



Descriptive biogeography of *Tomicus* (Coleoptera: Scolytidae) species in Spain

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ABSTRACT

Aim, location *Tomicus* (Coleoptera, Scolytidae) species are some of the principal pests of Eurasian forest and are represented by three coexisting species in Spain, *Tomicus piniperda* (Linnaeus, 1758), *Tomicus destruens* (Wollaston, 1865) and *Tomicus minor* (Harting, 1834). The distribution of two taxa are unknown as they have until recently been considered separate species. Therefore, we model the potential distribution centres and establish the potential distribution limits of *Tomicus* species in Iberia. We also assess the effectiveness of different models by comparing predicted results with observed data. These results will have application in forest pest management.

Methods Molecular and morphological techniques were used to identify species from 254 specimens of 81 plots. For each plot, a Geographical Information System was used to extract a set of 14 environmental (one topographic, six climatic) and biotic variables (seven host tree distributions). General Additive Models and Ecological Niche Factor Analysis models are applied for modelling and predicting the potential distribution of the three species of *Tomicus*.

Results The results of both modelling methodologies are in agreement. *Tomicus destruens* is the predominant species in Spain, living in low and hot areas. *Tomicus piniperda* occurs in lower frequency and prefers wet and cold areas of north-central Spain. We detected sympatric populations of *T. destruens* and *T. piniperda* in Northern coast of Spain, infesting mainly *P. pinaster*. *Tomicus minor* is the rarest species, and it occupies a fragmented distribution located in high and wet areas. The remarkable biotic variable is the distribution of *P. sylvestris*, incorporated into the models of *T. destruens* and *T. piniperda*.

Main conclusions These results indicate that in wet areas of north-central Spain where *T. piniperda* occurs (and possibly the high altitudes of the southern mountains), *T. destruens* has a climatic distribution limit. In the northern border of this area, both species overlap their distributions and some co-occurrences were detected. *Tomicus minor* potentially occurs in high and wet fragmented areas.

Keywords

Tomicus, Scolytidae, forest pest, climate, General Additive Model, Ecological Niche Factor Analysis, potential distribution, Spain.

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INTRODUCTION

Tomicus species (Coleoptera, Scolytidae) are important pests of pine forest in Eurasia (Schroeder, 1987; Bouhot *et al.*, 1988; Hui, 1991), Europe (Langström, 1983; Schroeder, 1987; Bouhot *et al.*, 1988; Hui, 1991; Guerrero *et al.*, 1997; Dajoz,

2000) and Mediterranean regions (Triggiani & Santini, 1987; Monleón *et al.*, 1996; Nanni & Tiberi, 1997). Three widespread species occur in the Iberian Peninsula (Gil & Pajares, 1986; Lombardero, 1994; Gallego & Galián, 2001).

According to Wood & Bright (1992), *T. piniperda* has holarctic distribution, after their introduction in North

America, whereas *T. destruens* is a circummediterranean and macaronesican species. *Tomicus minor* occurs in the palaearctic region, coinciding with *T. piniperda* in the major part of its distribution. The distribution of the *Tomicus* species in the Iberian Peninsula was revised in two studies (Gil & Pajares, 1986; Lombardero, 1994), showing that *T. piniperda* occupies the major part of Spain, whereas *T. minor*, most occasional, is only present in some regions. In those papers *T. destruens* was not considered as a valid species, so that its distribution is unknown in the Iberian Peninsula.

Tomicus destruens has been considered as an ecotype of *Tomicus piniperda* (Carle, 1973; Schwerdtfeger, 1981), or as a different species (Lekander, 1971; Wood & Bright, 1992; Pfeffer, 1995). Recent molecular studies have demonstrated consistent differences between them as expected for distinct species (Gallego & Galián, 2001; Kerdelhué *et al.*, 2002; Kohlmayr *et al.*, 2002). *Tomicus minor* differs morphologically from *T. destruens* and *T. piniperda* in the second row of setae that continues uninterrupted through the declivity, although some females of *T. piniperda* also shows this character (Passoa & Cavey, 1993). Studies on reproductive flight period showed a clear difference between *T. destruens* and *T. piniperda*. *Tomicus piniperda* flies in early spring whereas the flight of *T. destruens* occurs in autumn-early winter (Carle, 1973; Langström, 1983; Triggiani & Santini, 1987; Hui, 1991; Monleón *et al.*, 1996; Nanni & Tiberi, 1997). Furthermore, the flight of *T. piniperda* in spring is strongly influenced by the maximum daily temperatures, with a flight threshold estimated at 12 °C in Europe (Bakke, 1968) and northeastern US (Haack *et al.*, 1998) and 13 °C in the Chinese Kunming region (Hui, 1991). In contrast, Monleón (1995) reported that *T. destruens* flies above a temperature of around 24 °C in pine forests near Barcelona (Spain). The three species of *Tomicus* attack several species of *Pinus* (Wood & Bright, 1992), with a life cycle similar to that described for *T. piniperda* by Carle (1973).

