



Climate constrains range expansion of an allochronic population of the pine processionary moth

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ABSTRACT

Aim Allochronic speciation occurs when sympatric populations sharing similar feeding regimes diverge because they mate at different times. Such speciation mode is fascinating because it permits the study of subsequent adaptations and/or geographic range shifts undergone by the populations that face new ecological constraints. Moreover, exploring whether intraspecific differentiation is accompanied by niche divergence is crucial for planning efficient biodiversity management and invasive species control. Here, we address the topic of potential climatic niche divergence between two sympatric populations of the pine processionary moth *Thaumetopoea pityocampa* (PPM) that diverged under allochrony. The larval development of a PPM population recently discovered in coastal regions of Portugal, referred to as the summer population (SP), occurs in the spring–summer instead of the autumn–winter as for all other populations of this species.

Location Portugal.

Methods We carried out intensive field sampling in the area where both populations are sympatric and calibrated spread (MigClim approach) and species distribution models (ensemble forecasting approach) to depict the response of SP to environment and predict its potential range under current and future climatic conditions.

Results Since its discovery in 1997, the distribution of SP has been expanding along the Western coasts of Portugal. Still, its establishment in inland regions failed, even though suitable hosts occur. Our models identify maximal temperatures as the main constraint explaining SP absence from inland regions. The coastal area where winter populations and SP co-occur displays unique climatic conditions (moderate maximal and minimal temperatures), which enable the coexistence of these populations with totally different phenologies. The models predict a future decrease of SP range due to climate warming.

Main conclusions We show here that a climatic niche shift occurred following allochronic divergence. This study highlights how climate differentially affects allochronic populations and how considering intraspecific diversity is crucial when predicting species responses to climate change.

Keywords

allochronic speciation, intraspecific diversity, MigClim, niche shift, phenology change, *Thaumetopoea pityocampa*.

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INTRODUCTION

There is increasing evidence that intraspecific diversity should be accounted for when the potential distribution of

species is predicted for purposes of conservation or pest management. Disregarding the potentially different responses of genetically divergent populations to environmental conditions may lead to inefficient biodiversity management plans

(Benito Garzón *et al.*, 2011; D'Amen *et al.*, 2013) or invasion risk assessments (Peterson & Holt, 2003; Rey *et al.*, 2012; Godefroid *et al.*, 2015, 2016). Allochronic speciation is an increasingly documented important driver of intraspecific differentiation in several groups of organisms (Miyatake *et al.*, 2002; Abbot & Withgott, 2004; Yamamoto & Sota, 2009). Allochronic speciation arises when sympatric populations with similar feeding regimes and similar habitat requirements diverge because they mate at distinctly different times (Alexander & Bigelow, 1960). Populations that have experienced a drastic shift in reproduction time are expected to have overcome new ecological barriers through adaptations (Santos *et al.*, 2011a) and/or subsequent geographic range shifts. For that reason, exploring niche dynamics during allochronic speciation is an attractive field for evolutionary ecologists and provides an ideal context to understand the response of organisms to environmental changes and forecast the impact of ongoing global warming upon biodiversity.

The pine processionary moth (PPM), *Thaumetopoea pityocampa* (Denis & Schiffmüller) (Lepidoptera: Notodontidae), is a pine-feeding insect that occurs throughout southern Europe and northern Africa, including the Atlantic coast (Kerdelhué *et al.*, 2009). Adults typically emerge and reproduce during summer, and larvae develop during fall and winter (Démolin, 1969). An obligate nymphal diapause occurs until adult emergence takes place in the following summer (Démolin, 1969). The PPM exhibits this phenology over its whole range, and such typical populations are referred as to the 'winter populations', hereafter WPs (Kerdelhué *et al.*, 2009). In 1997, an atypical population exhibiting divergent phenology was discovered in Portugal in Mata Nacional de Leiria (National Forest Park of Leiria), hereafter MNL, where it was sympatric with WP (Pimentel *et al.*, 2006) and fed on needles of *Pinus pinaster* Aiton. Larvae of this newly discovered population develop during the summer while adults mate in the spring. This unique population is referred to as the 'summer population', hereafter SP, in opposition to the WP. In September 1997, the SP was found in an outbreak condition, yet its distribution was restricted to a few squared km inside MNL (M-R Paiva, pers. obs.). Since the discovery of the SP, its geographical range has slowly expanded along the Western coast (Battisti *et al.*, 2015). Today the range of the SP is restricted to a coastal section of central Portugal, while WPs occur wherever pines are present, that is over most of Portugal. No other population of PPM with such abruptly shifted life cycle has been observed in other regions of either Europe or North Africa.

Both the SP and the sympatric WP exhibit low phylogenetic differentiation based on nuclear internal transcribed spacer 1 (ITS-1) and mitochondrial cytochrome oxidase 1 (CO1) (Santos *et al.*, 2007; Burban *et al.*, 2016), which suggests a recent, local origin of the SP. However, the two sympatric populations are highly differentiated based on population genetics data (microsatellite markers), suggesting a founder effect and limited gene flow (Santos *et al.*, 2007,

2011b; Burban *et al.*, 2016). Based on these results, it was hypothesized that mutation(s) in a phenology-related gene(s) caused the relatively recent local foundation and emergence of SP, which is further consistent with high heritability of the shifted phenology (Branco *et al.*, 2016). Allochrony then abruptly disrupted gene flow between the sympatric populations that subsequently diverged in several adaptive and morphological traits (Santos *et al.*, 2011a, 2013). The currently observed system is thus likely to reflect the incipient stage of an ongoing allochronic speciation (Santos *et al.*, 2007, 2011b). The PPM is, consequently, an ideal organism to study the response of closely related populations facing new environmental selective pressures. However, the response of SP to the environment as well as the ecological factors allowing WP and SP to co-occur locally in Portugal are still poorly understood (but see Santos *et al.*, 2011a, 2013). Understanding the ecological aspects of allochronic divergence requires accurate depictions of both the geographic range and the ecological niche of the SP, which are currently lacking.

