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Geographical variation in climatic drivers of the pine processionary moth population dynamics

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A B S T R A C T

Geographical variation in forest insect sensitivity to environmental conditions is often overlooked. Yet considering regional variation in response to climate is necessary to better predict the consequences of climate change on pest population dynamics and associated damage.

We investigated the climatic drivers of demographic fluctuations in a forest tree defoliator, the pine processionary moth (PPM), in 8 biogeographical regions in France. We studied the effects of precipitation and temperature for both cold and warm periods, in accordance with PPM biology. We trained second-order log-linear models of infestation dynamics based on records spanning over 32 years (1981–2014) and 1239 forest plots, and tested their forecast accuracy on two additional years (2013–2014).

PPM population growth rate decreased with higher precipitations in 5 regions and increased with increasing temperatures in the cold period in 4 regions. The magnitude and direction of temperature effects in the warm period varied among biogeographical regions. Our results also revealed that PPM population dynamics were largely triggered by density-dependent factors independent from climatic drivers. Short-term forecasts were generally accurate irrespective of the inclusion of climatic variables into the models.

To better predict the consequences of climate change on insect population dynamics, it is advisable to take geographical variability of species response into account and develop regional forecasting models.

1. Introduction

Climate change is expected to exacerbate abiotic and biotic disturbances in forests (Ayres and Lombardero, 2000; Cannon, 1998; Dukes et al., 2009; Volney and Fleming, 2000; Williams et al., 2010), threatening the health of forests and their ability to provide major ecosystem services (Boyd et al., 2013; Littell et al., 2010) such as the maintenance of the global carbon balance (Kurz et al., 2008; Stinson et al., 2011; Volney and Fleming, 2000).

1.1. Population dynamics of insects exhibit intraspecific variations in climatic drivers

Herbivore insects are among the most widespread natural sources of biotic disturbances in forests (Schelhaas et al., 2003). However these biotic disturbances are not independent of abiotic conditions. Indeed climate is a key driver of insect species distribution and dynamics through effects on growth rates and biotic interactions (Post et al., 2009). The nature, direction and magnitude of climatic effects on insect population dynamics vary at the intraspecific and interspecific level (Harrison et al., 2015; Haynes et al., 2014; Nice et al., 2014; Wallis De Vries et al., 2011). Different populations of a given species may thus exhibit different sensitivities to a given climatic variable (Marini et al., 2013) or even differ in the main climatic driver of their dynamics, due to local adaptation or plasticity (Robinet et al., 2015). Identifying intraspecific variations in pests sensitivity to climate is therefore a foreground preliminary step to accurately predict their future impact on forest health.

1.2. Multiple-site monitoring for studying geographical variation of insect population dynamics

Forest insect population dynamics are often quantified with indirect estimates of population abundance, for example based on the effects of

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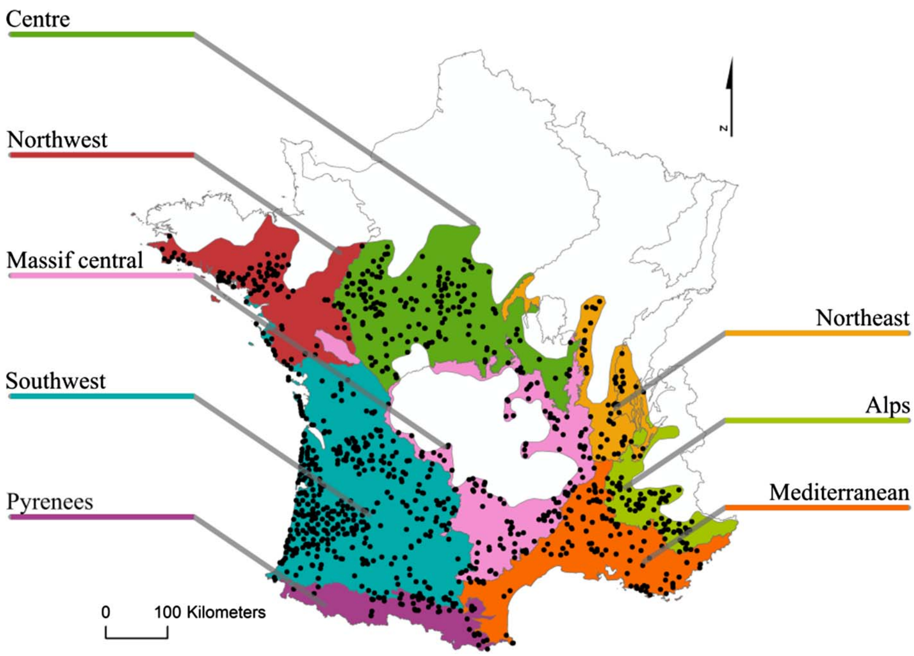