The presence of the three species in the Iberian Peninsula, led us to hypothesize that this is a region where the limits of the distribution areas of the three species coincide. Perhaps, the peninsula includes the extreme ranges of *T. piniperda* and *T. destruens*. The fragmented distribution of *T. minor*, according to Gil & Pajares (1986) and Lombardero (1994), may be due to a patched occurrence for high specialization or less tolerance. If this scenario is correct, a study of the factors that condition distributions among the three species become a stimulating field for research.

Several authors (Ungerer *et al.*, 1999) have proposed that the distribution of a species of bark beetle could be determined by some or all of these three factors (i) the occurrence of its host plant, (ii) a lower lethal temperature and (iii) spatial variations in community interactions. Historical records of air temperature were used for interpreting some aspects of the biology and large-scale distribution of *T. piniperda* (Haack *et al.*, 1998) and *Dendroctonus frontalis* (Ungerer *et al.*, 1999).

The spatial prediction of species distributions is an important tool for conservation and management planning, by using a wide variety of statistical approaches and Geographical

Information Systems (GIS) (Austin, 2002). The availability of a map of potential distribution for cryptic species such as *T. destruens* and *T. piniperda*, morphologically indistinguishable also from some individuals of *T. minor*, is useful in pest forest management (Liebhold *et al.*, 1993). The use of a Digital Elevation Model (DEM) constitutes a basis for generating maps of environmental variables (Guisan & Zimmermann, 2000). A DEM has basic derivatives, as altitude, slope or aspect, with influence in the distribution of the organisms. Other environmental variables, as temperature and water availability are important factors in the distribution of the bark beetles species and their host trees (Amman, 1973; Logan & Bentz, 1999; Perkins & Roberts, 2003). These factors influence the life cycle of the beetle and define its northern distribution limits by lower lethal temperature (Ungerer *et al.*, 1999). The distribution pine host trees are influenced by these two factors (Leathwik & Mitchell, 1992; Leathwik, 1995; Chaparro, 1996; Leathwik & Rogers, 1996; Zaniewski *et al.*, 2002). The influence of the host tree distribution in the distribution of both *T. destruens* and *T. piniperda* in Southern France was proposed by Kerdelhué *et al.* (2002). According to these authors *T. piniperda* could only attack the continental *Pinus* species (*P. sylvestris*, *P. nigra* and *P. mugo*), whereas *T. destruens* infests the Mediterranean pine species (*P. pinaster*, *P. halepensis*, *P. pinea*, *P. brutia* and *P. canariensis*).

Generalized additive models (GAM) are a nonparametric extension of GLM models that fit predictor variables independently by smooth functions (Hastie & Tibshirani, 1990; Yee & Mitchell, 1991). The presence/absence data sets are the data most commonly used in GAM models (Hui, 1991; Austin & Meyers, 1996; Leathwik & Rogers, 1996; Leathwik *et al.*, 1996; Bio *et al.*, 1998; Lehmann, 1998; Pearce & Ferrier, 2001; Lehmann *et al.*, 2002; Zaniewski *et al.*, 2002), for inferring species distributions related to the spatial distribution of environmental variables, and to generate predictive models of potential distribution of species (Franklin, 1995; Guisan & Zimmermann, 2000; Guisan & Zimmermann, 2000; Scott *et al.*, 2002).

The determination of the true absences is the main problem of many animal presence/absence data sets (Hirzel *et al.*, 2002; Zaniewski *et al.*, 2002). Some techniques based on heuristic models incorporate presence-only data, as bioclimatic analysis and prediction system (BIOCLIM) and Ecological Niche Factor Analysis (ENFA) (Hirzel *et al.*, 2002). ENFA creates habitat suitability maps using marginality and tolerance indices. These maps are the result of the location of the species within the multidimensional environmental volume that is defined by considering all mapping units within the study area (Guisan & Zimmermann, 2000). The habitat suitability maps indirectly reveal the species potential distribution (Hausser, 1995; Hirzel *et al.*, 2002).

The aims of this study are as follows:

1. To study the distribution of the three species of *Tomicus* in the Iberian Peninsula and to evaluate the centres and range limits of these species.
2. To generate maps of potential distribution as a tool for pest forest management.

METHODS

Study area

The study area included the Spanish territory of the Iberian Peninsula and the Balearic islands, with a total landmass of 489,400 km². Peninsular Spain is a plateau framed by two great mountain ranges, the Cantabrian–Pyrenean Mountains, direction E–W at the North, and the Betic Mountains, direction NE–SW at the South, parallel to their coastlines, respectively. Another mountain range, the Central Mountains, direction E–W, divides the plateau into two Northern and Southern sub-plateaus. Finally, the Iberian Mountains is the border between the eastern side of the Northern Plateau and the Ebro River Valley, direction NW–SE. The Balearic Islands, an eastern extension of the Betic Mountains, are a group of four large islands and three small islands. Majorca, the higher island, has a mountain range, direction SW–NE, and a mean altitude around 900 m (Lautensach, 1964). The climate depends on three factors, continentality, orography and atmospheric circulation. At a great scale, different zones can be climatologically differentiated. One, the coolest and with high precipitations in winter and spring, is located at the North of the Central Mountains, and at a high altitude in the Betic Mountains. The second zone, warmer and drier with precipitations in spring and autumn, occupies the Southern area of Central Mountains, the Mediterranean coast, the Ebro Valley and an area of the Northern Plateau with small altitude. Thirdly, another area occupies the Southeastern corner of the Peninsula, with the warmest and driest climate (Font-Tullot, 1983).

