Effects of climate and density-dependent factors on population dynamics of the pine processionary moth in the Southern Alps

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Abstract Forest pest populations can fluctuate dramatically in relation to climate and density-dependent factors. Although the distributional range of the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera Notodontidae) appears to be expanding northward and upslope with climate warming, the relative importance of climate and endogenous, density-dependent factors has not been clearly documented. We analyzed the population dynamics of the moth using long-term data from two provinces in the Southern Alps (Trento: 1990–2009, Bolzano/Bozen: 1975–2011) to evaluate the relative importance of climate and density-dependent factors as regional drivers. Both summer temperatures and rainfall significantly affected population growth rate, with different outcomes depending on the local conditions. Although previous studies indicated that low winter temperatures have negative effects on insect performance, our analyses did not show any negative effect on the population dynamics. A negative density dependent feedback with a 1-year lag emerged as the most important factor driving the population dynamics in both regions. Potential mechanisms explaining the observed negative density feedback include deterioration of host quality, increased mortality caused by pathogens, and increase of prolonged diapause as an adaptive mechanism to escape adverse conditions.

1 Introduction

Population dynamics of forest pests often depends on complex interactions between abiotic and biotic regulation factors (Turchin et al. 2003; Klapwijk et al. 2012). During the last decades

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climate change has been demonstrated to have important consequences for forest pest outbreaks and population dynamics of several species (Dale et al. 2001; Solomon et al. 2007). The direct effects of warmer temperatures on herbivorous insects are expected to be generally positive as a result of increased winter survival, faster development rates, and sometimes increased number of generations per year (Sinclair et al. 2003; Klapwijk et al. 2012). Indirectly climate can affect population dynamics of herbivores through modification of host plant quality (Marini et al. 2012; Jactel et al. 2012) and natural enemy impacts (Berggren et al. 2009). Despite these predictions about effects of climate change on insect herbivores, density-dependent factors such as intra-specific competition for resources or top-down interactions may be dominant drivers of population dynamics for several species (Marini et al. 2013). In this context, analyses of long time-series can help elucidating the relative importance of both endogenous and exogenous processes on pest population dynamics.

The pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera, Notodontidae) is one of the most important pests of pine forests in Europe and Northern Africa. The insect is active throughout the winter as larva, feeding nocturnally on pine needles and causing increment loss in the attacked stands (Jacquet et al. 2012). This pest represents also a threat to public health since caterpillars release urticating setae causing allergic reactions in humans and domestic animals (Battisti et al. 2011). Larvae exhibit strong social and gregarious behavior building up silky tents, commonly called nests, on host plants during all the development stage. At the beginning of spring the larvae form a head-to-tail line (procession) and move to pupate in the soil. A variable part of the colony enters in extended diapause which may last up to 7 years (Démolin 1969; Battisti et al. 1998). Adult emergence is immediately followed by mating and egg laying. Among several pest control techniques tested, the applications of chemical and biological insecticides are by far the most widespread choice for pest control (Battisti et al. 1998). Recent short-term studies, however, have brought into question the cost effectiveness of insecticide applications during outbreaks, indicating that population may collapse irrespective of the treatment (Cayuela et al. 2011). More research to elucidate the relative importance of climate and density-dependent factors should improve our ability to predict and manage pest outbreaks under a climate change scenario.

Several climatic parameters are expected to affect moth population dynamics. Winter temperatures are the main limiting factor for moth development and range expansion in the northern part of the pest geographical distribution (Battisti et al. 2005; Buffo et al. 2007; Huchon and Demolin 1970) and over the few last decades, temperature warming has been associated with expansion in both latitude and elevation (Hódar and Zamora 2004; Battisti et al. 2005). Warmer climate may contribute to improve larval performance (Klapwijk et al. 2012), and increase winter survival, because of decreased probability of lower lethal temperatures (Hódar et al. 2003). Other potential important climatic factors are rainfall (Pimentel et al. 2011; Hódar et al. 2012a) and effects of summer temperatures on adult dispersal (Battisti et al. 2006).