Additionally to being an ideal biological model for research purposes, the PPM is an economically important defoliator species that causes large losses to pine forests (Hódar *et al.*, 2002) and severe allergic reactions in humans due to the urticating setae released by the larvae (Vega *et al.*, 2004). In the SP, the urticating life stages occur at the end of the summer, coinciding with the main touristic season, by contrast with the typical WP larvae that are present during the colder months. The SP deserves higher attention from biosecurity agencies as this population is currently expanding in Portugal and, consequently, may constitute a serious threat for forestry, public health and tourism economy. While climate tolerances of WP are well depicted and predictions of its future potential distribution are available (Robinet *et al.*, 2007; Battisti *et al.*, 2015), climatic niche requirements of the SP are still poorly understood impeding an accurate prediction of its future distribution. Management of the SP might be impaired by these knowledge gaps regarding its present and future distribution across Portugal and the Mediterranean basin. Predictions of SP future spread are thus required for the development of management programs of this recently discovered population.

In this study, we explore the potential intraspecific climatic niche divergence between the allochronic WP and SP and made predictions about the evolution of the SP distribution range over time. For that purpose, we (1) performed an intensive field sampling to document the current distribution of SP in Portugal; (2) ran multivariate analyses and calibrated species distribution models (SDMs) to depict the response of SP to climate and identify the underlying environmental constraints acting on the geographic range of this population; (3) fitted spread models (MigClim approach; Engler & Guisan, 2009) to predict the potential spread of SP with regard to climate and landscape constraints, as well as dispersal abilities; (4) used SDMs to forecast the potential range of SP under future climate conditions.

METHODS

Distribution data

The range of SP has been closely monitored since the date of its first detection in Portugal by field surveys and pheromone traps (Pimentel *et al.*, 2006; Santos *et al.*, 2007, 2011b; Battisti *et al.*, 2015; Burban *et al.*, 2016). Based on this information, we carried out an intensive field sampling at the end of the summer 2014, to depict as accurately as possible the limits of the SP distribution. A total of 131 sampling stations separated by short distances (ranging from *circa* 0.5 to 4 km) were selected according to the presence of pine stands (Appendix S1 in Supporting Information). As our sampling was primarily focused on the borders of the SP range, distances separating neighbour stations within the core of SP distribution were occasionally superior to this range of values. Sampling effort in each station consisted in a thorough inspection of pine stands within a *ca.* 500-m radius circle for assessment of SP presence/absence. In addition, we performed road sampling of SP nests, a technique that is routinely used to assess the expansion of the WP in northern

France (Rousselet *et al.*, 2013). This approach consisted in driving along the main roads between sampling stations, making frequent stops to assess with naked eyes or using binoculars the presence/absence of SP nests in pine stands boarding the roads.

Fifty-seven occurrences were obtained from this campaign and from the different field surveys performed during the period 1997–2014 (Fig. 1 and Appendix S1). Our dataset was restricted to occurrences of nests with living larvae because this kind of record constitutes a good indicator that a PPM population can truly get established in a given locality (contrary to trap records that may encompass individuals that passively or actively dispersed into unsuitable regions). Transferability of correlative bioclimatic models highly increases when models are calibrated with ‘true’ absences (climatically unsuitable areas for the establishment of an organism) rather than with ‘false’ absences (climatically suitable localities where an organism is not present because of dispersal constraints or biotic interactions; Elith *et al.*, 2010). We consequently constructed two absence datasets to perform our analyses. A first absence dataset (‘ABS1’) was assumed to include only true absences and used to calibrate

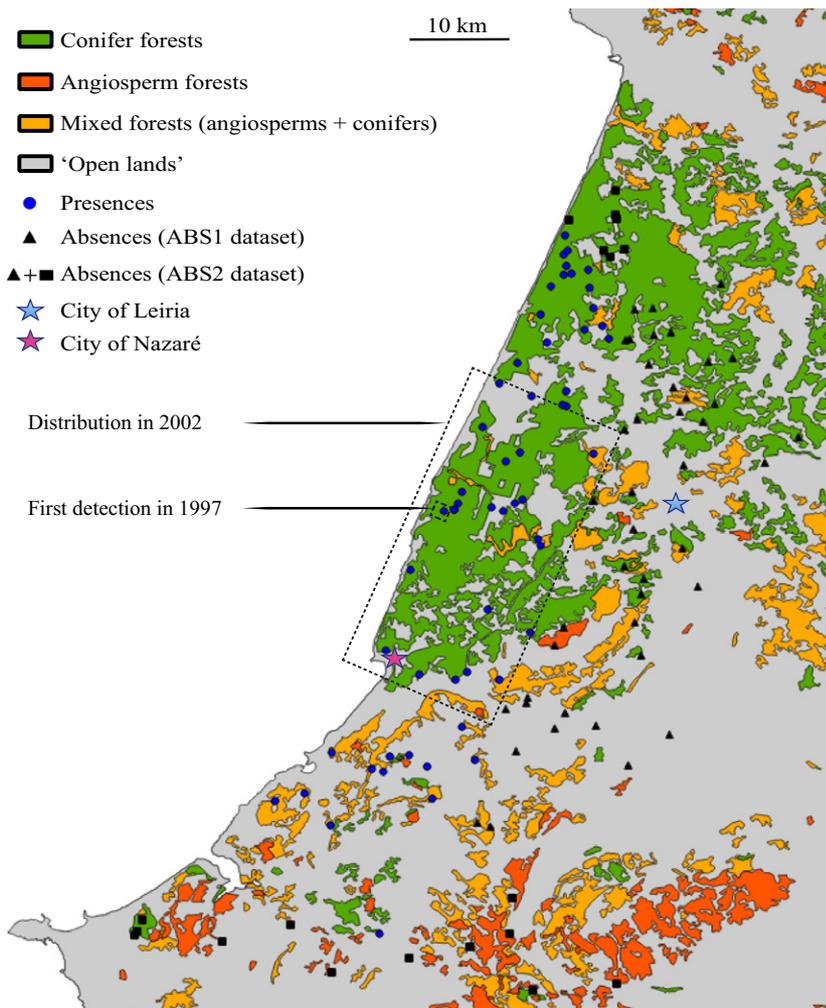


Figure 1 The presences and absences of the summer population (SP) of *Thaumetopoea pityocampa* used in species distribution and spread modelling. All absence data were obtained during field sampling performed in 2014. Two absence datasets were constructed. The ‘ABS1’ dataset comprised the absences located outside the minimum convex polygon encompassing presence records and not situated around the northern and southern fronts of expansion of SP. The second absence dataset (‘ABS2’) comprised the absences of the ABS1 dataset associated with the absences located at the northern and southern expansion fronts of SP. Colour figure can be viewed at wileyonlinelibrary.com