Species data

We have studied 254 specimens of 81 plots of *Tomicus* collected in different sites of the study area. A random sampling was carried out, by field surveys, between 1999 and 2002. Infested trees, found randomly in pine forests, were

barked and the adults present in the galleries were collected; larvae and pupae were also occasionally collected. Some adults were also caught in shoots and in window traps. The insects were preserved in absolute ethanol or dried in silica gel, until molecular identification. For each plot, a database was compiled including information on latitude/longitude co-ordinates, altitude, collection date and host-tree species.

Insects were identified by the molecular test, based in RFLP-PCR of the rDNA proposed by Gallego & Galián (2001) for separating *T. destruens* from *T. piniperda*. *Tomicus minor* was also included in the molecular analysis for solving the morphological similarity showed by Passoa & Cavey (1993), also found in Spain for *T. destruens* (R. Hernandez, pers. com.). We define a grid of 10 × 10 km for all study area and make a presence/absence map for each of the tree species ($n = 4894$).

Environmental data

We used three types of environmental data to describe every 10 × 10 km unit grid of the study area: climatic estimates, topographical characteristic and biotic data (Table 1). Climatic estimates of temperature and water availability was obtained from 1572 climatic records, registered between 25 and 37 years, which is adequate for climatic interpolation (Kurtzman & Kadmon, 1999; Felicísimo *et al.*, 2001; Marquinez *et al.*, 2003). This data are available in the official Spanish Government website.

We used a DEM of the Iberian Peninsula, with a pixel of 1 × 1 km for calculating the altitude of the 10 × 10 km grid, using Spatial Analyst extension of Arcview 3.2 GIS. This DEM are available in the Gtopo project website. Aspect and slope, were not used in this work because of the inappropriate scale.

We performed an interpolation of climatic estimates for every 10 × 10 km grid of the study area by universal linear method of kriging interpolation (Dingman *et al.*, 1988; Collins & Bolstad, 1996; Price *et al.*, 2000; Felicísimo *et al.*, 2001; Jeffrey *et al.*, 2001; Joly *et al.*, 2003), using Spatial Analyst extension of ArcView3.2 GIS (Table 1). We have studied the

Table 1 Environmental predictors used to model *Tomicus destruens*, *T. piniperda* and *T. minor* distributions

Variable	Code	Min/max value	Types
Altitude (m)	Alt	0/3172	
Frost (no. of months)	Cooln	0/10.66	
Maximum absolute mean temperature (°C)	Maxabmt	17.79/37.57	
Minimum absolute mean temperature (°C)	Minabmt	−14/10.12	
Annual mean temperature (°C)	Tmann	7.2/21.71	
Temperature seasonality (°C)	Tmseas	0.3/1.89	
Annual mean water deficit (mm)	Wdefann	−1877.6/788	
Presence of <i>Pinus halepensis</i>	Phale		Presence, absence
Presence of <i>P. nigra</i>	Pnigr		Presence, absence
Presence of <i>P. pinaster</i>	Ppina		Presence, absence
Presence of <i>P. sylvestris</i>	Psylv		Presence, absence
Presence of <i>P. radiata</i>	Pradi		Presence, absence
Presence of <i>P. uncinata</i>	Punci		Presence, absence
Presence of <i>P. pinea</i>	Ppine		Presence, absence

influence of the temperature using three variables: mean maximum absolute temperature (Maxabmt), mean minimum absolute temperature (Minabst) and mean annual temperature (Tmann). The degree of deviation from the expected temperature is calculated by an index of temperature seasonality (Tmseas), inversely related to continentality gradient (Leathwick *et al.*, 1996; Lehmann *et al.*, 2002; Zaniewski *et al.*, 2002). Water availability was estimated by the mean annual water deficit index (Wdefann), as annual potential evapo-transpiration minus annual precipitation. Positive values of this index indicate drought conditions.

Biotic dataset was extracted from the maps of distribution of all species of pine trees, available in digital version (Ruiz, 2002). We have extracted the distribution of pine species and we have made seven maps of presence/absence of single pine species, without differentiating whether the pine species are dominant or secondary in the forest. With this dataset, we can test the dependence of single species of host tree in the distribution of their potential herbivorous (*Tomicus*), characterized for their less specificity of host selection (Wood & Bright, 1992). Biological data set are used only in the GAM model procedure.

We calculated the correlations between all predictors to allow removal of the correlated predictors, for avoiding the problem of estimating responses. Lehmann *et al.* (2002) consider that a correlation of 0.793 was not high enough to justify removing any variables. The highest absolute value of correlation in our dataset is 0.839. We do not consider necessary removing any variable.

