

# Predicting the distribution of the two bark beetles *Tomicus destruens* and *Tomicus piniperda* in Europe and the Mediterranean region

Agnès Horn\*, Carole Kerdelhué†, François Lieutier\*<sup>1</sup> and Jean-Pierre Rossi†<sup>1</sup>

\*Laboratoire de Biologie des Ligneux et des Grandes Cultures UPRES EA 1207, Université d'Orléans, Rue de Chartres, BP 6759, F-45067 Orléans Cedex 2, France, and †INRA, UMR CBGP (INRA/IRD/Cirad/Montpellier SupAgro), Campus International de Baillarguet, CS 30016, F-34988 Montpellier-sur-Lez Cedex, France

- Abstract**
- 1 Various factors such as climate and resource availability influence the geographical distributions of organisms. Species sensitive to small temperature variations are known to experience rapid distribution shifts as a result of current global warming, sometimes leading to new threats to agriculture and forests. *Tomicus piniperda* and *Tomicus destruens* (Coleoptera, Curculionidae, Scolytinae) cause economic damage to pines in Europe and around the Mediterranean Basin. However, their respective potential distributions have not yet been studied at a large scale. The present study aimed to investigate the influence of climatic and host factors on the geographical distributions of both *Tomicus* species in Europe and around the Mediterranean Sea, and to establish maps of suitable areas.
  - 2 Using 114 published localities where the presence or absence of both species was unambiguously recorded, we gathered WorldClim meteorological records to correlate the occurrence of insects with bioclimatic variables and to build potential distribution maps.
  - 3 The two studied *Tomicus* species presented parapatric distributions and opposite climate demands, with *T. destruens* occurring in locations with warmer temperatures, whereas *T. piniperda* occurs under a colder climate. Amongst the investigated climate variables, temperature appeared to be most correlated with both species distributions.
  - 4 The potential ranges of both species were further restricted by the availability of pine hosts. It appeared that setting new pine plantations in regions where *T. destruens* or *T. piniperda* are still absent could favour a rapid expansion of their distributions. Our data will be useful when aiming to apply management strategies adapted to each species, and to forecast their potential range expansions/contractions as a result of climate warming.

**Keywords** Bark beetles, climate, geographical distribution, *Pinus*, species distribution modelling, *Tomicus*.

## Introduction

Geographical distributions can be subjected to various modifications depending on the intrinsic and ecological requirements of the considered species (Gaston, 2003). Climate is probably the most well-known factor influencing species repartitions.

Correspondence: Agnès Horn; Tel.: + 41 21692 4218; fax: + 41 21692 4165; e-mail: agneshorn@gmail.com

<sup>1</sup>These authors contributed equally to this study.

Current global warming has caused the occurrence of rapid shifts in the distributions of some species that are sensitive to small temperature variations (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Battisti *et al.*, 2005; Parmesan, 2006; Thomas *et al.*, 2006; Thomas, 2010). In particular, climate has a major impact on survival, development and growth rates among insects (Bale *et al.*, 2002), although other factors such as trophic resource availability can also affect species distribution.

Bark beetles are coleopterans of the family Curculionidae, subfamily Scolytinae. They necessarily develop on a species

(or a group of species) of host plant(s), where the larvae develop by feeding in the inner bark (Sauvard, 2004). Climate and host accessibility (i.e. the presence of susceptible trees) are generally considered as the two main variables that affect geographical distributions of bark beetles (Coulson, 1979). In Europe, the pine shoot beetle *Tomicus piniperda* (L.) is well known as a result of the economic damage that it causes in European pine forests (Långström, 1983; Sauvard *et al.*, 1988; Långström & Hellqvist, 1990, 1991). Its life cycle consists of a phase of adult dispersion and sexual reproduction in the inner bark of the trunks at the end of winter followed by oviposition and *in situ* larval development and nymphosis. The callow adults then emerge and disperse to infest shoots for an obligate maturation period during the warm season. A high proportion of attacked shoots may weaken the trees and therefore induce overall growth losses. Mature adults then overwinter either in the shoots or in the outer bark and disperse again before reproduction at the end of the next winter (Chararas, 1962). Another species of the same genus, named *Tomicus destruens* (Woll.), has long been mistaken for *T. piniperda* as a result of their morphological similarity. Because its life cycle differs only by an earlier reproduction period (i.e. in autumn) and the apparent absence of overwintering, *T. destruens* has long been considered as a Mediterranean eco-type of *T. piniperda* occurring in the southern edge of its distribution (Carle, 1973). However, the taxonomic status of *T. destruens* has long been debated (Pfeffer, 1994). Recent molecular studies using mitochondrial as well as nuclear markers have confirmed that they are two separate species (Gallego & Galian, 2001; Kerdelhué *et al.*, 2002; Kohlmayr *et al.*, 2002; Duan *et al.*, 2004). A morphological analysis was then conducted to provide diagnostic morphological characters (Faccoli, 2006; Kirkendall *et al.*, 2008).

The definitive recognition of these two different species raised doubts about their respective distributions in Europe and the Mediterranean region, as well as about the damage for which they are responsible. Indeed, *T. piniperda* has long been assumed to be present in North Africa and along the northern coast of the Mediterranean Sea, although molecular studies have so far shown that *T. piniperda* only rarely occurs in these regions (Horn *et al.*, 2006, 2009). This is particularly striking because *T. piniperda* was considered to cause heavy damage in those regions, which likely should now be attributed to *T. destruens* (Masutti, 1969; Triggiani, 1983; Lieutier, 1984).