SDMs. We rasterized the minimum convex polygon encompassing presence records with a resolution of 30 arc seconds ('mcp-raster'). The ABS1 dataset comprised the absences located outside this mcp-raster and not situated around the northern and southern fronts of expansion of SP (Fig. 1). Given the recent emergence of SP in Portugal, the absence of this population in regions situated at higher and lower latitudes in this country might, indeed, be explained by dispersal constraints rather than climatic unsuitability of these regions. However, we included in ABS1 most of the absences recorded eastward of the current distribution of SP dataset, as these points were located in regions where the host *P. pinaster* occurs, at distances from the area where SP was first discovered in MNL that were inferior to the maximum distances of spread reached between 1997 and 2014. This fact indicates that SP spread to inland regions can neither be attributed to its dispersal ability nor to host-related constraints. In fact, host-pine plantations of *Pinus pinaster* extend almost continuously over MNL and surrounding areas (M. Godefroid, pers. obs.) (Fig. 1). The second absence dataset ('ABS2') comprised the absences of the ABS1 dataset associated with the absences located at the northern and southern expansion fronts of the SP (Fig. 1). The ABS2 dataset was exclusively used to evaluate the predictive power of spread models.

Landscape and bioclimatic data

We used current and future bioclimatic variables from WORLDCLIM version 1.4 at a resolution of 30 arc seconds (Hijmans *et al.*, 2005). We selected estimations of future climate used in the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC). To enhance the transferability of our bioclimatic models, we calibrated SDMs with a restricted climatic dataset encompassing four ecologically relevant variables according to the biology of the SP. We selected the mean temperature of the warmest month ('bio5') since heat stress is thought to constraint the range of SP (Santos *et al.*, 2011a). Average minimal temperatures recorded in May ('bio20') were considered since the reproduction of SP occurs during spring. To convey a possible moisture stress for pupae, we integrated the mean annual precipitation of the coldest quarter ('bio19') in our climatic dataset. Finally, mean temperature of the coldest month ('bio6') was selected since cold strongly constrains the geographic range of WPs, to test whether this variable could also affect the SP (Battisti *et al.*, 2005).

The climatic data from WORLDCLIM (annual trends between 1950 and 2000) do not perfectly reflect the conditions experienced by the SP over the period 1997–2014. We constructed a set of new climatic rasters ('NC bioclimatic rasters') by averaging the 1950–2000 climatic layers with layers corresponding to predictions of future climate by 2020, under the A2 scenario used in the Fourth Assessment Report of the IPCC. These predictions were obtained from the global

climate model INGV-ECHAM4 (Gualdi *et al.*, 2008). Mean differences in the values of bio5, bio6, bio19, bio20 encountered in the SP range among classical 1950–2000 climatic layers, and these newly constructed rasters were, respectively, 0.601 °C pixel⁻¹, 0.225 °C pixel⁻¹, 12.18 mm pixel⁻¹ and 0.217 °C pixel⁻¹ (Appendix S2). Although the NC bioclimatic rasters do not perfectly represent climatic conditions experienced by the SP during 1997–2014, this procedure mainly aimed at depicting uncertainty associated with our climatic data by avoiding underestimation of climatic tolerances of SP and consequently minimizing omission errors in the predictions.

We simulated the future potential distributions of SP in 2050 and 2070 using two different global climatic models (GCMs), that is the Hadley Centre Global Environmental Model version 2 HadGEM2-ES (Collins *et al.*, 2011) and the Model for Interdisciplinary Research on Climate version 5 MIROC5 (Watanabe *et al.*, 2010). We selected these GCMs because their predictions of future temperature and precipitation rank among the most reliable according to model evaluation procedures used in AR5 of IPCC (Flato *et al.*, 2013). For each GCM, we ran simulations using two different climatic datasets relative to the representative concentration pathways RCP4.5 and RCP8.5, which assume moderate and extreme global warming, respectively (Van Vuuren *et al.*, 2011).

Landscape data for Portugal were obtained from the CORINE land cover 2006 database (CEC, 1993) for the period 1990–2000. We used the distribution maps of three land cover categories at a resolution of 30 arc seconds: (1) pure conifer forests, (2) mixed conifer-angiosperm forests and (3) pure angiosperms forests (Fig. 1). All pixels not belonging to one of these three land cover categories were assigned to a uniform land cover category referred to as 'open lands' (Fig. 1).

Species distribution modelling

A principal component analysis (PCA) was first performed using the R package ADE4 (Dray & Dufour, 2007) to explore the spatial variability of climate in Portugal. We ran this PCA by considering all pixels of a 30-arc second raster of Portugal as individuals and 20 bioclimatic descriptors as variables and mapped the scores of each pixel on the two-first principal components of the PCA.

We used four SDM algorithms to model the distribution of SP: the generalized linear model with a binomial family (GLM), the classification and regression trees (CART), the boosted regression trees with a binomial family (BRT; Friedman *et al.*, 2000; Elith *et al.*, 2008) and the MAXENT algorithm based on the maximum entropy approach (Phillips *et al.*, 2006) using the R packages DISMO (Hijmans *et al.*, 2013), TREE (Ripley & Ripley, 2014) and GBM (Ridgeway & Ridgeway, 2004). To avoid the problem of separation in GLM with binary response (Heinze & Schemper, 2002), we used an approach based on a penalized likelihood correction

to the standard binomial GLM score function in the R package *GLMNET* (Friedman *et al.*, 2010).

Eighty percentage of presences and absences from ABS1 dataset were used to calibrate models while the remaining 20 percentage of data were kept for model evaluation. All probability maps were converted into the presence/absence binary maps by implementing the ‘lowest presence threshold’ (LPT; Pearson *et al.*, 2007) that minimizes the omission error. For each climatic scenario, we mapped the number of models predicting a presence in any pixel in Portugal and the Mediterranean basin (ensemble forecasting approach; see Araújo & New, 2007). In addition, for the current climatic conditions, we constructed a consensus binary prediction (C-prediction) by assigning a presence to each cell that was predicted suitable for at least 75% of models.