GAM models

The GAM models were performed in S-PLUS 2000 under MS WINDOWS environment using Generalized Regression Analysis and Spatial Predictions (GRASP-S; Lehmann *et al.*, 2002). The three species were individually modelled using a logistic link and a binomial error term, using the seven continuous variables and the seven qualitative variables (Table 1):

$$\text{logit}(p) = \log p / 1 - p = b + \sum \text{flixi} \quad (1)$$

where p is the probability of presence/absence of species, b is a regression constant and f is an arbitrary smooth function selected by spline smoothers. We use a both directional stepwise procedure to include only those variables with $P < 0.01$ in the model (Zaniewski *et al.*, 2002). For all species, a quasi-binomial model was chosen. Starting models including all predictors smoothed with 4 d.f. An ANOVA (F -test) for quasi models was used for testing the significance of the smooth terms (Lehmann *et al.*, 2002).

ENFA models

The ENFA models were performed by BIOMAPPER 2.1 (Hirzel *et al.*, 2002), that is an autonomous program that generates habitat suitability models and maps. BIOMAPPER, using a similar procedure to principal component analysis, summarizes the environmental (eco-geographical) variables in two types of

uncorrelated factors: (1) marginality factor, that describes how far is the species optimum from the mean habitat in the study area and (2) tolerance factors, that describe how specialized is the species in relation to the available range of habitat in the study area (Hirzel *et al.*, 2002). These factors define a hypervolume of space corresponding to the Hutchinsonian ecological niche of the species (Hirzel *et al.*, 2002). Only presence data together with the environmental continuous data are introduced into BIOMAPPER. Environmental data are normalized using the Box-Cox transformation. The maps were transformed in Arcview 3.2 format by Av2IIdris extension.

Evaluation and comparisons of models

We have used a cross-validation by ROC test (Fielding & Bell, 1997) for validating the results of GAM. In ENFA models it is not possible to use the same evaluation method, because it uses only presence data. The validation procedure of the ENFA models is included in BIOMAPPER: performed by a Jack-knife cross-validation process (Fielding & Bell, 1997), by partition of each species data set (Reutter *et al.*, 2003).

Both model methods use different kinds of selection and incorporation predictor variables in the model. ENFA includes all continuous variables, with different weight; however GAM incorporates only those predictors (continuous and qualitative) that explain a significant percentage of null deviance, after a stepwise procedure. Models obtained by both procedures are evaluated by the method described in Zaniewski *et al.* (2002). We conducted random selections of 1000 points from the three grids of distribution of each species, species data sets grid, probability of presence grid and habitat suitability index grid. These selections were repeated 1000 times. Mean and standard deviations were calculated for comparison between observed and predicted values.

RESULTS

Sampling of *Tomicus* species

We have detected the presence of *T. destruens* in 49 sites (60.5%), *T. piniperda* in 26 sites (32.1%) and *T. minor* in 11 sites (13.6%) (Figure 1). *Tomicus destruens* occurs in a large area of the East, South, Central and Northern coast of Spain and in the Balearic Islands. *Tomicus piniperda* is restricted to Northern plateau and Cantabrian and Pyrenees Mountains. *Tomicus minor*, less frequent and more fragmented, occurs in the Central and Betic Mountains, as well as in the Northern Plateau. *Tomicus destruens* was collected from the sea level up to 1,300 m. *Tomicus piniperda* between 200 and 1800 m. *Tomicus minor* was collected between 800 and 1600 m. *Tomicus destruens* was collected in a large number of host tree species: *P. halepensis*, *P. pinaster*, *P. nigra*, *P. radiata* and *P. pinea*. *Tomicus piniperda* is caught in *P. pinaster*, *P. radiata* and *P. sylvestris*. *Tomicus minor* is found in *P. nigra*, *P. pinaster* and *P. sylvestris*. The collection of

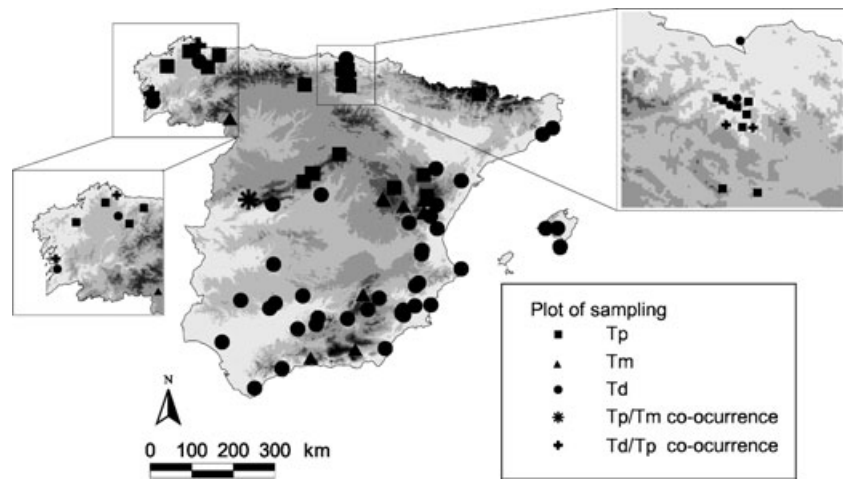


Figure 1 Spatial location of the *Tomicus* populations sampled. A DTM (1 km²) is shown (white: low altitude; black: high altitude). Molecular identification of the species is indicated by symbols, Td, *T. destruens*; Tp, *T. piniperda*; Tm, *T. minor*. Details of areas of sympatric co-occurrence of *T. destruens* and *T. piniperda* are magnified.