During the last decade, several studies have provided reliable data concerning the respective distribution ranges of both *Tomicus* species in Europe and the Mediterranean region. These data are so far discrete presence/absence data obtained in a number of localities. Overall, *T. destruens* was found all around the Mediterranean Basin up to the Atlantic regions of France and develops on several Mediterranean *Pinus* species (Kerdelhué *et al.*, 2002; Gallego *et al.*, 2004; Horn *et al.*, 2006; Vasconcelos *et al.*, 2006; Faccoli, 2007, 2009). Conversely, the distribution of *T. piniperda* was confirmed over a large part of Europe from Scandinavia to France, Italy and the northern half of the Iberian Peninsula (Gallego *et al.*, 2004; Ritzerow *et al.*, 2004; Vasconcelos *et al.*, 2006; Horn *et al.*, 2009). This polyphagous species was observed on several *Pinus* species but

its main host in Europe appears to be *Pinus sylvestris* (Gallego *et al.*, 2004; Horn *et al.*, 2009). These recent studies have also allowed a better description of the phenology of both species. Adult flight activity and reproduction of *T. destruens* was observed in both autumn and spring in North Africa and Italy (Nanni & Tiberi, 1997; Horn *et al.*, 2006), whereas this species reproduces only in autumn in all other regions. Concerning *T. piniperda*, reproduction occurs in late winter or early spring in Europe. Therefore, *T. piniperda* has one generation per year, whereas *T. destruens* could be either uni- or bivoltine depending on local conditions. Both species have sister broods (i.e. the female can oviposit successively in different individual host trees).

Because *T. destruens* and *T. piniperda* have different phenologies and generally do not reproduce during the same season, it is critical to acquire knowledge on their potential distributions and their ecological requirements to allow the adaptation of silvicultural practices and to more accurately anticipate the potential consequences of climate warming (Mason *et al.*, 2011). To date, only one study has inferred the influence of climatic factors on both *Tomicus* species and generated maps of potential distribution, although this was restricted to Spain (Gallego *et al.*, 2004). It was shown that the two species had contrasting requirements in terms of climate and pine hosts: *T. destruens* was found in warm and dry parts of Spain, whereas *T. piniperda* preferred more humid and colder areas. Gallego *et al.* (2004) provided new data that proved useful in managing these damaging insects in Spain (i.e. at the known southern edge of the range of *T. piniperda*). The main conclusions in Gallego *et al.* (2004) may therefore not apply to the rest of the species' ranges in Europe, where environmental conditions are different. An equivalent study over the entire range of both species is now essential for completing the picture in Europe.

In the present study, we investigated, for the first time, the distributions of *T. piniperda* and *T. destruens* based on samples all over Europe and the Mediterranean Basin gathered from published data. The main goals of the present paper are: (i) to use the presence/absence data obtained from published studies with unambiguous molecular identification to build predictive maps of the present geographical distributions for *T. destruens* and *T. piniperda* and (ii) to determine the influence of abiotic (temperature and rainfalls) factors on their respective distributions.

## Materials and methods

### Data source

A total of 114 sites with *T. destruens* or/and *T. piniperda* was gathered (see Supporting information, Doc. S1). Each site was obtained from previously published studies carried out in Europe and around the Mediterranean Basin, and was kept only if *Tomicus* individuals were identified to the species level based on molecular markers. Previous results using mitochondrial and nuclear markers showed that molecular barcoding is an efficient and reliable way of identifying *Tomicus* species (Duan *et al.*, 2004). Hence, the present study is based on data taken from Gallego and Galian (2001), Kerdelhué *et al.* (2002), Kohlmayr

et al. (2002), Ritzerow et al. (2004), Faccoli et al. (2005), Horn et al. (2006), Vasconcelos et al. (2006) and Horn et al. (2009).

Moreover, the statistical analyses conducted in the present study require both presence and unambiguous absence data. Presence data were readily accessible, although interpreting the absence data may be difficult. In some cases, both species were systematically searched in each site (i.e. trap trees set up both in fall and in the end of winter, using all available host species, observations conducted in shoots; information was found either from the literature or directly from the respective authors). In such cases, when one of the species was not found, it was considered as absent. In cases of doubt, we considered the corresponding species as missing data (see Supporting information, Doc. S1) and excluded it from the analysis of the distribution of that species.

#### Environmental data

We used a set of 19 bioclimatic variables available from the WorldClim database, version 1.4 (<http://www.worldclim.org>; Hijmans et al., 2005; Table 1). These data are derived from monthly temperatures and rainfalls and constitute biologically meaningful variables expressing annual trends (e.g. mean annual temperature), seasonality (e.g. annual range in

**Table 1** List of the 19 bioclimatic variables obtained from the WorldClim database over the period 1950–2000 (Hijmans et al., 2005)

Code	Variable name	Formula
BIO1	Annual mean temperature	
BIO2	Mean diurnal range	[Mean of monthly (maximum temperature – minimum temperature)]
BIO3	Isothermality	[(BIO2/BIO7) × 100]
BIO4	Temperature seasonality	(SD × 100)
BIO5	Maximum temperature of warmest month	
BIO6	Minimum temperature of coldest month	
BIO7	Temperature annual range	(BIO5–BIO6)
BIO8	Mean temperature of wettest quarter	
BIO9	Mean temperature of driest quarter	
BIO10	Mean temperature of warmest quarter	
BIO11	Mean temperature of coldest quarter	
BIO12	Annual precipitation	
BIO13	Precipitation of wettest month	
BIO14	Precipitation of driest month	
BIO15	Precipitation seasonality	
BIO16	Precipitation of wettest quarter	
BIO17	Precipitation of driest quarter	
BIO18	Precipitation of warmest quarter	
BIO19	Precipitation of coldest quarter	