We constructed Multivariate Environmental Similarity Surface (MESS) maps that measure the dissimilarity between the climatic spaces of the training and projected areas (Elith *et al.*, 2010). The predictive power of each model was evaluated by calculating the area under the curve of the receiving-operator curve (AUC; Fielding & Bell, 1997).

Modelling the spread of SP

Since the range of SP in 2002 was relatively well defined (Pimentel *et al.*, 2006), we divided the presence dataset in two subsets, that is localities that were reached by SP before and after 2002 (Fig. 1). However, data were inadequate to accurately depict the range of SP for the remaining years, between 1997 and 2014. Still, we recognize that in 2002, the southern border of the SP range was not established with perfect exactitude, as SP nests were detected in the surroundings of Nazaré but were not precisely georeferenced.

We calculated the ratio between the spreading distances (i.e. distance separating the area where SP was firstly detected in 1997 and the occurrences of SP situated at latitudinal extremes across its geographic range) and the spreading time for three periods: the 1997–2014, the 1997–2002 and the 2003–2014 periods.

We used the MigClim model (Engler & Guisan, 2009) in *MIGCLIM* R package (Engler *et al.*, 2012) to model the spread of SP. We ran numerous MigClim simulations by varying the values of the dispersal kernel (more than 115 combinations) to identify the parameters’ combinations best explaining the current distribution of SP. The models maximizing the sum of sensitivity (i.e. true positive rate) and specificity (i.e. true negative rate) were considered as the most accurate. We did not consider the distribution of SP in 2002 when estimating the predictive power of MigClim models because the distribution data of SP in 2002 were relatively imprecise and the outbreak experienced by SP in 1997 probably inflated the initial spread rate of this population.

A small patch of 2 km² within MNL corresponding to the first detection of SP larvae in 1997 (Pimentel *et al.*, 2006) was considered as the source of the SP in MigClim simulations (Fig. 1). The consensus ‘C-projection’ map was used as

the input binary map of climatic suitability. A dispersal step was generated each year, and a newly colonized cell was considered prone to generate dispersing propagules 1 year after colonization (*iniMatAge* = 1, *PropaguleProd* = 1; Engler *et al.*, 2012). Even if long-distance dispersal events occurred during the spread of PPM in France (Robinet *et al.*, 2012), our measures of SP spread suggest that human-mediated dispersal events have not occurred for this population. We consequently did not consider long-distance dispersal events in models. The pure angiosperm forests were considered as barriers to dispersal (‘weak barriers’ to dispersal according to Engler *et al.* (2012)). As preliminary results showed that the spread rate of SP was anisotropic (see below), we independently ran two set of MigClim simulations that accounted for northward and southward spread of SP and subsequently merged both sets of projections.

RESULTS

The realized climatic niche of the SP

The first principal component of the PCA corresponded to a north–south climate gradient well depicted in Fig. 2(a,c). The second axis separated the Western coasts of Portugal in relation to moderate maximal temperatures (*bio5*) and low temperature seasonality (*bio2*, *bio4*, *bio7*; Fig. 2).

All SDMs have significant predictive power displaying AUCs superior to 0.93. All models identified the summer temperatures as the variable best explaining the current range of SP. Most models predicted only a narrow band along the Atlantic coast as climatically suitable for the SP in Portugal (Fig. 3). In contrast, inland regions of Portugal were considered climatically unsuitable by all models (Fig. 3). Models globally predicted that the current climatic conditions encountered in most lowland regions of the Mediterranean basin, except some coastal areas in Morocco and Northern Spain, would be unsuitable for SP establishment (Fig. 3). Some lowland regions of the Mediterranean basin (coasts of Israel, Italy and Greece) were predicted as suitable by only one model (Fig. 3). Some models, but not all, predicted European mountainous regions as climatically suitable (Fig. 3). Caution is needed, however, when interpreting the SDM predictions for these elevated regions in Europe as these areas display climatic conditions different from our calibration dataset (MESS values < 0; Fig. 2c). Models calibrated with the NR bioclimatic rasters displayed similar predictions (Fig. S1 in Appendix S3).

Depending on the GCM and the RCP considered in this study, the summer mean temperatures within the current geographic range of SP are expected to increase from 1.4 to 3 °C by 2050 compared to the period 1950–2000 and to become similar to those encountered in the adjacent inland regions where the SP is currently absent (Fig. S2 in Appendix S3). Most models predicted that large parts of the current range of the SP might become unsuitable by 2050 and 2070 (Figs 4 & S3 in Appendix S3). Most models