T. piniperda in seven plots (26%) infesting *P. pinaster*, a Mediterranean species of *Pinus*, is not in accordance to Kerdelhué *et al.* (2002).

It is noticeable that *T. destruens* and *T. piniperda* were collected together in four sites, as previously reported by Kerdelhué *et al.* (2002) in one plot in Southern France. This sympatric co-occurrence happens in the Northern Coast of Spain (Fig. 1), attacking *P. pinaster* (three sites) and *P. radiata* (one site). We confirmed here a spatial-temporal coincidence in the same host tree of these sibling species. Also, we have detected a sympatric population of *T. piniperda* and *T. minor* in the central mountains, according to the reports of Fernández (1997) in the Northern Plateau.

Some authors noted a frequent problem for estimating the presence of rare species (Venette *et al.*, 2002; Zaniewski *et al.*, 2002). It is of the generalized tendency to search for rare species in contrast to common species, i.e. Museum data set are biased to rare species over common species. *Tomicus minor* is the rarest species of the genus *Tomicus* in our data set as it is in published reports (Gil & Pajares, 1986; Lombardero, 1994), but the random sampling of *Tomicus* species and the molecular identification presumably minimizes this bias.

GAM models

The stepwise selection of predictors for the three species selects the following models (see Table 1 for codes):

$$\begin{aligned} T. destruens \text{ probability} : & s(\text{Alt}, 4) + s(\text{Cooln}, 4) \\ & + s(\text{Maxabmt}, 4) + s(\text{Tmann}, 4) \\ & + s(\text{Tmseas}, 4) + \text{Phale} + \text{Pradi} + \text{Psylv}; \\ & \text{explained deviance} : 93.35\%(58.44\text{d.f.}) \end{aligned} \quad (2)$$

$$\begin{aligned} T. piniperda \text{ probability} : & s(\text{Alt}, 4) + s(\text{Wdefann}, 4) \\ & + s(\text{Cooln}, 4) + s(\text{Minabmt}, 4) \\ & + s(\text{Tmann}, 4) + s(\text{Tmseas}, 4) + \text{Phale} \\ & + \text{Ppina} + \text{Pnigr} + \text{Pradi} + \text{Psylv} \\ & + \text{Ppine}; \text{explained deviance} : 95.05\%(51.73\text{d.f.}) \end{aligned} \quad (3)$$

$$\begin{aligned} T. minor \text{ probability} : & s(\text{Alt}, 4) + s(\text{Wdefann}, 4) \\ & + s(\text{Cooln}, 4) + s(\text{Maxabmt}, 4) \\ & + s(\text{Minabmt}, 4) + s(\text{Tmseas}, 4) + \text{Phale} \\ & + \text{Ppina} + \text{Pnigr} + \text{Pradi} \\ & + \text{Psylv}; \text{explained deviance} : 98.58\%(54.69\text{d.f.}) \end{aligned} \quad (4)$$

where *s* is the spline smoother, 4 is d.f. for the spline smoother. The dispersion parameters estimated for quasi-binomial models are 0.07 for *T. destruens*; 0.06 for *T. piniperda* and 0.01 for *T. minor*. The cross-validation and simple validation of each species presented high ROC values (Table 2). The small differences between both values indicate good model stability.

For the interpretation of the models we show the partial responses curves of each species (Figs 2–4) and we analyse the contribution of each variable to the models. As far as partial responses is concerned, *T. destruens* (Fig. 2) has a strong negative response to altitude, negative with a plateau to number of month of frost and maximum absolute temperature mean temperature and positive response to annual mean temperature and temperature seasonality. Besides, *T. destruens* selected presence of *P. halepensis* and absences of *P. radiata* and *P. sylvestris*. *Tomicus piniperda* (Fig. 3) shows a unimodal response to altitude and annual mean temperature, positive to temperature seasonality, positive with plateau to number of month of frost and minimum absolute mean temperature and negative with plateau to annual mean water deficit. This

Table 2 Values of cross-validation ROC and validation ROC in validation method of generalized additive models for all three species

	Cross-validation ROC	Validation ROC
<i>Tomicus destruens</i>	0.91	0.97
<i>T. piniperda</i>	0.81	0.98
<i>T. minor</i>	0.86	0.97