Fig. 1. Biogeographical forest regions covered by the dataset. Black dots represent the plots. White areas in the northern half and the central part of the country correspond to the biogeographical forest regions outside the distribution range of the PPM.

defoliation on individual tree growth which can be reconstructed from tree-ring chronosequences (Berg et al., 2006; Esper et al., 2007; Flower et al., 2014; Konter et al., 2015; Paritsis and Veblen, 2011). However, because climatic variables can influence tree growth both directly through tree physiology and indirectly through pest impacts, outcomes of such dendrochronological analyses are difficult to interpret in terms of climatic effects on insect demography. A few long term studies of forest insect population dynamics relied on empirical multiple-site data (Haynes et al., 2009; Ims et al., 2004; James et al., 2010; Jepsen et al., 2008; Johnson et al., 2005; Klemola et al., 2006; Liebhold et al., 2006), using direct counts of insects (e.g., trapping) or defoliation monitoring. However, only few have considered the possibility of intraspecific variations of insect population dynamics in response to climate (Marini et al., 2013; Tamburini et al., 2013). Here we took advantage of a long term, multiple-site monitoring of a forest pest to investigate geographical variations in the climatic determinants of its population dynamics.

1.3. Temperature and precipitation are key determinants of insect metabolic rates

As poikilothermic organisms, insect are particularly sensitive to external variations of temperature, which regulate their metabolic rates and longevity (David et al., 2016; Robinet and Roques, 2010; Vasseur et al., 2014). Change in precipitation regimes, particularly extreme events like heavy rains or droughts, can also affect insects' survival and fitness, directly or through host plant physiology (Jacquet et al., 2012; Netherer and Schopf, 2010; Rouault et al., 2006). Climate changes are thus likely to influence insect survival and development rate (Jepsen et al., 2008; Netherer and Schopf, 2010), to modify insect-host phenological synchrony (Stireman et al., 2005; van Asch and Visser, 2007), to favor multi-voltinism (Altermatt, 2010), and to cause expansion of species ranges (Robinet and Roques, 2010).

1.4. Pine processionary moth population dynamics

We focused on the pine processionary moth (PPM), *Thaumetopoea pityocampa* (*Denis* and *Schiffermüller*, *1775*), the most devastating defoliator of pine forests around the Mediterranean basin (Roques et al., 2015). Severe defoliations caused by PPM can lead to significant tree growth losses (Jacquet et al., 2012). Furthermore, PPM caterpillars release urticating setae in the air, threatening mammal and human health (Battisti et al., 2011). Since the beginning of the nineties, PPM has extended its range towards northern latitudes and higher altitudes in response to climate warming, with a shift of 120 m upward in the Italian Alps between 1975 and 2004 (Battisti et al., 2006, 2005; Robinet et al., 2007). However how the frequency and amplitude of PPM outbreaks will change with climate in colonized regions remains an unresolved question (Tamburini et al., 2013). Thus PPM is a highly relevant biological model for studying geographical variations in climatic drivers of pest population dynamics. Frequency of PPM outbreaks have been shown to be regular, suggesting cyclicity in population dynamics, which would be mainly driven by density-dependent factors (Li et al., 2015). In addition, periodicity varied at the national scale in France, with a return period of outbreaks ranging from 7 to 9 years in the different regional areas. The sinusoidal model adjusted to demographic fluctuations of PPM populations did however not account for changes in amplitude of outbreaks (Li et al., 2015). And yet extrinsic variables, and particularly climatic drivers (Tamburini et al., 2013), are major determinants of outbreak intensity.

1.5. Study objectives and hypotheses tested

The study of the climatic determinants of PPM population dynamics is not trivial as different life stages can be impacted by different weather conditions at different times of the year. We seek to investigate the intraspecific variability in the climatic drivers of PPM population dynamics at a national scale (France). We expected an effect of both density-dependant factors and climate, specifically we made the hypothesis that the direction and magnitude of temperature and precipitation effects varied across regions according to limiting factors of PPM survival and development at different life stages. We considered separately the cold period, where low temperatures and high precipitations may cause high mortality in larval stages, and the warm period where pupae and moths could be exposed to adverse high temperatures and high precipitations. In a second step we compared the short-term, forecasting accuracy of PPM population dynamic models based on direct and delayed density-dependent factors *vs*. models also including relevant climatic variables. We used continuous temporal series covering up to 34 years of PPM infestation recorded in 8 biogeographical regions encompassing the natural range of the insect in France. We developed explanatory models with climatic variables using