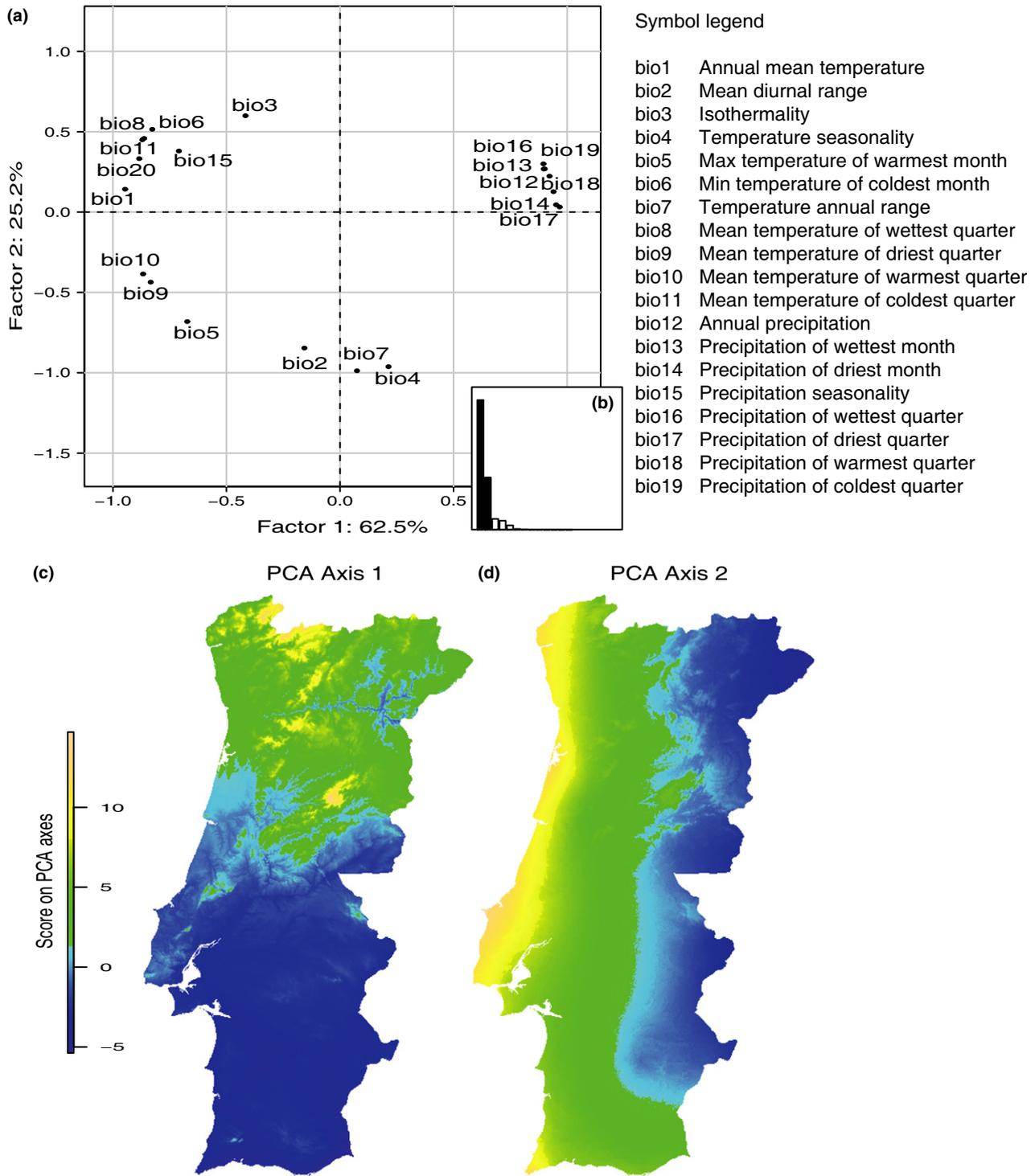


Figure 2 Principal component analysis (PCA) performed on 20 bioclimatic variables extracted from all pixels in a raster of Portugal extracted from WORLDCLIM (Hijmans *et al.*, 2005). Circle of correlation (a), eigenvalues diagram (b) and maps of scores of all pixels in Portugal on PCA axis 1 (c) and axis 2 (d) are represented. Colour figure can be viewed at wileyonlinelibrary.com

predicted some coastal regions of Portugal (i.e. the surroundings of the towns of Peniche and Aveiro) to remain climatically suitable by 2050 and 2070 under the scenario 4.5 (Figs 4 & S3 in Appendix S3). These trends were globally similar when calibrating SDMs with NR climatic layers (Figs

S2 & S4 in Appendix S3). However, the effects of global changes were predicted to be slightly more intense when calibrating SDMs with classical 1950–2000 climatic layers. The reduction of the extent of suitable climatic conditions in Portugal was predicted to be higher under the RCP 8.5

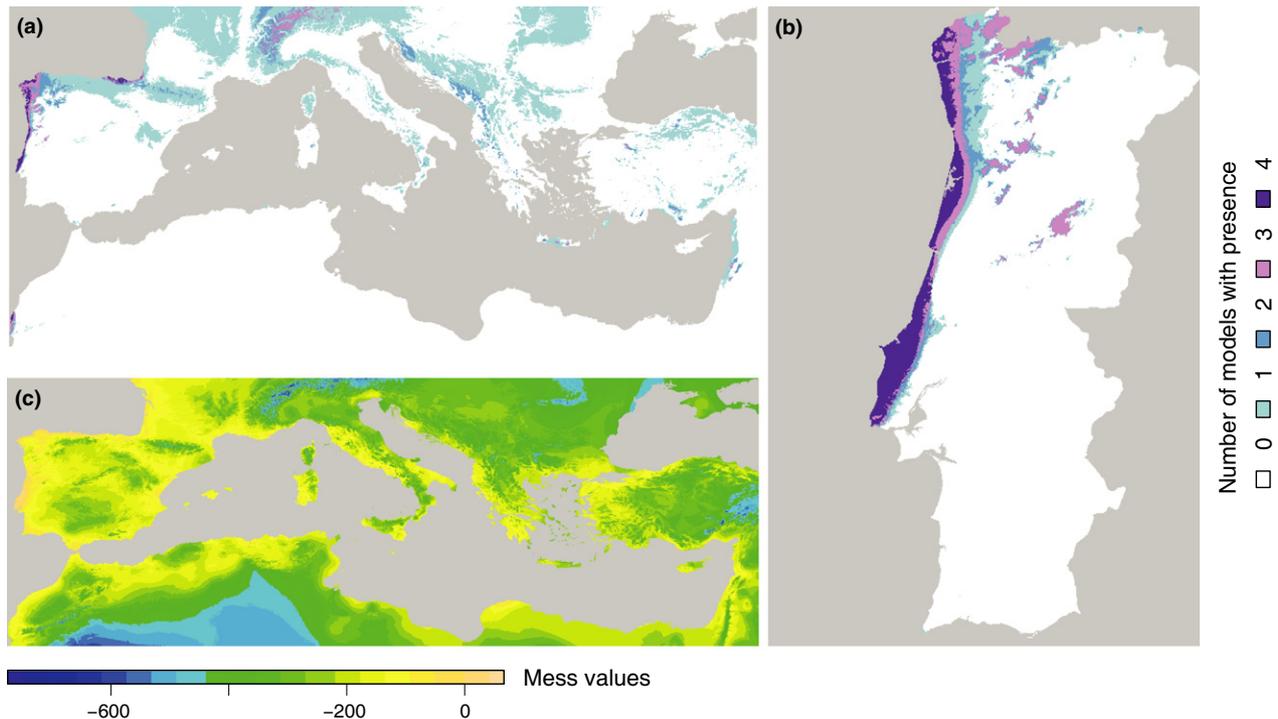


Figure 3 Potential distribution of the summer population (SP) of *Thaumetopoea pityocampa* in (a) the Mediterranean basin and in (b) Portugal under current climate predicted by four bioclimatic models (boosted regression trees, generalized linear model, classification and regression trees, MAXENT) calibrated with variables extracted from WORLDCLIM (Hijmans *et al.*, 2005). We mapped the number of models predicting a presence in these regions when implementing the lowest presence threshold (Pearson *et al.*, 2007). (c) Multivariate environmental similarity surfaces (MESS maps). Colour figure can be viewed at wileyonlinelibrary.com

(Figs 4 & S3 in Appendix S3). The Mediterranean basin, except for the extreme north-east of Spain and some mountainous regions, was predicted to globally remain climatically unsuitable by 2050 and 2070 (Figs S5 & S6 in Appendix S3).