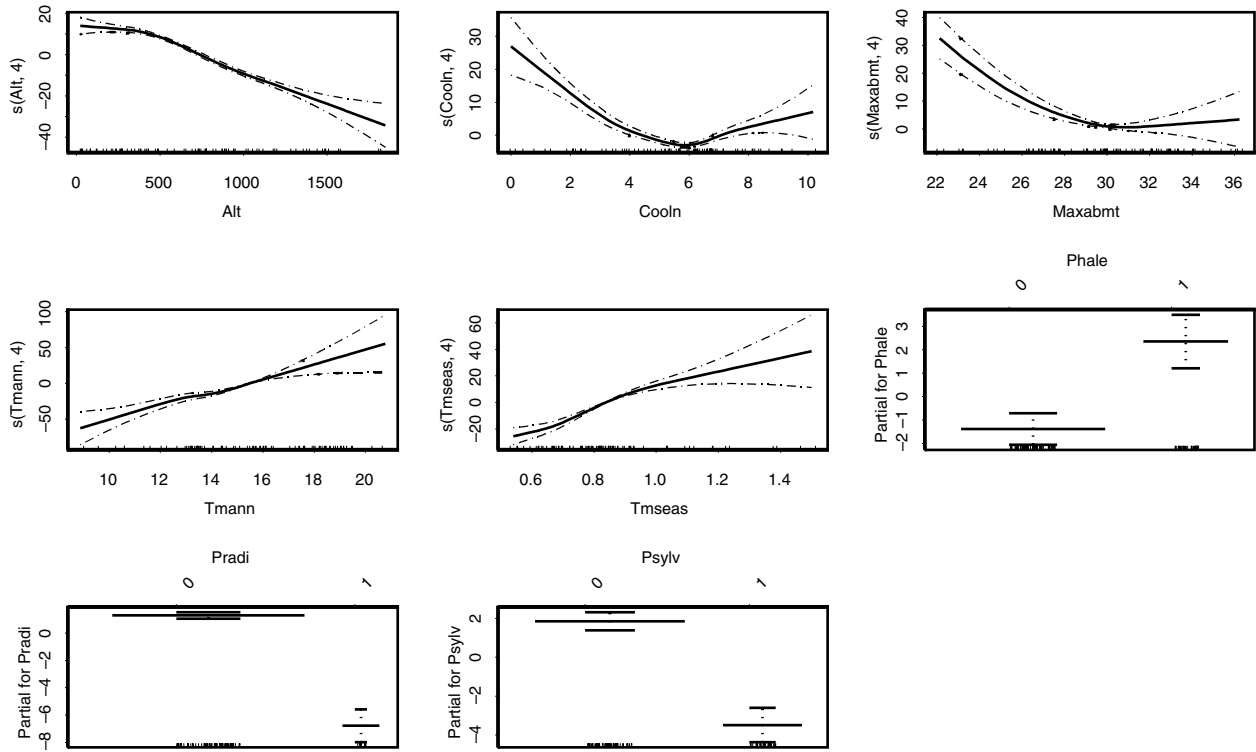


Figure 2 Partial response curves of *Tomicus destruens* model.

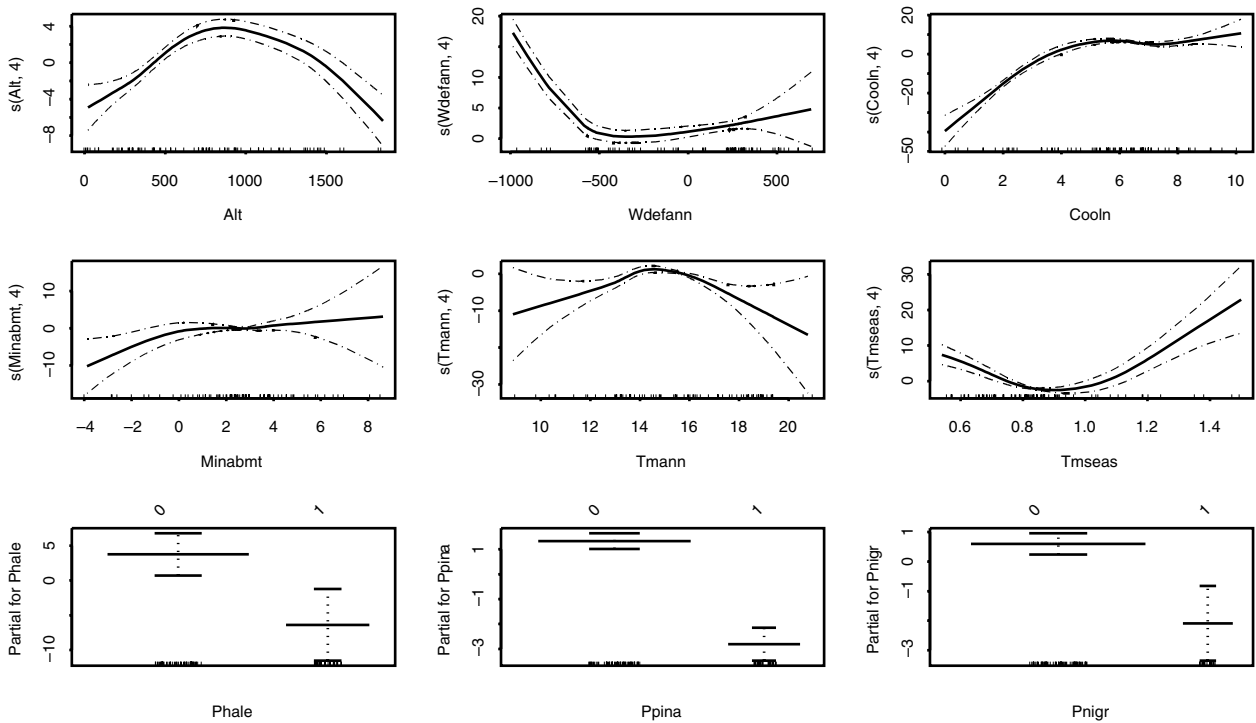


Figure 3 Partial response curves of *Tomicus piniperda* model.

species has a strong relation to presence of *Pinus sylvestris*. Finally, *T. minor* (Fig. 4) has a strong positive relation to altitude (close linear), unimodal to annual mean water deficit

and negative to number of month of frost, maximum and minimum absolute mean temperature, temperature seasonality, and presence of *P. pinaster* and *P. nigra*.