Despite the clear effect of climate on range expansion, effects of climate change on population dynamics and outbreak propensity have not been fully elucidated yet. Hódar et al. (2012a) recently found strong correlations between several climate indexes and *Th. pityocampa* defoliation. It remains important to further evaluate the relative importance of single climatic variables and to consider their effect in combination with endogenous, density-dependent factors to better understand and predict the moth population dynamics.

Quite surprisingly, factors involved in driving the population dynamics of *Th. pityocampa* have been seldom studied using long-term data. For instance, it is still unclear if density-dependent negative feedbacks contribute to population collapse during outbreak conditions. Some small scale studies have indicated that outbreaks usually result in deterioration of food quality and quantity that seem to be important factors responsible for population collapses

(Battisti 1988; Hódar et al. 2004). Considering the natural enemy species associated with *Th. pityocampa*, a relatively large number of predators and parasitoids are expected to respond numerically to moth density potentially producing negative density feedback on host populations (Zovi et al. 2006, 2008). Due to the gregarious behavior of the larvae, high population density during outbreaks is further expected to facilitate spread of viral diseases with potential negative effects on populations (Weseloh et al. 1993).

Scarce knowledge about the drivers of population dynamics in this system prevents effective prediction about large-scale response of the species to climate change. Even if temperature effects on the insect physiology are well known, the influence of single climatic variables on the population dynamics is still largely unclear (but see Pimentel et al. 2011). This is probably due to the paucity of studies based on long time-series that are able to give a comprehensive view of the moth's population dynamics and interaction with exogenous factors. Hódar et al. (2012a) provided a first step in this direction, showing the potential of climatic models to forecast forest defoliation by *Th. pityocampa*. In the present study, we analyzed two time-series of *Th. pityocampa* population dynamics in two regions of the Southern Alps. We aimed at evaluating the relative importance of both climatic and density-dependent factors in driving inter-annual fluctuations of *Th. pityocampa* populations and underscore their potential importance for planning pest management in Alpine forests.

2 Material and methods

2.1 Study area

The study areas were the province of Trento and Bolzano/Bozen located in northern Italy (Fig. 1a). Both provinces are mainly dominated by alpine habitats (75 % of the territory lies above 1,000 m). Pine forests composed of scots pine (*Pinus sylvestris*) and black pine (*P. nigra*) cover 57,775 ha (8 % of the total regional forest surface). During the last century the intensive use of *P. nigra* for reforestation in both provinces significantly extended the area suitable for colonization by the pine processionary moth, especially at low elevation. Because of this, black pine forms mainly pure stands whereas scots pine grows also in mixed stands with broadleaf species. In the province of Trento, temperature and rain conditions are influenced by the Mediterranean climate in the southern part, while the northern part has more continental climate. Average annual rainfall is 815 mm. Pine forests (20,740 ha) represent the 6 % of the total forest area and lie between 200 and 1,900 m, with a mean of c. 650 m. Black pine formations constitute 28 % of total pine forests. Bolzano/Bozen province is characterized by higher elevation and generally colder temperatures. The climate is more continental, with an annual rainfall regime of 790 mm. Pine forests (37,035 ha) represent 11 % of the total forest area. Black pine stands constitute less than 1 % of total pine forests and were also planted at low elevation. Although the two provinces are neighbors, they were considered separately because the data came from two independent monitoring campaigns and the length of the time-series were very different (see below).