Modelling the spread of SP

The measured distances between the area where SP was firstly discovered in 1997, and both the southern and northern limits of its distribution in 2014, were, respectively, 42.69 and 28.25 km. Consequently, the estimates of southward and northward spread rates, respectively, yielded values of 2.51 and 1.66 km year⁻¹ over the period 1997–2014. The estimates of the distances covered by SP southwards and northwards, during the period 1997–2002, yielded values of 16.90 and 12.25 km, respectively. The estimates of the northward rates of spread of SP in the periods of 1997–2002 and 2003–2014 yielded values of 2.5 and 1.36 km year⁻¹, respectively. The estimates of the southward rates of spread of SP in the periods 1997–2002 and 2003–2014 yielded values of 3.38 and 2.48 km year⁻¹, respectively.

The parameters of the MigClim models best explaining the distribution of SP in 2014 are summarized in Table S1 (Appendix S4). The future range expansion of SP was predicted to remain confined to a narrow strip, along the Atlantic coast of Portugal (Fig. 5). Without considering future

climatic changes, the SP was predicted to reach the district of Lisbon and the district of Aveiro in the centre region around 2050 (Fig. 5). Some regions in north Portugal were predicted as climatically suitable by 2050 or 2070 (Fig. 4) but out of reach of the SP with respect to landscape heterogeneity and dispersal constraints (Fig. 5).

DISCUSSION

A climatic niche shift induced by allochronic speciation

Allochronic speciation may induce geographic range shifts or adaptations (through phenotypic plasticity or evolutionary changes) in the populations that abruptly face new environmental conditions. Both phenomena have been observed in PPM. Thus, laboratory experiments have shown the presence of adaptations to high temperatures in SP larvae in comparison with classical WPs (Santos *et al.*, 2011a). Yet, our study clearly demonstrates that the distribution of SP is strongly constrained by environmental parameters and only a subset of the geographic range of the classical WP (i.e. the Mediterranean basin) is currently climatically suitable for the long-term establishment of the SP.

Considering that our models were calibrated with a majority of true absences that enhance the predictive power of

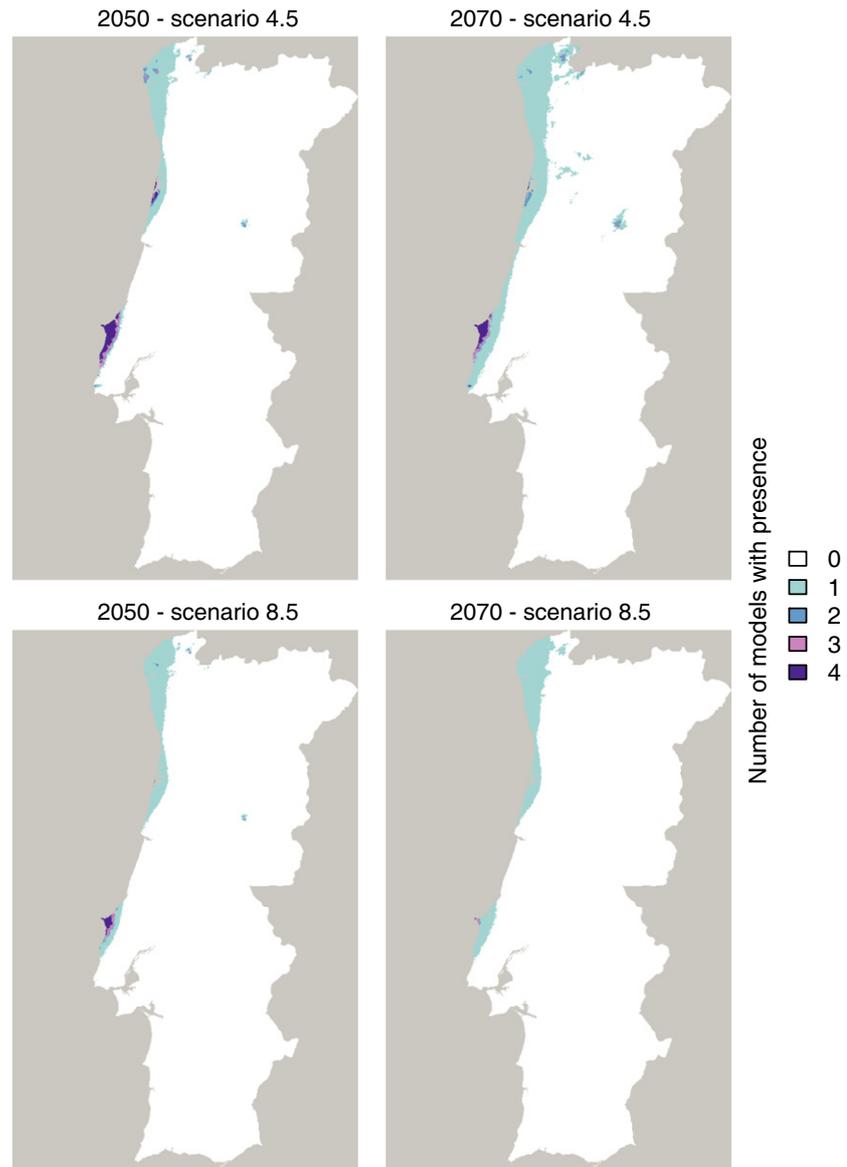


Figure 4 Potential distribution of the summer population (SP) of *Thaumetopoea pityocampa* in Portugal in 2050 and 2070 predicted by four bioclimatic models (boosted regression trees, generalized linear model, classification and regression trees, MAXENT) calibrated with variables extracted from WORLDCLIM (Hijmans *et al.*, 2005). Future climate data were obtained from the Hadley Centre Global Environmental Model version 2 HadGEM2-ES (Collins *et al.*, 2011). We predicted the future distribution of SP with two hypothetical scenarios of future greenhouse gas emissions (4.5 and 8.5). We mapped the number of models predicting a presence in these regions when implementing the lowest presence threshold (Pearson *et al.*, 2007). Colour figure can be viewed at wileyonlinelibrary.com

bioclimatic models (Elith *et al.*, 2010), the present study may be expected to accurately depict the niche of SP and provide reliable predictions. Despite intensive searching between 1997 and 2014, nests of SP have only been detected within a narrow strip along the Atlantic coast of the country, but never across inland regions.