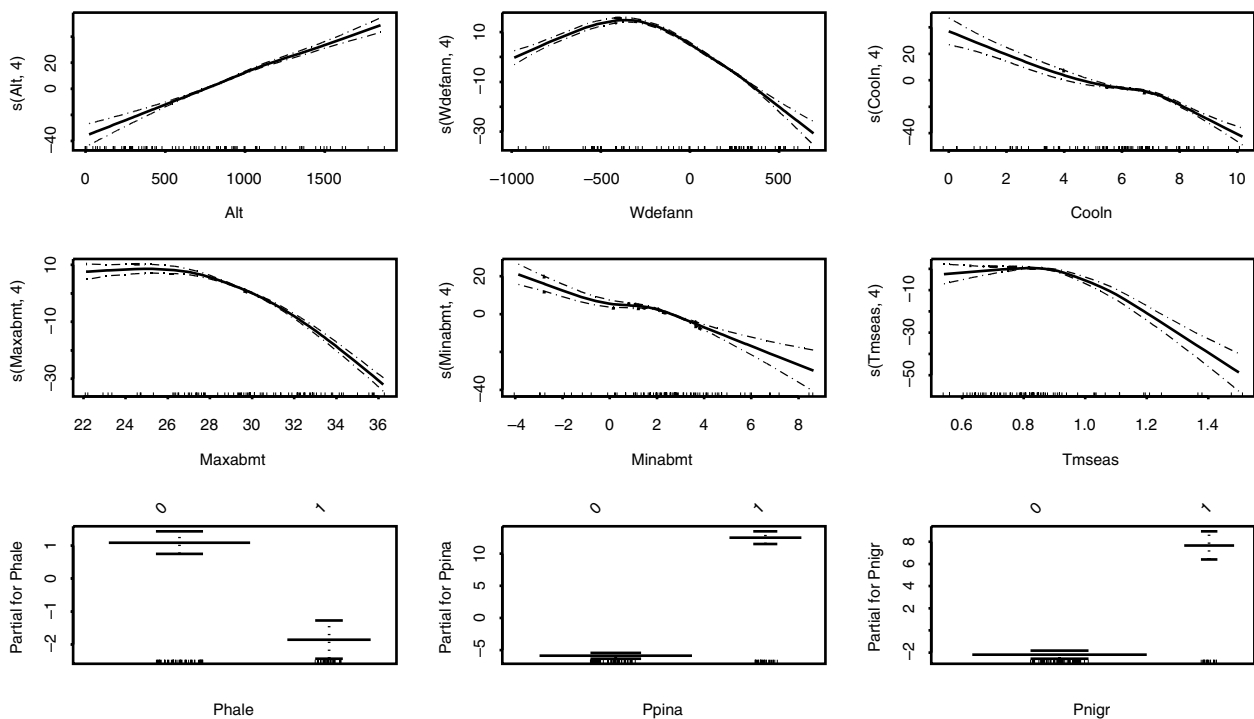


Figure 4 Partial response curves of *Tomicus minor* model.

Drop contribution indicates the marginal contribution of each variable, when we drop it from the model and calculate the associated change in deviance. For *T. destruens* and *T. minor*, altitude is the dominant variable, whereas in *T. piniperda* are two co-dominant variables: annual mean water deficit and distribution of *P. sylvestris*. Alone contributions are the explanation of models with only one predictor. Annual mean temperature is the best alone predictor for *T. destruens* and *T. piniperda*, and altitude is for *T. minor*. Other predictors are ranked in different order for each species from host predictors, underlining the high explanation of distribution of *P. sylvestris* for *T. destruens*, distribution of *P. halepensis* and distribution of *P. sylvestris* for *T. piniperda* and distribution of *P. nigra* for *T. minor*.

Figure 5 shows the plot of combined response curves of the three species. We found a clear segregation between the pair *T. destruens*/*T. minor*, and not as clear between the other pairs. Thus, a more or less defined border of altitude (1000 m), the number of month of frost and mean temperature (12 °C) segregates *T. destruens*, that occupies the hottest and lowest areas, with some months of frost but without extreme lowest temperature, whereas *T. minor*, occurs in highest and coldest. The pair *T. destruens*/*T. piniperda* has a segregation by water availability, that is, wettest areas for the presence of *T. piniperda* and driest for *T. destruens*. Finally, continentality are the variable that segregates the presence of *T. minor* from *T. piniperda*.

The spatial prediction of the three species are shown in Fig. 6. *Tomicus destruens* has the largest potential distribution of the three species. It potentially occupies the southern half of

Spain, the coastal band of Spain, the Ebro and the Duero Valleys, and it is absent at great altitudes of the Betic Mountains. *Tomicus piniperda* has a high probability of presence in an area that occupies the mountains of the northern plateau and the Pyrenees and some areas of the Betic Mountains in the south. Areas of similar size have less probability in parts of the Ebro and Duero Valleys and the Iberic Mountains of the Southern Plateau. *Tomicus minor* has a fragmented potential distribution, with areas of high probability of presence divided for the mountains of the Northern Plateau, connected by areas of low probability. The Pyrenees, at the north, and the Betic Mountains, at the south, are apparently unconnected areas of high probability.