2.2 *Thaumetopoea pityocampa* data

Time-series data came from two extended campaigns of forest monitoring based on field observations. In Trento province, the data series started in 1990 and ended in 2009 (20 years). The data series for Bolzano/Bozen province started in 1975 and ended in 2011 (37 years). Data consisted of the area of forest attacked by the moth, as estimated from ground-
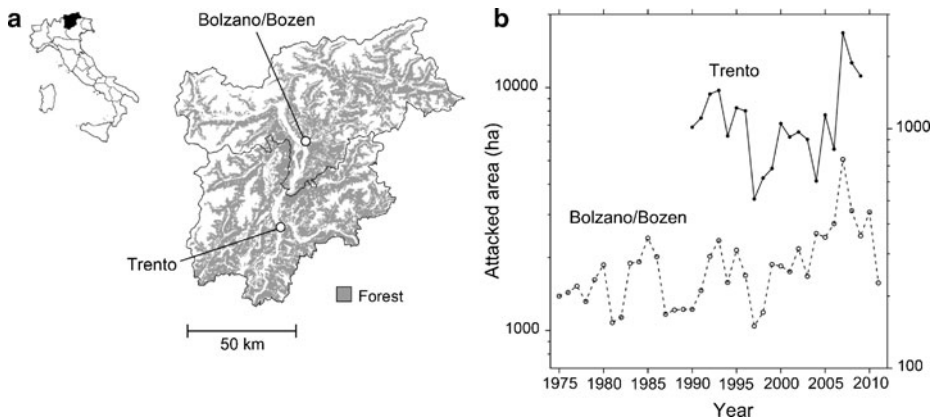
Fig. 1 **a** Geographical distribution of the forest in the two provinces and **b** annual time series of attacked area separately for Trento (*left y-axis*) and Bolzano/Bozen province (*right y-axis*). The y-axis is log-transformed. Forest included both conifer and broadleaf tree species from CORINE (www.eea.europa.eu)

based observations (see below) over the whole provincial territory. Although pest control treatments were applied in the vicinity of urban settlements and hiking paths, the extent of treatment (<5 % of area affected) was so small that we do not expect significant effects on regional population dynamics. The spatial resolution of the infested area data was the management unit area (average area c. 14 ha). Each forest unit area was surveyed every year and classified as infested if more than 10 nests per hectare were present during the winter survey, when they are particularly conspicuous and easy to detect. For each year, the area of all the infested units was summed to build a time series of infestation at the provincial scale. The area of attacked forest cannot be considered as a true population abundance measure but it is expected to be monotonically and positively correlated with population size at large spatial scale (see also Friedenberg et al. 2008; Marini et al. 2012). We therefore used a population dynamics model to explain the inter-annual variation in attacked area over time (see below).

2.3 Abiotic variables with direct effects

We used a range of climatic parameters to explain inter-annual fluctuations of moth population. We included variables that likely have direct effects on insect growth, i.e., variables based on temperature and rainfall. *Th. pityocampa* is active during winter usually as larva in the third and fourth instar feeding on pine needles as long as the night temperature is above 0 °C. Winter temperatures are considered the principal larval mortality factor during this period of the year (Huchon and Demolin 1970; Battisti et al. 2005). We also took into account temperature during the summer months, as this period is of crucial importance for insect dispersal. Swarming takes place usually from the end of June until the beginning of September. Expansion of infestation is facilitated by warm summer nights, contributing to long-distance (more than 2 km) dispersal of females (Battisti et al. 2006). Population of pine processionary moth might be also affected by high amounts of rainfall that can affect insect development during the larval stages, especially during autumn (early development stages) and spring (last development stages), although the direction of the effect can be contrasting according to timing and site (Huchon and Demolin 1970; Buffo et al. 2007; Pimentel et al. 2011).

Consequently, we defined four climatic parameters expected to influence specific aspects of life history: *T-winter$_{t-1}$* (the mean of the minimum temperatures registered during