Temperatures are given in Celsius; precipitations are given in millimetres.

temperature) and extreme or limiting environmental factors (e.g. temperature of the coldest and warmest months). Monthly temperatures and rainfalls are themselves interpolations of observed data representative of the years 1950–2000 (Hijmans et al., 2005). Based on the published data used to select the presence/absence data (see Supporting information, Doc. S1), the known pine host species of *T. piniperda* in Europe are *Pinus halepensis*, *Pinus nigra*, *Pinus pinaster*, *Pinus sylvestris*, *Pinus uncinata* and *Pinus radiata*, whereas those of *T. destruens* are *P. halepensis*, *Pinus pinea*, *P. pinaster*, *Pinus brutia*, *P. nigra* and *P. radiata*. European distributions of most of these species are available from the European Forest Genetic Resources Program (Euforgen) (<http://www.euforgen.org/>), except for the introduced species *P. radiata* and for *P. uncinata*. However, it must be noted that some planted areas and fragmented stands do not appear in the Euforgen database. Accordingly, we did not use these host data to model *Tomicus* species distribution but rather to refine the potential distributions of *Tomicus* species to places where at least one host species occurs. It should be noted that the pine distribution maps used in the present study are more restricted than the actual host occurrence. Data were in the form of rasters and were managed using the geographical information system software GRASS (GRASS Development Team, 2010), which was interfaced with R statistical software (R Development Core Team, 2010) by means of the R packages SPGRASS6 (Bivand, 2007) and RASTER (Hijmans & van Etten, 2010).

#### Generalized linear model (GLM) fitting, evaluation and prediction

A GLM was used to model the occurrence data (both presence and absence) of both *Tomicus* species using environmental predictors (here, the bioclimatic variables). Each species was analyzed separately. A GLM is a generalization of ordinary least squares regression (Faraway, 2006). GLMs are robust tools and are commonly used in species distribution modelling (Guisan et al., 2002; Franklin, 2009). We used basic GLMs relating species occurrence and all predictors without interaction. Each insect species was individually analyzed using the R package MASS (Venables & Ripley, 2002). We performed a stepwise model selection by Akaike information criterion (AIC). The performance of the resulting models were assessed by cross-validation for a set of confusion matrices and threshold values (Fielding & Bell, 1997) using the R package DISMO (Hijmans et al., 2010). For each species, we used the threshold corresponding to the maximum of the sum of the sensitivity (true positive rate) and specificity (true negative rate) to set the areas where species were considered as present (raw model prediction above threshold) or absent (raw model prediction below threshold).

We additionally evaluated each model using the area under the receiver operator curve (AUC) that is a measure of rank-correlation. High values indicate that high (low) predicted values tend to be areas of known presence (absence) of the species under study. Model evaluation was performed using the R package DISMO. We modelled the distributions of both *Tomicus* species across a large area comprised between 10°W, 40°E, 30°S and 70°N.

**Table 2** Summary statistics for generalized linear models linking the presence and absence of *Tomicus destruens* and *Tomicus piniperda* and a set of bioclimatic variables

Species	Code	Variable name	Coefficients	Std. error	z value	P
<i>Tomicus destruens</i>	BIO6	Minimum temperature of coldest month	-0.11041	0.07983	-1.383	0.1666
	BIO10	Mean temperature of warmest quarter	0.08099	0.03796	2.133	0.0329
	BIO11	Mean temperature of coldest quarter	0.19789	0.10069	1.965	0.0494
<i>Tomicus piniperda</i>	BIO1	Annual mean temperature	1.46464	0.65345	2.241	0.02500
	BIO3	Isothermality	-0.79970	0.56922	-1.405	0.16005
	BIO5	Maximum temperature of warmest month	0.33861	0.17052	1.986	0.04706
	BIO6	Minimum temperature of coldest month	0.30129	0.14367	2.097	0.03599
	BIO8	Mean temperature of wettest quarter	-0.08786	0.04347	-2.021	0.04324
	BIO9	Mean temperature of driest quarter	-0.04342	0.02308	-1.881	0.05997
	BIO10	Mean temperature of warmest quarter	-1.34178	0.58422	-2.297	0.02164
	BIO11	Mean temperature of coldest quarter	-0.89429	0.34606	-2.584	0.00976
	BIO14	Precipitation of driest month	-0.09713	0.06471	-1.501	0.13338
	BIO16	Precipitation of wettest quarter	-0.01660	0.01006	-1.651	0.09873

The resulting presence/absence maps are reported as 'climate-based potential distributions' of both insect species because they are based solely on climatic data. We also report the intersection between these maps and the geographical distribution of host pine species, aiming to obtain a more realistic picture of the occurrence of species.

## Results

### General linear models

In the case of *T. destruens*, the stepwise model selection by AIC resulted in the selection of three bioclimatic variables (AIC = 37.16) among which two significantly contributed to the model (Table 2). These variables were mean temperature of warmest quarter and mean temperature of coldest quarter (Table 2). The AUC was 0.97, which indicated good model performances [i.e. that sites with high (low) predicted suitability values tended to be areas of known presence (absence)]. Overall, the presence of *T. destruens* was associated with the highest temperatures (Fig. 1).

The stepwise model selection by AIC yielded a 10 bioclimatic variables model in the case of *T. piniperda* (AIC = 50.5; Table 2). Among these, six significantly contributed to the final model: annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, mean temperature of wettest quarter, mean temperature of warmest quarter and mean temperature of coldest quarter (Table 2). Again, the AUC value was high (0.99), indicating a good performance of the model.

