO-3	−0.029	0.016	460.59	0.005	0.059
Scots					
Intercept	−2.171	0.073	514.73		<0.001
NAO	0.133	0.037	500.38	0.028	<0.001
NAO-1	−0.109	0.035	483.93	0.032	0.002
NAO-2	−0.354	0.027	299.76	0.358	<0.001
NAO-3	−0.098	0.023	282.16	0.034	<0.001

Central Europe, while negative values of NAO mean mild temperatures and wet conditions in Southern Europe, and specifically in the Iberian Peninsula (Rodó et al. 1997; Gouveia et al. 2008). In the South of the Iberian peninsula, the relationship between NAO and climate is straightforward for precipitation but not so clear with temperature (Rodó et al. 1997; Sáenz et al. 2001; Gouveia et al. 2008), although anyway the strength of the relationship depends of the period of the year considered and, interestingly, of altitude, being the
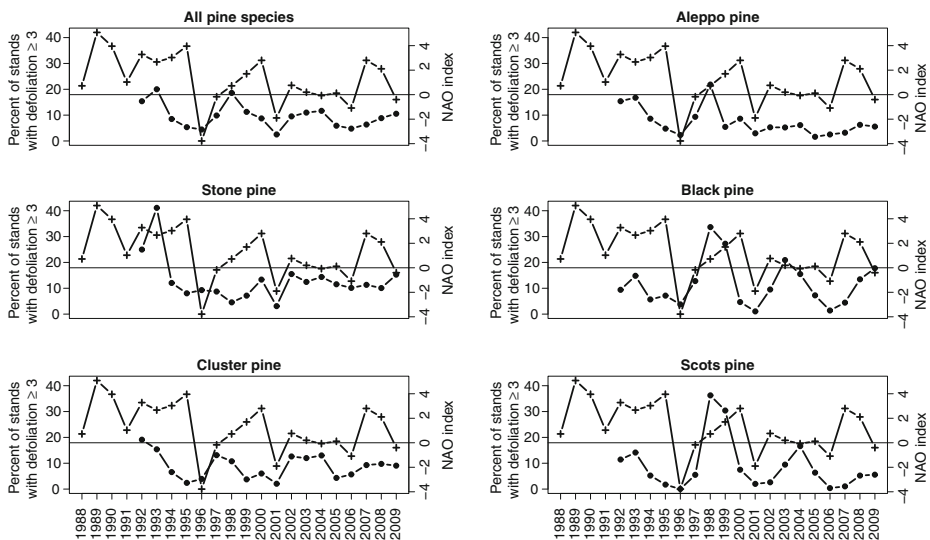
Fig. 2 Defoliation dynamics (black dots) in relation to the winter NAO index (crosses) in all pine woodlands and in stands dominated by stone (*Pinus pinea*), cluster (*P. pinaster*), Aleppo (*P. halepensis*), black (*P. nigra*) and Scots pine (*P. sylvestris*). The horizontal solid line indicates zero winter NAO values

relationship stronger in mountains than in lowlands (López-Moreno et al. 2011). Previous works have shown the key role played by the topography in modulating the large-scale NAO variability over Europe (Bojariu and Giorgi 2005). Our analysis found in general a direct significant relationship between winter NAO values and PPM incidence for a given winter, but an inverse one for the following winters (Table 2), being this relationship stronger for pines living at the higher altitudes of eastern Andalusia. That is, a typical PPM cycle would start with a winter with negative NAO and a minimum population of PPM, then population increases during the one-two following winters of positive NAO, and after that collapses.

While the pattern is clear, the biological mechanisms behind this pattern are not, since specific knowledge on underlying relationships between climate and insect development are far from being fully understood (Netherer and Schopf 2010). In the case of PPM, recent studies have disentangled very much on the relationships between PPM larval survival and minimum winter temperatures, either directly on larval survival (Buffo et al 2007; Pimentel et al. 2011) or indirectly by altering parasitism rates (Pimentel et al. 2011). However, other important aspects of climate, as rainfall or sun radiation, and their effects in other phases of the life cycle, as pupal diapause and moth emergence, remain doubtful. Nevertheless, at least two different mechanisms, not mutually exclusive, can be proposed to explain the pattern found.