December, January, and February), *T-summer$_{t-1}$* (the mean temperature of July and August), *Rain-spring$_{t-1}$* (the rainfall sum of March and April), and *Rain-autumn$_{t-1}$* (the rainfall sum of September, October, and November). All the climatic variables described above were used to explain defoliations of the following year (at time t) and derived using daily data from 10 weather stations distributed throughout the study area: 5 in Trento province (San Michele all'Adige 205 m, Borgo Valsugana 385 m, Arco 91 m, Trento 194 m, Cles 660 m) and 5 in Bolzano/Bozen province (Bolzano/Bozen 254 m, Silandro/Schlanders 698 m, Merano/Meran 330 m, Bressanone/Brixen 560 m, Vipiteno/Sterzing 943 m). The different elevation of the weather stations affects the absolute value of temperatures but not the interannual fluctuation of the climatic signal, which is what we expect to explain the moth population variation over time (see Marini et al. 2012). For quality control, we evaluated the correlation structure among climate stations for yearly data. Although the stations were located at different elevations, the annual time series of monthly mean temperature and monthly rainfall of the single stations were highly correlated. For temperature in Trento we found an average $r_s=0.68$ while in Bolzano/Bozen an average $r_s=0.69$. For rainfall in Trento we found an average $r_s=0.73$ while in Bolzano/Bozen an average $r_s=0.69$. We therefore averaged each of the climatic variables described above across the stations within each province to obtain a single regional climatic signal for each year. The absolute values of the temperature-related variables are not important as they depend on the elevation of the meteorological stations; what is important for our analyses is the interannual variation. These annual time series were then used to explain the population growth rate in the two provinces.

2.4 Data analysis

As we assumed that the area attacked by *Th. pityocampa* should be monotonically related to population size, we used a discrete model of population dynamics (e.g. Day et al. 2010; Marini et al. 2012) to explain interannual fluctuation of *Th. pityocampa* populations. Thus, we calculated the population growth rate as $R=\ln(N_t/N_{t-1})$ (where N_t=attacked area of year t). First, we included a density feedback term to test whether the attacked forests of the previous year N_{t-1} affects R. We hypothesized that interannual variation would provide a negative density dependent feedback as follows:

$$R = f(N_{t-1}, N_{t-2}) + \varepsilon,$$

with ε representing sampling error in the estimation of population growth rate plus exogenous (i.e. density independent) effects on R. The density feedback term N_{t-1} represented direct (1-year lag) density dependent regulation and should mostly be related to competition for food or to other endogenous process that exhibit no lagged responses. On the contrary N_{t-2} is usually tested to detect potential effect of natural enemies (Berryman and Turchin 2001). As natural enemies usually respond with a 1-year lag to increase in host or prey density they are expected to exhibit a 2-year lag relationship with R. As in preliminary analyses N_{t-2} presented no relationship with R, we included only N_{t-1} in further analyses. We omitted this variable from the analyses presented here to reduce model complexity in the multi-model inference analyses (see below).

As exogenous variables (ε) we included in the model *T-winter$_{t-1}$*, *T-summer$_{t-1}$*, *Rain-autumn$_{t-1}$* and *Rain-spring$_{t-1}$*

$$R = f(N_{t-1} + T{-}winter_{t-1} + T{-}summer_{t-1} + Rain{-}autumn_{t-1} + Rain{-}spring_{t-1})$$

All the climatic variables were included with a 1-year lag as they are expected to directly influence population density. As we had no clear ecological hypotheses about indirect effects

of climate through host plant variation, we did not include any abiotic variable with more than a 1-year lag.

Due to the different time-series length we ran this model within each province (Trento and Bolzano/Bozen), separately. We used general linear models to estimate model parameters as residuals approximated a normal distribution. To evaluate the relative importance of exogenous and endogenous variables, we used an information theoretic approach to evaluate alternative competing models within each province, separately (Burnham and Anderson 2002). Compared to single model inference and traditional null-hypothesis testing, multimodel inference is a useful approach in observational explanatory analyses when a single hypothesis is difficult to construct (Johnson and Omland 2004). $R = \ln(N_t/N_{t-1})$ was used as the response variable in these models. Our information-theoretic approach compared the fit of all the possible candidate models obtained by the combination of predictors using second-order Akaike's information criterion (AICc) corrected for small sample size. The AICc is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to generate it. The best fitting model is the one with the lowest AICc ($AICc_{MIN}$). The difference in AICc values between models indicates the relative support for the different models. In a set of n models each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta AICc_i = AICc_i - AICc_{MIN}$). A model is usually considered plausible if its $\Delta AICc$ is below 2 (Burnham and Anderson 2002). From the set of plausible models we omitted the models with uninformative parameters, i.e. models with $\Delta AICc$ below 2 but including only one additional parameter compared to the best model (Arnold 2010). For each model i, we also calculated an Akaike's weight (w_i), which sums to 1 and has a probabilistic interpretation: of all the candidate models, w_i is the probability that model i would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham and Anderson 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. To gauge the relative importance of each predictor, we summed the w_i across the models in the set ($\sum w_i$) in which the predictor occurred. The sum of model weights can vary between 0 and 1. The multimodel inference analyses were performed using the 'MuMIn' package (Barton 2010) implemented in R version 2.12.0 (R Development Core Team 2012).