The observed maximal distance of spread by SP during the period 1997–2014 (*ca.* 40 km) largely exceeds the distances separating some of the absence records situated in inland regions and the area where SP was first discovered (Fig. 1). Some absences were indeed recorded in locations where *P. pinaster* stands are distributed over large areas (Fig. 1), up to 10 km from the area where the SP was first discovered in MNL. Such observations strongly suggest that SP dispersal ability and host-related constraints alone cannot explain that expansion into inland regions did not take place. Therefore, climate can probably be identified as the most

relevant factor explaining why the geographic range of SP has remained confined to part of the coastal regions of Portugal. In addition, density of SP nests (i.e. number of nests m^{-2}) gradually decreases between the coast and the inland regions of Leiria province (Godefroid, personal observation), which is consistent with the most parsimonious hypothesis that coastal regions are climatically more suitable for SP long-term establishment. With regard to reliability of our absences data, this study clearly demonstrates that a niche shift occurred during allochronic speciation in PPM and proves the crucial importance of accounting for intraspecific diversity when calibrating SDMs for conservation, invasion and pest control purposes.

All models captured the average maximal summer temperature as the climatic variable presenting the highest contribution to discriminate our presence and absence data, confirming that tolerance of larvae to heat probably

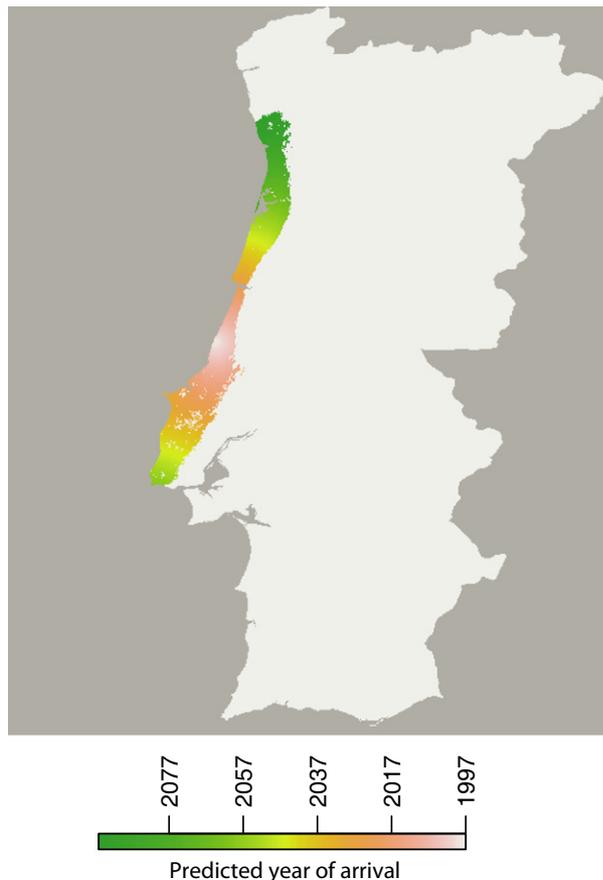


Figure 5 Potential spread of the summer population (SP) of *Thaumetopoea pityocampa* in Portugal predicted by MigClim model. This projection was constructed by merging the outputs of two MigClim models that were calibrated independently to model the past spread SP northward and southward, respectively. Colour figure can be viewed at wileyonlinelibrary.com

constitutes the main constraint relative to a shift in the phenology of PPM. Adaptations of SP to high temperatures (Santos *et al.*, 2011a) are probably neither sufficient to allow for the expansion of SP into the inlands of Portugal nor into most regions of the Mediterranean basin. The extreme temperatures observed in the summer in most areas of the Mediterranean basin are indeed lethal for SP larvae (Santos *et al.*, 2011a) and impede SP long-term establishment in these regions. Beyond summer heat, other climate characteristics such as winter and spring temperatures act as serious constraints upon the phenological shift of SP. The relative contributions of these climatic descriptors were, however, globally small in our correlative SDMs. It is generally expectable that relatively high spring temperatures should be required for SP reproduction, as mating takes place at night in May and cold weather may prevent adult activity. Regarding WPs, a threshold of 14 °C below which WP females have low flight activity was identified by Battisti *et al.* (2006). However, Zhang & Paiva (1998) showed that temperatures above 22 °C can hinder reproductive activity and that

females first started calling when air temperatures dropped below that threshold. Low winter temperatures and high soil moisture are thought to cause high mortality to overwintering pupae of PPM in the soil (Markalas, 1989). However, in some cases, diapausing pupae of WP were observed to remain in the soil for over 8 years before emergence, suggesting that they are prone to resist cold winter temperatures (Aimi *et al.*, 2006; Salman *et al.*, 2016). Preliminary experiments showed that soil temperatures (at 10 and 20 cm depth) measured during the winter of 2008 in localities where SP is present, ranged from 5 to 14 °C. In this context, outputs of some correlative SDMs might seem surprising as they predict high climatic suitability in mountainous areas, where very cold winter temperatures and fresh spring temperatures are common (Fig. 3). As these areas show a climate very different from the climatic space of the calibration dataset (see MESS maps in Fig. 3), our predictions for these areas have a low reliability and should be interpreted with caution (Elith *et al.*, 2010). In this context, the question of how spring and winter temperatures interact to shape the geographic distribution of SP should be explored in depth to improve the reliability of the model predictions.