Firstly, the direct significant relationship between winter NAO values and PPM incidence for a given winter suggests that a dry (although cold) winter is better for PPM larval survival in Southern Spain. Positive winter NAO values usually render dry winters in Southern Spain (Rodó et al. 1997; Sáenz et al. 2001; Gouveia et al. 2008) and in general these winters can be classified as warm, even if minimum temperatures are rather low, because maximum temperatures are rather high (López-Moreno et al. 2011). In fact, maximum winter temperatures show a direct and significant correlation with winter NAO in Sierra Nevada (López-Moreno et al. 2011), which is surely related with the direct and good

correlation that NAO shows in the area with sun irradiance (Sánchez-Lorenzo et al. 2005). Perhaps larvae develop better in a dry environment and with sunny days, even if nights are cold, than in a wet winter with mild temperatures (see e.g. Démolin 1969a; Battisti et al. 2005; Robinet et al. 2007; Pimentel et al. 2011, on the effects of low temperatures and solar radiation on the winter nests). Apart of this direct effect of temperature on larval survival, it is known that humidity increases the attack of pathogens on Lepidoptera larvae (Weseloh et al. 1993; Sierpiñska 1998), and activate larval and pupal parasitoids (Pimentel et al. 2011), explaining the negative effect of wet winters (negative NAO values) on PPM defoliation. A very wet soil can be also a problem for PPM larvae trying to bury in soil for pupation (obs. pers.).

Secondly, the inverse significant relationship between winter NAO values and PPM incidence for the following winter suggest that, after a rainy winter with low populations of PPM, plants grow better (Gouveia et al. 2008), increasing the quantity of vegetal tissue and reducing the induced defenses accumulated during the periods of defoliation (Battisti 1988; Hódar et al. 2004), thus constitute a better and more abundant food for PPM larvae. Furthermore, after the population crash during the wet winter, the PPM density (and also the densities of specialists parasitoids) becomes very low, and the conditions for the rising phase of the cycle are optimal. This in turn explains why the variance in defoliation explained by NAO is maximum and with inverse sign one or two years after a negative NAO (Table 2), because the PPM population needs time to take advantage of conditions and increase its population, while the relationship with the current winter NAO is positive, being defoliation favoured by dry winters with high irradiance and high maximum temperatures. Some other relationships, however, remain unexplained, as for instance the direct and very significant between NAO and PPM defoliation of Aleppo pine with a three-years delay (Table 2, Fig. 1).

Stone pine is the species showing a poorest fit with this pattern. Stone pine is mainly distributed at lower altitudes in the western side of the region (and thus more prone to be influenced by the NAO effect), and does not show a clear relationship in its defoliation with NAO values. The zones dominated by this pine species have a mild climate in winter, conducive to PPM development irrespectively of NAO phases. Pines in these areas need to be resistant to PPM because its incidence is chronic, and predators and parasitoids probably have more diverse and developed populations than in high-mountain sites, and it is known that stone pine is the species least susceptible to the PPM (Démolin 1969b; Avtzis 1986; Breuer et al. 1989; Devkota and Schmidt 1990; Tiberi et al. 1999). As a result, the defoliation dynamics in the woodland stands dominated by stone pine differ sharply from those of more palatable pines (black or Scots pine, Fig. 2), and does not show a clear relationship with the NAO phases. On the contrary, as altitude increases and temperature decreases, the probability of defoliation reduces, pines are less resistant to PPM (black and Scots pines are very palatable species, Hódar et al. 2002), the incidence of parasitoids is scant, and defoliation occurs after mild winters. This suggests that, although the NAO as a global effector may determine the periods of outbreak in the PPM, the local characteristics of the site, namely altitude or pine species, greatly modulate the intensity of the defoliation.

The fact that the areas subject to heavy defoliations coincide with those with palatable pines prone to the PPM, which need suitable climatic conditions for PPM development, and the delay between the climatic signal and the defoliation, suggests that the PPM outbreaks can be predicted with one or two years in advance, and this is a key result for forest management. One of the great difficulties in managing pests such as the PPM is that, once the outbreak begins, the possibilities of control are nil (Cayuela et al. 2011). Most control

procedures against PPM require costly and extensive programs of population estimates, first to determine whether the population is increasing and eventually approaching outbreak levels, and then to act before the outbreak level is reached. Our study shows that NAO is a straightforward early-warning system for the population dynamics of the PPM, and hence can be used as predictor in order to program the appropriate managements to reduce or prevent the possibility of outbreaks. A strong effort in downscaling the prediction of PPM incidence is needed, but this is a promising path to explore.

A noteworthy point is that, while the general trend of temperatures is increasing (Gitai et al. 2002), the NAO tendency shows a predominance of positive phases (thus increasing temperatures all over Europe), but a decrease in the probability of negative NAO-phases (Moreno 2005; Stephenson et al. 2006; Bojariu and Giorgi 2005; López-Moreno et al. 2011). The first is positive for the development of the PPM, while the second, as suggested our results, would be at the end negative, since these rainy winters create the conditions for the start of the cycle. The future tendency of the damage by PPM in the pine woodlands of southern Spain will depend of the interaction between these two opposite trends. The future scenario will likely include a higher level of chronic defoliation, as a consequence of rising temperatures, and a rarefaction but intensification of the outbreaking events, due to the new pattern of the NAO negative phases. This scenario, combined with the predicted reduction of precipitation for Mediterranean regions and a concomitant increase of drought stress in plants (Gouveia et al. 2008; López-Moreno et al. 2011), would be extremely negative for the pine woodlands. In particular, it will be very harmful for the populations more susceptible to PPM and drought, such as the relict Scots pine populations in south-eastern Spain (Hódar et al. 2003; Hódar and Zamora 2004).