3 Results

The area attacked by *Th. pityocampa* was very different between the two provinces. In the Trento province, it varied from a minimum of 3,480 ha to a maximum of 16,781 ha year^{-1} (81 % of the province's pine forests) and in Bolzano/Bozen from 150–744 ha year^{-1} (2 % of the province's pine forests). In spite of this difference, fluctuations in attacked area had comparable trends between the two provinces, particularly appreciable during the years of highest peaks (1993 and 2007). In both time-series peaks of attacks occurred with lapses of 4–10 years (Fig. 1b).

In both provinces only one model was selected as plausible, i.e. no other models had $\Delta AICc < 2$. Model selection uncertainty was relatively low. In both provinces the sum of model weights indicated that the population dynamics was mostly related to the attacked area in the previous year (N_{t-1}), showing a direct (1-year lag) negative density, i.e. population growth rate decreased after years with large attacks (Fig. 2).

In relation to the climatic variables we found different effects in the two provinces. In the Trento province, the population growth rate was further negatively explained by autumnal rainfall (*Rain-autumn$_{t-1}$*) and positively by spring rainfall (*Rain-spring$_{t-1}$*). We also found a
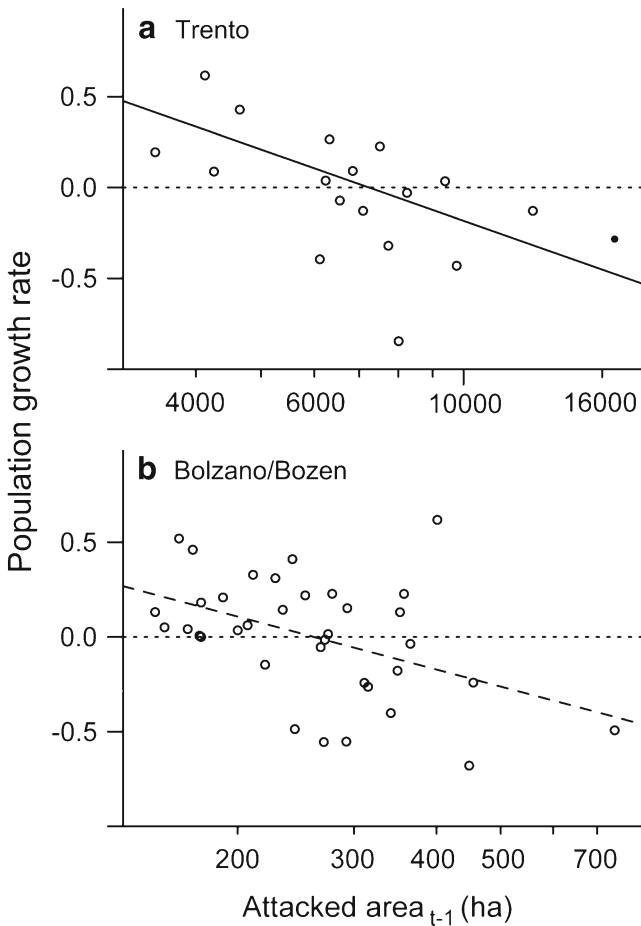
Fig. 2 Relationship between population growth rate between year t-1 and t and the attacked area in year t-1 separately for (**a**) Trento and (**b**) Bolzano/Bozen provinces. The x-axis is log-transformed

weak indication for a positive effect of minimum winter temperatures ($T\text{-}winter_{t-1}$). The best model explained c. 65 % of the total variation in R (Table 1). In the Bolzano/Bozen province, summer temperatures ($T\text{-}summer_{t-1}$) further explained part of the variation in the population growth rate showing a positive effect. The best model explained c. 30 % of the total variation in R (Table 1).