Two of the significant variables (mean temperature of warmest quarter and mean temperature of coldest quarter) were linked to the distribution of both species but the sign of the relationship was opposite (Fig. 1). These results illustrated that the species had opposite preferences.

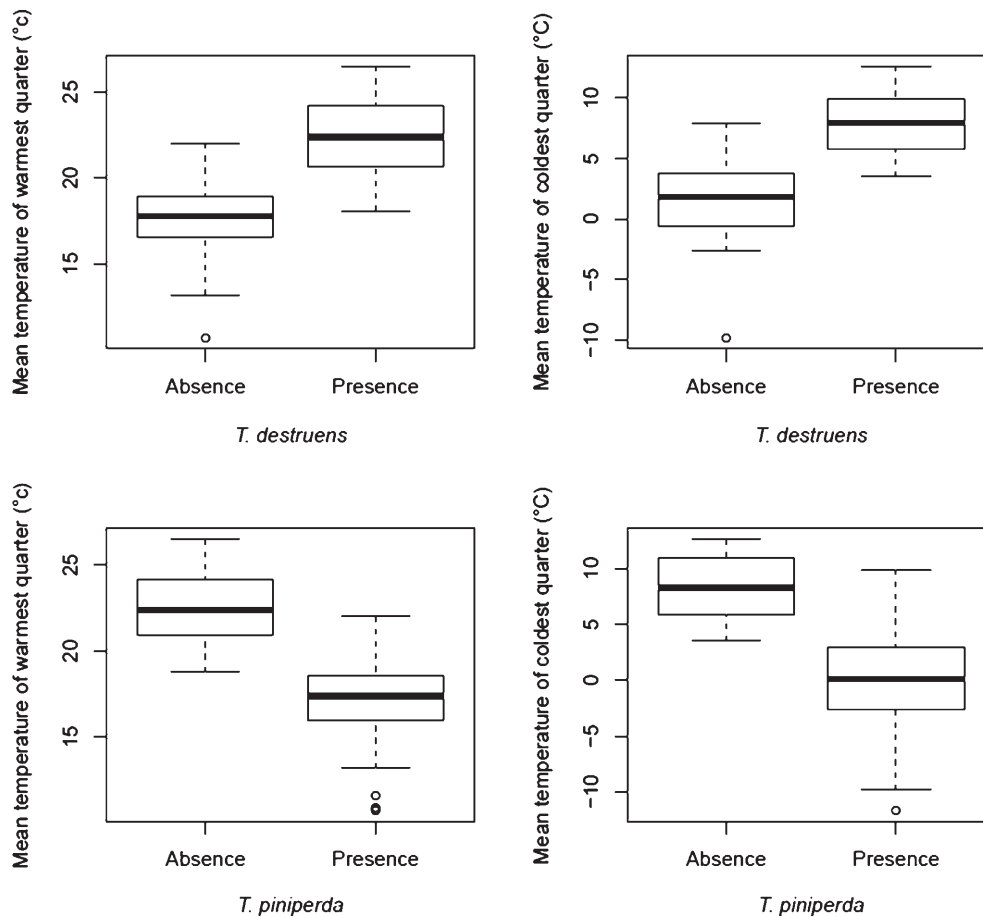
### Maps of geographical distributions

GLMs were used to predict the geographical distributions of *T. destruens* and *T. piniperda* using the bioclimatic data.

The threshold values corresponding to the maximum of the sum of the sensitivity and specificity were 0.038 and 0.475 for *T. destruens* and *T. piniperda*, respectively. The resulting species distribution maps are shown in Figs 2 and 3. Figure 2 shows the estimate of the potential distributions of both species on the basis of the GLMs alone. Figure 3 is derived from the former estimations but the range of each species was restricted to the areas where at least one of its known hosts is naturally present (in accordance with information from the Euforgen database). Based on these results, *T. destruens* was expected to be present continuously around the Mediterranean Basin, except at high altitude in mountainous regions (Figs 2 and 3). Moreover, its presence was also predicted along the Atlantic Ocean up to Oléron Island (France), as well as around the Black Sea in the Middle East. The model fitted to *T. piniperda* known occurrences yielded an almost opposite pattern because the species was expected in most of Europe, at latitudes higher than 45°N or below this latitude in mountainous areas. It was also expected to occur at lower latitudes outside of Europe, such as in Morocco, Algeria, Tunisia and Turkey, although it was restricted to regions of high altitude (Figs 2 and 3). For both species, the predicted distribution ranges included regions where they have not yet been studied (i.e. where no sampling point is currently available). The regions of sympatry were mainly located in the northern part of the Mediterranean Basin where both species are known to occur, although data are still scarce. The countries with the largest predicted areas of sympatry were Portugal, Spain, France and Italy, as well as Morocco, Algeria, Tunisia, Bulgaria, Turkey and Syria (Fig. 2). It is worth noting that no confirmed occurrence of any of the two species is available in some of these latter countries. When restricted to areas where at least one pine host species is present, potential areas of sympatry were mostly estimated in the Iberian Peninsula and France (Fig. 3).

## Discussion

By using the available molecular data on the presence/absence of *T. piniperda* and *T. destruens* in Europe and around the Mediterranean Basin, we were able to draw maps of suitable geographical ranges for both species as a function of bioclimatic



**Figure 1** Box plots of two bioclimatic variables that significantly contributed to the generalized linear model linking climate descriptors to *Tomicus destruens* and *T. piniperda*. Each bioclimatic variable is expressed in Celsius (°C). Absence and Presence represent the observed occurrence of each species.