In conclusion, our study shows that the defoliation dynamics by PPM in southern Spain is determined by a global-scale climate index, the NAO, but that the global effects are strongly modulated by the local conditions, mainly the pine species and the elevation. These results highlight the necessity of using global drivers in order to understand the overall consequences of global change on a regional scale, helping to reduce the uncertainty in regional predictions, and opens the window to the development of NAO-based predictive models on a regional scale while incorporating local drivers.

References

AEMET (2011) Iberian climate atlas. Air temperature and precipitation (1971–2000). AEMET, Agencia Estatal de Meteorología, Ministerio de Medio Ambiente y Medio Rural y Marino. Madrid. URL http://es.scribd.com/doc/52596832/6/Koppen-Climate-Classifcation-for-the-Iberian-Peninsula

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Proceedings of the second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Avtzis N (1986) Development of *Thaumetopoea pityocampa* Schiff. (Lepidoptera: Thaumetopoeidae) in relation to food consumption. For Ecol Manag 15:65–68

Ayres MP, Lombardero MJ (1998) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Smyrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob Chang Biol 8:1–16

Battisti A (1988) Host-plant relationships and population dynamics of the pine processionary moth *Thaumetopoea pityocampa* (Denis and Schiffermüller). J Appl Entomol 105:393–402

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096

Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Glob Chang Biol 12:662–671

Bjørnstad ON, Grenfell DT (2001) Noisy clockwork: time series analysis of population fluctuations in animals. Science 293:638–643

Bojariu R, Giorgi F (2005) The North Atlantic Oscillation signal in a regional climate simulation for the European region. Tellus 57 A:641–653

Breuer M, Devkota B, Douma-Petridou E, Koutsaftikis A, Schmidt GH (1989) Studies on the exposition and temperature of nests of *Thaumetopoea pityocampa* (Den, Schiff.) (Lep., Thaumetopoeidae) in Greece. J Appl Entomol 107:370–375

Briers RA, Gee JHR, Geoghegan R (2004) Effects of the North Atlantic Oscillation on growth and phenology of stream insects. Ecography 27:811–817

Brunet M, Jones PD, Sigro J, Saladie O, Aguilar E, Moberg A, Della-Marta PM, Lister D, Walther A, López D (2007) Temporal and spatial temperature variability and change over Spain during 1850–2005. J Geophys Res 112:D12117

Buffo E, Battisti A, Stastny M, Larsson S (2007) Temperature as a predictor of survival of the pine processionary moth in the Italian Alps. Agr Forest Entomol 9:65–72

Cayuela L, Hódar JA, Zamora R (2011) Is insecticide spraying a viable and cost-efficient management practice to control pine processionary moth in Mediterranean woodlands? For Ecol Manag 261:1732–1737

Dajoz R (1998) Les insectes et la forêt. Technique et Documentation, Paris

Junta de Andalucía (2003) Adecuación del Plan Forestal Andaluz. URL http://www.juntadeandalucia.es/medioambiente/planesmed/planforestal/adecuacion.pdf

Junta de Andalucía (2006) Actuaciones forestales. In: Medio Ambiente en Andalucía. Informe 2005. Consejería de Medio Ambiente, Junta de Andalucía, Seville, Spain, pp 224–225

Démolin G (1969a) Bioecología de la procesionaria del pino *Thaumetopoea pityocampa* Schiff. Incidencia de los factores climáticos. Bol Serv Plagas For 12:9–24

Démolin G (1969b) Comportement des adultes de *Thaumetopoea pityocampa* Schiff. Dispersion spatiale, importance écologique. Ann For Sci 26:81–102

Devkota B, Schmidt GH (1990) Larval development of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lepidoptera: Thaumetopoeidae) from Greece as influenced by different host plants under laboratory conditions. J Appl Entomol 109:321–330

Esteban-Parra MJ, Rodrigo FS, Castro-Díez Y (1995) Temperature trends and change points in the Northern Spanish plateau during the last 100 years. Int J Climatol 15:1031–1042

Gitai H, Suárez A, Watson RT, Dokken DJ (2002) Climate change and biodiversity. IPCC Technical paper V. IPCC, Geneva

Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. Glob Chang Biol 16:1082–1106

Gouveia C, Trigo RM, DaCamara CC, Libonati R, Pereira JMC (2008) The North Atlantic Oscillation and European vegetation dynamics. Int J Climatol 28:1835–1847

Gray DR (2008) The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Clim Change 87:361–383

Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75

Hódar JA, Zamora R (2004) Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. Biodivers Conserv 13:493–500

Hódar JA, Zamora R (2009) Influencia de los factores abióticos y bióticos en la defoliación por la procesionaria del pino (*Thaumetopoea pityocampa*) en los pinares andaluces. Proceedings of the 5th Spanish Forestry Congress, Ávila, Spain

Hódar JA, Zamora R, Castro J (2002) Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. Ecol Entomol 27:292–301

Hódar JA, Castro J, Zamora R (2003) Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. Biol Conserv 110:123–129

Hódar JA, Zamora R, Castro J, Baraza E (2004) Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*. Acta Oecologica 26:203–210

Hodkinson ID (1999) Species response to global environmental change or why ecophysiological models *are* important: a reply to Davis et al. J Anim Ecol 68:1259–1262

Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269:676–679

Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. J Anim Ecol 77:257–264

López-Moreno JI, Vicente-Serrano SM, Morán-Tejeda E, Lorenzo-Lacruz J, Kenawy A, Beniston M (2011) Effects of the North Atlantic Oscillation (NAO) on combined temperature and precipitation winter modes in the Mediterranean mountains: Observed relationships and projections for the 21st century. Global Planet Change 77:62–76

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl A, Defila C, Donnelly A, Filella I, Jatczak K, Måge F, Mestre A, Nordli O, Peñuelas J, Pirinen P, Remisová V, Scheifinger H, Striz M, Susnik A, Wielgolaski F-E, van Vliet A, Zach S, Zust A (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976

Montoya R, Hernández R (1991) La procesionaria del pino. In: Romanyk N, Cadahia D (eds) Plagas de insectos en las masas forestales españolas. MAPA, Madrid, pp 59–73

Moreno JM (coord) (2005) A Preliminary Assessment of the Impacts in Spain due to the Effect of Climate Change. OECC, MMA, Madrid, Spain

Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests – General aspects and the pine processionary moth as specific example. For Ecol Manag 259:831–838

Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952–2000 in the Mediterranean region. Glob Chang Biol 8:531–544

Pimentel C, Calvão T, Ayres MP (2011) Impact of climatic variation on populations of pine processionary moth *Thaumetopoea pityocampa* in a core area of its distribution. Agric Forest Entomol 13:273–281

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Robinet C (2006) Mathematical modelling of invasion processes in ecology: the pine processionary moth as a case study. PhD thesis, EHESS, Paris

Robinet C, Baier P, Pennerstorfer J, Schopf A, Roques A (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den, Schiff.) (Lep., Notodontidae) in France. Glob Ecol Biogeogr 16:460–471

Rodó X, Baert E, Comín FA (1997) Variations in seasonal rainfall in Southern Europe during the present century: relationships with the North Atlantic Oscillation and the El Niño-Southern Oscillation. Clim Dyn 13:275–284

Sáenz J, Rodríguez-Puebla C, Fernández J, Zubillaga J (2001) Interpretation of interannual winter temperature variations over Southwestern Europe. J Geophys Res-Atmos 106(D18):20641–20652

Sánchez Lorenzo A, Martín Vide J, Calbó J, Cernocky T (2005) Aproximación a la influencia de la NAO en la insolación en la España peninsular y Baleares. 1st Congress Climatic Change, Agriculture and Environment. Junta de Castilla y León, November 10–12, 2005, Valladolid (Spain)

Sierpiñska A (1998) Towards an Integrated Management of *Dendrolimus pini* L. In: ML McManus, AM Liebhold (eds) Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service, Northeastern Research Station, General Technical Report NE-247, pp 129–142

Stenseth NC, Mysterud A (2005) Weather packages: finding the right scale and composition of climate in ecology. J Anim Ecol 74:1195–1198

Stephenson DB, Pavan V, Collins M, Junge MM, Quadrelli R (2006) North Atlantic Oscillation response to transient greenhouse gas forcing and the impact on European winter climate: a CMIP2 multi-model assessment. Clim Dyn 27:401–420

Tiberi R, Niccoli A, Curini M, Epifano F, Marcotullio MC, Rosati O (1999) The role of monoterpene composition in *Pinus* spp. needles in host selection by the pine processionary caterpillar *Thaumetopoea pityocampa*. Phytoparasitica 27:263–272

Vähätalo AV, Rainio K, Lehikoinen A, Lehikoinen E (2004) Spring arrival of birds depends on the North Atlantic Oscillation. J Avian Biol 35:210–216

Volney WJA, Fleming RA (2000) Climate change and impact of boreal forest insects. Agric Ecosyst Environ 82:283–294

Weseloh RM, Andreadis TG, Onstad DW (1993) Modelling the influence of rainfall and temperature on the phenology of infection of gypsy moth, *Lymantria dispar*, larvae by the fungus *Entomophaga maimaiga*. Biol Control 3:311–318