4 Discussion

Our study showed that both climate and density-dependent factors contributed to drive the interannual variation of *Th. pityocampa* populations in the Southern Alps. A negative density-dependent feedback emerged as the most important driver of population dynamics, i.e. where the population growth rate was negatively related to the area attacked in the previous year. Both temperature and rainfall further affected population dynamics with their relevance being dependent on the local conditions. We found that while high autumnal

Table 1 Estimated parameters from the plausible models (ΔAICc < 2) explaining changes in population growth rate $\ln(N_t/N_{t-1})$ in (a) Trento and (b) Bolzano/Bozen province. In both provinces, only one model was selected, i.e. no other model has ΔAICc < 2. R^2 and model weights (w_i) are also reported. Σw_i indicates the sum of model weights of the model in which each variable is included

| | (a) Trento | | (b) Bolzano/Bozen | |
	1st	Σw_i	1st	Σw_i
R^2	0.65		0.30	
ΔAICc	0.00		0.00	
Model w_i	0.52		0.37	
Intercept	3.626		0.587	
Attacked area$_{t-1}$	−0.411	0.82	−0.471	0.98
Rain-autumn$_{t-1}$	−0.002	0.95		0.27
Rain-spring$_{t-1}$	0.004	0.89		0.23
T-summer$_{t-1}$		0.09	0.100	0.89
T-winter$_{t-1}$	−0.135	0.75		0.23

From the set of plausible models we omitted the models with uninformative parameters, i.e. models with ΔAICc below 2 but including only one additional parameter compared to the best model (Arnold 2010)

rainfall and mild winters negatively influenced population growth rate, hot summers and high spring rainfall had a general positive effect on population growth. Although previous studies clearly indicated that low winter temperatures have negative effects on insect performance (Huchon and Demolin 1970; Battisti et al. 2005; Buffo et al. 2007), our analyses showed no clear effect of low temperature on the population dynamics at the regional scale (see also Hódar et al. 2012a). This suggests that factors clearly affecting individuals locally in a given year may have a different importance when considered the population dynamics over a larger spatial scale. In addition, *Th. pityocampa* did not show any tendency to express regular cycles, as previously observed in the French Alps (from 1959–1982, Geri and Millier 1985) and in Bolzano/Bozen province during the period preceding the one considered in this study (from 1950–1974, Hellrigl 1995).

4.1 Climatic variables

We found a positive effect of warm summer temperatures on population growth rate of the pine processionary moth in Bolzano. High temperatures may affect the dispersal of *Th. pityocampa* adult females increasing the take-off probability (Battisti et al. 2006) and probably also the distance flown (Ishiguri and Shirai 2004). Both of these impacts are expected to positively affect species dispersal. This factor did not emerge as significant in the Trento province probably because of its generally warmer climate.

Contrary to our expectations, winter temperature did not play an important role in population dynamics. In Trento province we found support for a weak positive effect. A positive effect of winter minimum temperature on larval growth was also observed by Pimentel et al. (2011) in Portugal and it was associated with higher radiation. Radiation is an important factor for food digestion during daytime (Battisti et al. 2005, 2013) and generally is associated with lower night temperatures because of clear sky. It may thus happen that an insect benefiting from high radiation in winter can better tolerate low temperatures in the core of its range (Hoch et al. 2009; Hódar et al. 2012a).

In contrast, several previous studies have shown that low winter temperatures are one of the most important factors negatively affecting *Th. pityocampa* populations and regulating its expansion at the margin of species distribution (Huchon and Demolin 1970; Battisti et al. 2005; Buffo et al. 2007). Considering the elevational distribution of the forests attacked, winter temperatures are unlikely to cause significant winter mortality. Winter temperatures are probably important only locally where population occur at the coldest part of its distributional range. Thus, they could certainly be a factor in climate-induced range expansion.