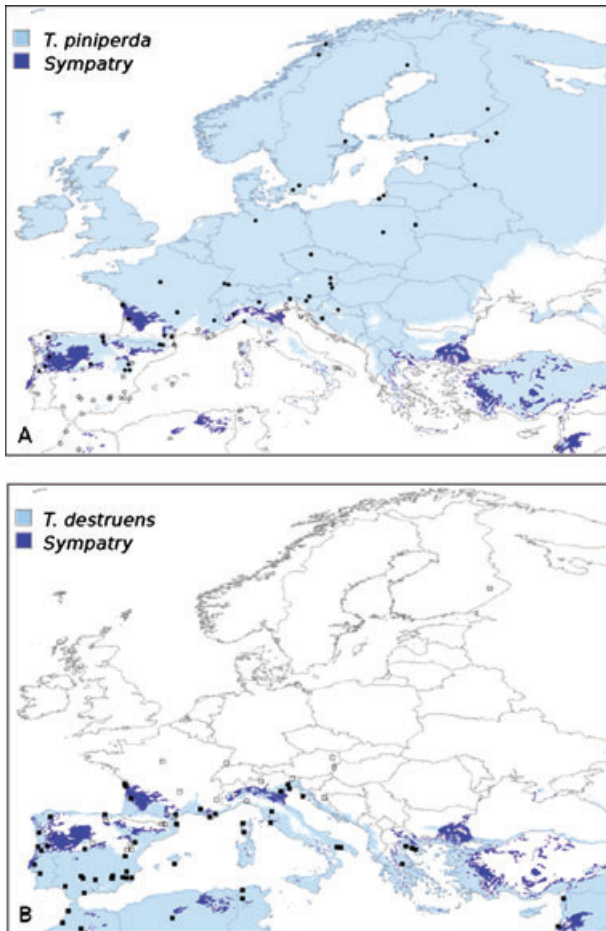
variables. All recent existing data suggested that the two species have parapatric distributions with few contact zones where they occur in sympatry (Kerdelhué *et al.*, 2002; Gallego *et al.*, 2004; Horn *et al.*, 2006, 2009; Vasconcelos *et al.*, 2006). The results obtained in the present work confirmed that *T. piniperda* and *T. destruens* broadly displayed parapatric distributions (Fig. 2). They shared limited regions of sympatry in the Iberian Peninsula, southern France and Italy, and also in rare places in the rest of the southern and northern limits of their respective ranges (Fig. 2). The present study offered a large-scale picture of the ecological requirements and plausible distribution ranges of the two species, which will help in pest diagnostics and adaptation of management strategies.

#### *The two Tomicus species have contrasted ecological requirements*

Occurrences of both *Tomicus* species were shown to be strongly correlated with bioclimatic variables, although with opposite patterns in terms of climatic requirements (Fig. 1). For example, the distributions of both species were significantly related to the same extreme environmental factors (mean

temperature of warmest quarter and mean temperature of coldest quarter) but the presence of *T. destruens* was associated with warm temperatures, whereas *T. piniperda* was associated with low values (Fig. 1). The present result is consistent with the trend shown by Gallego *et al.* (2004) at a regional spatial scale (i.e. Spain). The absence of *T. destruens* in localities with the coldest temperatures is in accordance with the ecology and life-history traits of this species, in which reproduction and larval development occur in autumn and winter (Sabbatini Peverieri *et al.*, 2008). Larval development is known to be a critical period when individuals may experience high mortality rates, especially as a result of extreme temperatures (Howe, 1967). No information is available about the lethal temperature for *T. destruens*, although preliminary results suggested that low temperatures probably limit larval development and increase mortality (Horn, 2006), which could explain the absence of *T. destruens* in the coldest regions.

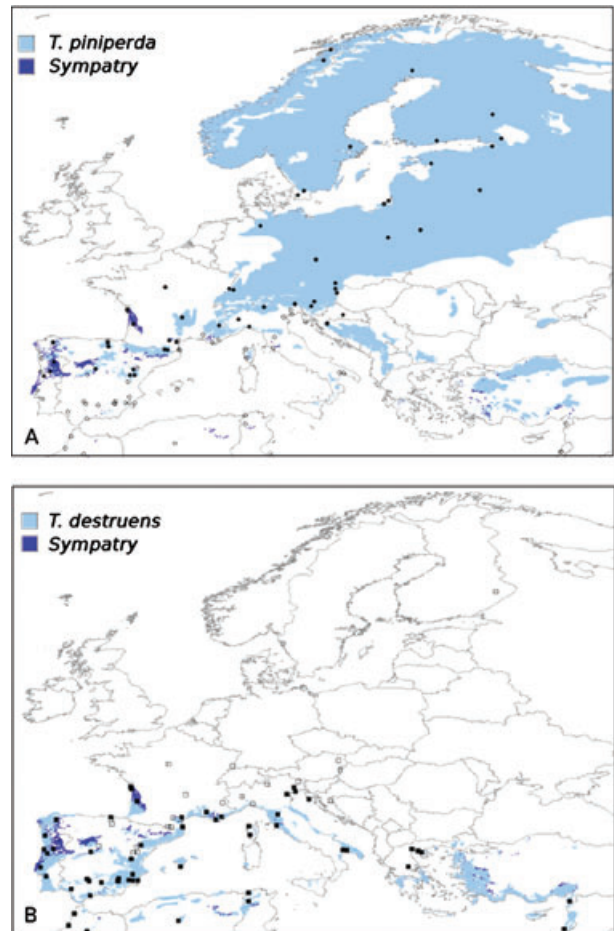
Similarly, the presence of *T. piniperda* appeared to be related to low values of variables such as mean temperature of warmest quarter or mean temperature of coldest quarter, which is in agreement with the species' biological traits (Fig. 1). *Tomicus piniperda* is known to be tolerant to cold temperatures (Bakke, 1968; Långström, 1983; Saarenmaa, 1985) because its ability