Special features on Portuguese coast could explain the successful establishment of the allochronic SP. Indeed, the climatic conditions encountered in this area are particular for Portugal and for Europe (i.e. oceanic climate with mild winters and moderately hot summers; Fig. 2) and have probably been little constraining with respect to the shift of the larval development period from winter to summer. Moreover, this region is characterized by elevated relative air humidity that perhaps may alter the tolerance of insects to extreme temperatures (Fields, 1992). The moderate temperatures and the high levels of relative humidity encountered in the summer across these coastal regions may interact to shape the current geographic distribution of the SP. Several phenology changes occurred during the evolutionary history of the *Thaumetopoea* genus (Santos *et al.*, 2007; Simonato *et al.*, 2013). One plausible hypothesis is that phenology is labile in *Thaumetopoea* species and that, consequently, other allochronically reproducing populations have diverged from the classical PPM in separate geographic regions but failed to get established over long term, presumably due to strong environmental constraints associated with phenological shift. For instance, in Greece, some adults of PPM were trapped in the spring by Athanassiou *et al.* (2007) but no other population of PPM with such abruptly shifted life cycle has ever been observed in the country. Still, further survey is needed to search for allochronic individuals that could recurrently occur in separate geographic regions and therefore confirm this hypothesis.

The geographic distribution of SP: the role of spread

The estimated rates of spread of SP over the period 1997–2014, ranging from 1.66 to 2.51 km year⁻¹, were globally similar to those reported for WP by Démolin (1969) and

Battisti *et al.* (2005). However, they were largely inferior to the rate of spread of PPM recorded in northern France, over the period 2000–2009 (*ca.* 5.6 km year⁻¹; Battisti *et al.*, 2005) and laboratory-estimated dispersal capacity by Robinet *et al.* (2012). Our moderate estimates of SP spread rate suggest that human-mediated long dispersal events have probably not occurred during SP range expansion as reported in WP (Robinet *et al.*, 2012).

The spread rate of SP has probably not been uniform across space and time since 1997. It appears that the SP spread faster over the period 1997–2002. This may be explained by the outbreak phase experienced by the SP in 1997, which has abruptly increased the population density and consequently raised the spread towards adjacent areas. The subsequent diminution of the SP spread rate might be explained by the decrease in population densities typical of post-outbreak phases. We observed that SP spread was slightly faster southward (2.51 km year⁻¹) than northward (1.66 km year⁻¹). Two hypotheses may explain this trend. On the one hand, wind regimes might play a main role in driving dispersal of SP across Portugal. It has already been mentioned by Pimentel *et al.* (2006) that the direction of dominant winds in Leiria province during the period of adult flight of SP (*i.e.* mainly south-eastward) might explain the faster southward range expansion of SP. It must be noted the PPM females has poor flight capacities and as such their dispersal may be markedly affected by dominant winds. On the other hand, it is likely that landscape fragmentation influences SP dispersal as reported for other forest insects (Morin *et al.*, 2009). In northern France, the PPM was shown to spread across large agricultural areas through the ecological continuities created by trees outside forests (mostly ornamental trees scattered across fields and towns; Rossi *et al.*, 2016). Although we did not directly sample the distribution of trees outside forests in Leiria province, it is likely that the large number of pines planted in open areas have facilitated the spread of SP southward (see ‘open lands’ in Fig. 1). However, field data are currently lacking, preventing a formal integration of these elements in our models.

What future for the SP?

Effects of global change are predicted to be particularly harmful for small-range organisms such as SP (Ohlemüller *et al.*, 2008). The present survey corroborates this trend as most of the SDMs predicted SP to be endangered following ongoing environmental changes. Within the current SP range, the average summer temperatures are expected to increase from 1.4 to 3 °C by 2050, depending on the scenario considered and become similar to those recorded in areas where SP is currently absent (Fig. S2 in Appendix S3). Moreover, the limited dispersal abilities of SP will probably enhance the detrimental effect of global change on this population. Some areas of northern Portugal are predicted to be climatically suitable for SP by 2050 but out of reach by natural dispersal (Figs 4 & 5). These trends

highlight the importance of coupling SDM with dispersal and demographic models when assessing the future distribution of species (Engler & Guisan, 2009). We cannot exclude the possibility that SP might be introduced and become established in other regions of Portugal or of the Mediterranean basin through human-mediated long dispersal events, as it has been the case for the WP (Robinet *et al.*, 2012). However, this hypothesis is unlikely for two main reasons: (1) importations of pines from Leiria province are currently prohibited by authorities of many countries because of the recent detection of the pine wood nematode *Bursaphelenchus xylophilus* (Steiner & Buhner) in forests of Portugal (Branco *et al.*, 2014); (2) the climate of most areas of the Mediterranean basin is predicted as unsuitable for long-term establishment of the SP (Fig. 3; Figs S5 & S6 in Appendix S3).

The reliability of SDM predictions must be considered with caution as these correlative tools mainly depict the *realized niche* of a species (*i.e.* inferred from its geographic distribution) rather than its *fundamental niche* (*i.e.* reflecting its physiological tolerances; Soberón & Peterson, 2005). Moreover, SDMs usually do not anticipate adaptations of species to environmental changes and implicitly assume niche conservatism across space and time. However, niche shifts are not uncommon and examples of adaptation to new environmental conditions by phenology shifts (Parmesan & Yohe, 2003) or increased thermal tolerances (Hill *et al.*, 2013) have been reported. There is thus an urgent need to model the adaptive potential of SP to new environmental conditions to allow proper assessment of its future distribution. Although uncertainty is inherent to SDM predictions, the trends presented in this study are clear and suggest that SP should be added to the long list of threatened organisms from ongoing global changes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Distribution of SP assessed with a field survey performed at the end of the summer 2014.

Appendix S2 Comparison of bioclimatic variables extracted from WORLDCLIM (period 1950–2000) with newly constructed climatic variables (NR rasters) in Portugal.

Appendix S3. Prediction of the potential distribution of SP in Portugal and in the Mediterranean basin under current and future climatic conditions.

Appendix S4. Parameters of the MigClim models best explaining the southward and northward spread of SP between 1997 and 2014.

BIOSKETCH

Research of **Martin Godefroid** (MG) focuses on evolutionary and ecological factors that shape the spatial structures of genetic diversity. MG is also interested in uncovering relationships between genetics and geographic ranges of species to improve modelling tools used in invasion risk assessment and conservation planning.

Author contributions: All authors conceived the ideas and contributed to data collection and writing. MG and JPR analysed the data.

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