Besides temperature, we found that rainfall was a further important factor only in the warmer area (Trento province). Abundant rainfall during autumnal months seemed to have negative effects on the population growth rate. A first explanation might be that rainfall physically hinders larval movements, affecting individual growth rate (Pimentel et al. 2011; Hódar et al. 2012a). A second explanation is that a high humidity, together with the decreased larval resistance to infection due to the limited feeding, may promote infections by pathogens, such as fungi and viruses (Weseloh et al. 1993). Furthermore autumnal rainfall may affect negatively pupae survival increasing the soil humidity (Markalas 1989) and alter moth emergence during summer (Hódar et al. 2012b). Conversely, spring rainfall was found to affect the moth population positively. Rainfall during this intensive feeding period could have indirect effects by limiting the activity of larval-pupal parasitoids (Battisti et al. 2000) without affecting the more vigorous caterpillars of fourth and fifth instars. It should be also considered that an element of great uncertainty in our analysis of the abiotic factors is the tendency of the insect to enter prolonged diapause in response to deteriorating climatic cues (Démolin 1969). If large proportions of the population enter diapause, the potential effect of climatic factors on population dynamics can be easily masked or confused.

4.2 Density negative feedback

We found strong indication that direct, negative density feedback regulates the population growth rate in *Th. pityocampa*. We can identify three potential mechanisms explaining the observed negative density feedback. First, severe defoliation may strongly modify host tree quality. Studies at the single stand scale have showed that black pines present considerable reduction in food quality and quantity after a complete defoliation by *Th. pityocampa* and that this can affect the next generation's development and cause population collapse after outbreak years (Battisti 1988). Survival of young larvae was particularly influenced by leaf quality (Hódar et al. 2004). High levels of intraspecific competition after abrupt growth of the population, intensified by food scarcity, could cause higher larval mortality leading to population decline.

Second, amongst moth natural enemies, pathogens are the only ones able to respond relatively quickly (1-year lag) to the host density (Weseloh et al. 1993; Battisti et al. 1998), while parasitoids should respond with a longer time delay (Zovi et al. 2006). However, the lack of data regarding parasitism and predation of these moths at the scale of the study is insufficient to support an understanding of their role in moth population dynamics. The lack of negative density feedback with 2-year lag, however, suggests that natural enemies do not play an important role in regulating pest density in these particular areas. Conversely, pathogens have been recognized as important in the regulation of *Th. pityocampa* population density (Battisti et al. 1998) as well as in promoting density fluctuations in cycling species of other forest Lepidoptera (Hochberg et al. 1990; Dwyer 1991; Myers 2000; Bjornstad et al. 2010). The resistance to disease of many lepidopteran larvae (as the gypsy moth *Lymantria dispar*) has been found to be inversely related to the population density at the time of infection (Hochberg 1991; Reilly and Hajek 2007).

Third, shortage of food in years following a population peak may induce prolonged diapause, which can be regarded as an adaptation ensuring escape from low quality food and high competition (Sims 1983; Hanski 1988; Saulich 2010). Prolonged diapause is a typical trait of the pine processionary moth at high elevations and latitudes and may appear to a large extent after abiotic and biotic disturbances of population growth (Démolin 1969). The biotic and abiotic triggers of the diapause remain, however, largely unknown.

5 Conclusions

Our study provides evidence for a strong negative density-dependent feedback in *Th. pityocampa* populations. It further indicates that abiotic variables influencing range expansion of *Th. pityocampa* do not have the same importance on local population dynamics. Although temperature warming appears to explain the upslope and northward expansion of the moth range in Europe (Robinet et al. 2007), and the establishment of human introductions beyond current range limits (Robinet et al. 2011), warming may not directly translate into a higher impact across the range. Although several climatic variables related to temperature and rainfall locally explained pest population dynamics confirming the potential for climate change to influence outbreak dynamics, the observed strong negative density feedback seems to be an important natural mechanism controlling *Th. pityocampa* outbreaks.

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