**Figure 2** Estimates of potential geographical distributions of *Tomicus piniperda* and *Tomicus destruens* in Europe and around the Mediterranean Basin based on the generalized linear models alone. (A) Potential distribution for *T. piniperda*. Black and empty dots indicate locations where the species has been found present and absent, respectively. (B) Potential distribution for *T. destruens*. Black and empty squares indicate locations where the species has been found present and absent, respectively. In both maps, dark areas correspond to regions where the presence of both species was predicted by models (sympatry).

to overwinter under the bark at the base of the trees during the cold season protects it from the most extreme temperatures. Its geographical distribution thus covers a large part of northern Europe (Fig. 2). On the other hand, the absence of the species in southern localities could reflect a susceptibility to high summer temperature, and it may also be a result of the lack of cold temperatures during the cold season, which are a prerequisite to trigger the obligate overwintering period of mature individuals of *T. piniperda*. The species may require marked differences between the cold and the warm seasons to complete its cycle, and could thus not perform well in regions with mild winters.

By contrast to the conclusions noted by Gallego *et al.* (2004), who predicted the presence of *T. piniperda* in humid regions of Spain, we found no significant correlation between the occurrence of the two species and precipitations when studying the whole distribution range. Humidity could be a limiting



**Figure 3** Estimates of potential geographical distribution of *Tomicus piniperda* and *Tomicus destruens* in Europe and around the Mediterranean Basin derived from the generalized linear models and restricted to areas where at least one pine host species is naturally present. (A) Potential distribution for *T. piniperda*. Black and empty dots indicate locations where the species has been found present and absent, respectively. (B) Potential distribution for *T. destruens*. Black and empty squares indicate locations where the species has been found present and absent, respectively. In both maps, dark areas correspond to regions where the presence of both species was predicted by models (sympatry).

factor for *T. piniperda* at the southern edge of its distribution (i.e. only in the southern and driest part of its range), which could explain why precipitation and humidity do not appear as important variables on a global spatial scale. Additional data documenting the fine-scale distribution of this species at other southern margins of its range, such as in southern France or Italy, are necessary to further test this hypothesis.

*How to further improve the maps of suitable environmental conditions?*

The predicted distribution maps obtained in this study gave useful information about suitable areas for *T. destruens* and *T. piniperda*, although they should be used with care. In

particular, it is important to keep in mind that these maps cannot be directly interpreted as plausible distributions for each species but rather as maps of suitable environmental conditions. The results obtained in the present study should now be used to build precise sampling designs aiming to specifically explore the regions where one species could occur but has not yet been observed. For example, mountainous regions of North Africa could be suitable for *T. piniperda* (Figs 2 and 3), although whether this species is actually present in the southern rim of the Mediterranean remains an open question. Sampling along altitudinal gradients coupled with molecular barcoding could provide some answers.

Moreover, as a first approach, our analysis focused on Europe and the Mediterranean Basin. However, *T. piniperda* has also been reported in Eastern Russia, Asia Minor and East Asia (Murayama, 1963; Pfeffer, 1994; Kulinich & Orlinskii, 1998) based on morphological identification. In the future, it will be important to enlarge the studied scale and draw maps of possible distributions from Europe to East Asia. This may prove difficult because recent studies have pointed out taxonomic ambiguities in these regions; two new species of *Tomicus* were recently described there (Kirkendall *et al.*, 2008; Li *et al.*, 2010), which could have previously been confounded with *T. piniperda*. In addition, the occurrence of *T. piniperda* has been confirmed in at least one province of China (Duan *et al.*, 2004). Consequently, a reliable dataset of presence/absence of the different *Tomicus* species will be a prerequisite before building species distribution models in the rest of Eurasia.

#### Applied implications

The present work provides an important tool for future studies involving *T. destruens* and *T. piniperda* as a first indicator to encourage the use of molecular identifications in doubtful areas, in particular in all regions located near the potential contact zone between both species.

Additionally, our results may be particularly useful for pest management strategies because we give: (i) a broad view of the distributions of both *Tomicus* species; (ii) the main bioclimatic factors influencing their distributions; and (iii) the predicted distributions of both species with climatic and pine host factors. A better knowledge of bark beetles biogeography will be a major tool when developing pest management strategies, in addition to the large amount of information reported so far on *Tomicus* and forest management (Komonen & Kouki, 2008). In the future, we propose that these strategies should be adapted to the plausible presence of each of the two species. For example, in regions where *T. destruens* occurs, preventive measures or monitoring surveys should be conducted earlier than those established for *T. piniperda* because host attacks occur months earlier for *T. destruens*.

Finally, predictive maps of damaging species could also comprise a useful tool for identifying areas where the expansion of pest populations could occur in the context of global warming. The distribution range of *T. destruens* will probably increase in future years because this species is highly tolerant of higher temperatures. Our approaches could help when drawing maps of regions where the risk of expansion (or invasion) is high, and also in the targeting of early monitoring and

management practices. Moreover, our data will be helpful for establishing predicted scenarios in the context of global warming by integrating the different temperature change estimates made by the Intergovernmental Panel on Climate Change (Core Writing Team, 2007), although this is far beyond the goals of the present study.

#### Acknowledgements

We would like to thank G. Roux-Morabito, F. Koutroumpa and C. Bertheau for scientific advice. This manuscript benefited from interesting discussions with D. Piou about forest management practices. We are also especially grateful to Britta Knight for English proofreading and to the five referees for their constructive suggestions that improved the earlier versions of the manuscript.

#### Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference:

10.1111/j.1461-9563.2012.00576.x

**Doc. S1.** List of the *Tomicus* populations gathered in Europe and the Mediterranean Basin and corresponding references. The recording occurrence of each species is also indicated (+, presence; —, absence; NA, not available).

Please note: Neither the Editors nor Wiley-Blackwell are responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

#### References

- Bakke, A. (1968) Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular references to the influence of temperature. *Meddelelser Norske Skogforsoksvesen*, **21**, 443–602.
- Bale, J.S., Masters, G.J., Hodkinson, I.D. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- 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. *Ecological Applications*, **15**, 2084–2096.
- Bivand, R. (2007) Using the R-GRASS interface: current status. *OSGeo Journal*, **1**, 36–38.
- Carle, P. (1973) *Le dépérissement du pin mésogéen en Provence. Rôle des insectes dans les modifications d'équilibre biologique des forêts envahies par Matsucoccus feytaudi Duc. (Coccoidea, Margarodidae)*. Thèse de Doctorat, Université de Bordeaux I.
- Chararas, C. (1962) *Scolytides des conifères*. Paul Lechevalier, Paris, France.
- Core Writing Team (2007) *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Switzerland.
- Coulson, R.N. (1979) Population dynamics of bark beetles. *Annual Review of Entomology*, **24**, 417–447.

- Duan, Y., Kerdelhué, C., Ye, H. & Lieutier, F. (2004) Genetic study of the forest pest *Tomicus piniperda* (Coleoptera, Scolytinae) in Yunnan province (China) compared to Europe: new insights for the systematics and evolution of the genus *Tomicus*. *Heredity*, **93**, 416–422.
- Faccoli, M. (2006) Morphological separation of *Tomicus piniperda* and *T. destruens* (Coleoptera, Curculionidae, Scolytinae): new and old characters. *European Journal of Entomology*, **103**, 433–442.
- Faccoli, M. (2007) Breeding performance and longevity of *Tomicus destruens* on Mediterranean and continental pine species. *Entomologia Experimentalis et Applicata*, **123**, 263–269.
- Faccoli, M. (2009) Breeding performance of *Tomicus destruens* at different densities: the effect of intraspecific competition. *Entomologia Experimentalis et Applicata*, **132**, 191–199.
- Faccoli, M., Piscedda, A., Salvato, P., Simonato, M. & Battisti, A. (2005) Genetic structure and phylogeography of pine shoot beetle populations (*Tomicus destruens* and *T. piniperda*, Coleoptera Scolytidae) in Italy. *Annals of Forest Science*, **62**, 361–368.
- Faraway, J.J. (2006) *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Chapman & Hall, CRC, Boca Raton, Florida.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Franklin, J. (2009) *Mapping Species Distributions. Spatial Inference and Prediction*. Cambridge University Press, U.K.
- Gallego, D. & Galian, J. (2001) The internal transcriber spacers (ITS1 and ITS2) of the rDNA differentiates the bark beetle forest pests *Tomicus destruens* and *T. piniperda*. *Insect Molecular Biology*, **10**, 415–420.
- Gallego, D., Canovas, F., Esteve, M. & Galian, J. (2004) Descriptive biogeography of *Tomicus* (Coleoptera: Scolytidae) species in Spain. *Journal of Biogeography*, **31**, 2011–2024.
- Gaston, K.J. (2003) *The Structure and Dynamics of Geographical Ranges*. Oxford University Press, U.K.
- GRASS Development Team (2010) *Geographic Resources Analysis Support System (GRASS) Software*. Open Source Geospatial Foundation [WWW document]. URL <http://grass.osgeo.org> [accessed on 22 March 2012].
- Guisan, A., Edwards, T.C. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.
- Hijmans, R.J. & van Etten, J. (2010) *Raster: Geographic Analysis and Modeling with Raster Data. R Package*, Version 1.6-22 [WWW document]. URL <http://CRAN.R-project.org/package=raster> [accessed on 22 March 2012].
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2010) *Dismo: Species Distribution Modeling. R Package*, Version 0.5-9 [WWW document]. URL <http://cran.r-project.org/web/packages/dismo/index.html> [accessed on 22 March 2012].
- Horn, A. (2006) *Comparaison des distributions passées et présentes de deux espèces proches de scolytes. Tomicus piniperda et T. destruens* (Coleoptera: Scolytinae). PhD Thesis, Université d'Orléans.
- Horn, A., Roux-Morabito, G., Lieutier, F. & Kerdelhué, C. (2006) Phylogeographic structure and past history of the circum-Mediterranean species *Tomicus destruens* Woll. (Coleoptera: Scolytinae). *Molecular Ecology*, **15**, 1603–1615.
- Horn, A., Stauffer, C., Lieutier, F. & Kerdelhué, C. (2009) Complex postglacial history of the temperate bark beetle *Tomicus piniperda* L. (Coleoptera, Scolytinae). *Heredity*, **103**, 238–247.
- Howe, R.W. (1967) Temperature effects on embryonic development in insects. *Annual Review of Entomology*, **12**, 15–42.
- Kerdelhué, C., Roux-Morabito, G., Forichon, J., Chambon, J.-M., Robert, A. & Lieutier, F. (2002) Population genetic structure of *Tomicus piniperda* L. (Curculionidae: Scolytinae) on different pine species and validation of *T. destruens* (Woll.). *Molecular Ecology*, **11**, 483–494.
- Kirkendall, L.R., Faccoli, M. & Ye, H. (2008) Description of the Yunnan shoot borer, *Tomicus yunnanensis* Kirkendall & Faccoli sp. n. (Curculionidae, Scolytinae), an unusually aggressive pine shoot beetle from southern China, with a key to the species of *Tomicus*. *Zootaxa*, **1819**, 25–39.
- Kohlmayr, B., Riegler, M., Wegensteiner, R. & Stauffer, C. (2002) Morphological and genetic identification of the three pine pests of the genus *Tomicus* (Coleoptera, Scolytidae) in Europe. *Agricultural and Forest Entomology*, **4**, 151–157.
- Komonen, A. & Kouki, J. (2008) Do restoration fellings in protected forests increase the risk of bark beetle damages in adjacent forests? A case study from Fennoscandian boreal forest. *Forest Ecology and Management*, **255**, 3736–3743.
- Kulinich, O.A. & Orlinskii, P.D. (1998) Distribution of conifer beetles (Scolytidae, Cucurilionidae, Cerambycidae) and wood nematodes (*Bursaphelenchus* spp.) in European and Asian Russia. *Bulletin OEPP/EPPO Bulletin*, **28**, 39–52.
- Långström, B. (1983) Life cycle and shoot-feeding of the pine shoot beetles. *Studia Forestalia Suecica*, **163**, 1–29.
- Långström, B. & Hellqvist, C. (1990) Spatial distribution of crown damage and growth losses caused by recurrent attacks of pine shoot beetles in pine stands surrounding a pulp mill in southern Sweden. *Journal of Applied Entomology*, **110**, 261–269.
- Långström, B. & Hellqvist, C. (1991) Shoot damage and growth losses following three years of *Tomicus* attacks in Scots pine stands close to a timber storage site. *Silva Fennica*, **25**, 133–145.
- Li, X., Zhang, Z., Wang, H., Wu, W., Cao, P. & Zhang, P. (2010) *Tomicus armandii* Li & Zhang (Curculionidae, Scolytinae), a new pine shoot borer from China. *Zootaxa*, **2572**, 57–64.
- Lieutier, F. (1984) Impact économique des scolytides: voies de recherche. *Comptes-Rendus de l'Académie d'Agriculture de France*, **70**, 835–843.
- Mason, P.G., Weiss, R.M., Olfert, O., Appleby, M. & Landry, J.-F. (2011) Actual and potential distribution of *Acrolepiopsis assectella* (Lepidoptera: Acrolepiidae), and invasive alien pest of *Allium* spp. in Canada. *Canadian Entomologist*, **143**, 185–196.
- Masutti, L. (1969) Pinete dei litorali e *Blastophagus piniperda* L. Una difficile convivenza. (Coast pine-stands and *Blastophagus piniperda* L. a difficult coupling). *Monti e Boschi*, **20**, 15–27.
- Murayama, J.J. (1963) *Studies in the Scolytid Fauna of the Northern Half of the Far East, V: Hylesininae*. Shukosha Press, Japan.
- Nanni, C. & Tiberi, R. (1997) *Tomicus destruens* (Wollaston): biology and behaviour in Central Italy. *Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests* (ed. by J. C. Grégoire, A. M. Liebhold, F. M. Stephen, K. R. Day and S. M. Salom), pp. 131–134. USDA Forest Service, General Technical Report NE-236. Vallombrosa, Italy.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Reviews of Ecology, Evolution and Systematics*, **37**, 637–669.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pfeffer, A. (1994) Zentral- und Westpaläarktische Borken- und Kernkäfer (Coleoptera, Scolytidae, Platypodidae). *Entomologica Basiliensia*, **17**, 5–310.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria. <http://www.R-project.org> [accessed on 22 March 2012].



- Ritzerow, S., Konrad, H. & Stauffer, C. (2004) Phylogeography of the Eurasian pine shoot beetle *Tomicus piniperda* L. (Coleoptera, Scolytidae). *European Journal of Entomology*, **101**, 13–19.
- Saarenmaa, H. (1985) The role of temperature in the population dynamics of *Tomicus piniperda* (L.) (Col., Scolytidae) in northern conditions. *Zeitschrift für Angewandte Entomologie*, **99**, 224–236.
- Sabbatini Peverieri, G., Faggi, M., Marziali, L. & Tiberi, R. (2008) Life cycle of *Tomicus destruens* in a pine forest of central Italy. *Bulletin of Insectology*, **61**, 337–342.
- Sauvard, D. (2004) General biology of bark beetles. *Bark and Wood Boring Insects in Living Trees, A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Gregoire and H. Evans), pp. 63–88. Kluwer Academic Publishers, The Netherlands.
- Sauvard, D., Lieutier, F. & Lévieux, J. (1988) L'Hylésine du pin (*Tomicus piniperda* L.) en forêt d'Orléans: répartition-dégâts-lutte. *Revue Forestière Française*, **1**, 13–19.
- Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.
- Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**, 415–416.
- Triggiani, O. (1983) Gravi attacchi di *Tomicus piniperda* L. (Col. Scolytidae) nelle pinetti del litorale ionico (nota preliminare). *Atti XIII Congresso Nazionale Italiano Entomologica*, pp. 391–398. Accademia Nazionale Italiana di Entomologia and Società Italiana di Entomologia, Italy.
- Vasconcelos, T., Horn, A., Lieutier, F., Branco, M. & Kerdelhué, C. (2006) Distribution and population genetic structure of the Mediterranean pine shoot beetle *Tomicus destruens* in the Iberian Peninsula and Southern France. *Agricultural and Forest Entomology*, **8**, 103–111.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York, New York.
- Walther, G.-R., Post, E., Convey, P. *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Accepted 25 February 2012

First published online 21 May 2012