ENFA models

The continuous environmental variables are normalized by Box–Cox transformation and incorporated into the models. The values of global marginality, specialization and tolerance of the three species are shown in Table 3. *Tomicus piniperda* occurs in habitats that differ from the average conditions in Spain (1.06 of marginality, 0.51 of tolerance), opposite to *T. destruens*, that lives in habitat that differ less from these conditions (marginality = 0.73; tolerance = 0.79). *Tomicus minor* has a global marginality value similar to *T. destruens*, but the global tolerance value indicates that its niche is linked to rare environmental conditions in the study area (marginality = 0.82; tolerance = 0.08).

The marginality axis describes marginality and the others specialization (Table 4). Marginality coefficient indicates that

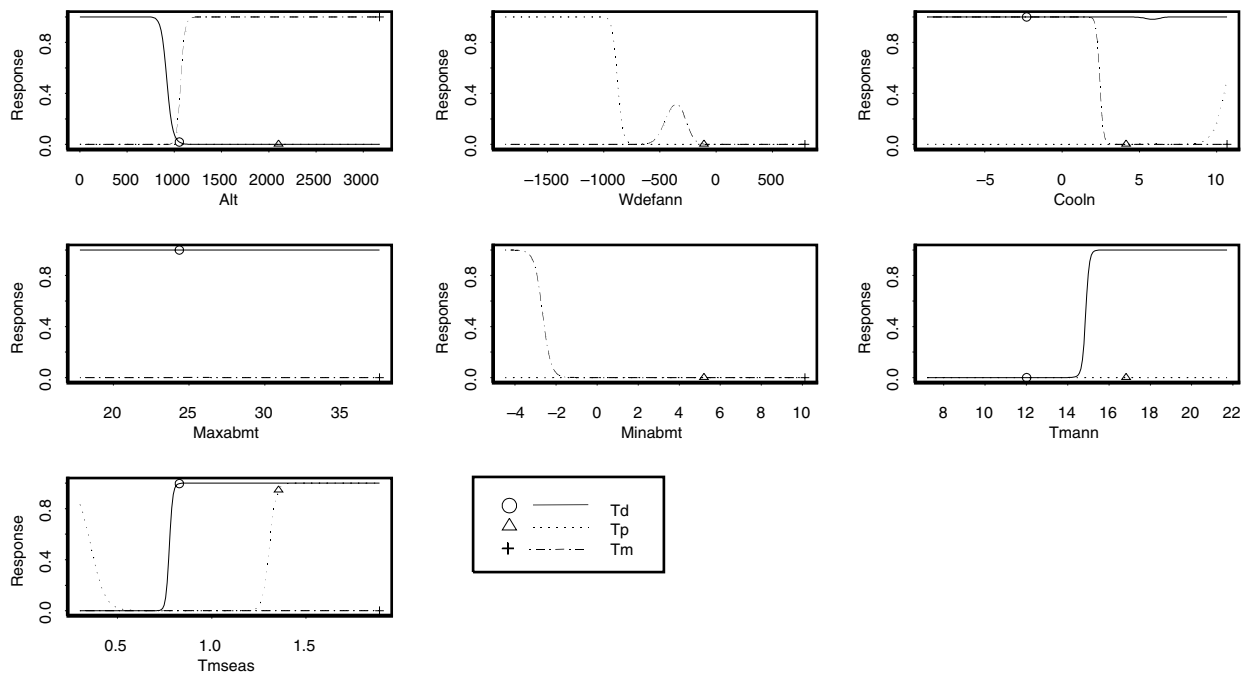


Figure 5 Combined response curves of the three species. Td, *Tomicus destruens*; Tp, *T. piniperda*; Tm, *T. minor*.

T. destruens is linked to warm and continental areas, with a large eigenvalue (39.4%). The other factors confirm these results. The values obtained by the Jack–knife cross-validation show the predicted suitability exceeds 0.5 in 56.7% of the validation cells (SD = 0.34). *Tomicus piniperda* has the largest eigenvalue of marginality axis (58.1%) and describes a preference for cold and wet areas (Table 4). The mean temperature is the most important eco-geographical variable for the model of this species. According to the Jack–knife cross-validation values of predicted suitability exceed 0.5 in 65% of de validation cells (SD = 0.32). The marginality factor of *T. minor* has the smallest eigenvalue (9.9%). The factor 2 accounts 86.1% of specialization. This species lives in high and cold areas. In this species, the values of Jack–knife cross-validation of predicted suitability exceed 0.5 in 80% of de validation cells (SD = 0.4).

The Fig. 6 shows the habitat suitability map performed for every species from the four factors. *Tomicus destruens* has the largest habitat suitability. It represents a fitted band along the coast of Spain, the Ebro Valley and extensive area of the Western of the Southern plateau with a high index value. The habitat suitability map for this species is differentiated from its probability map in the areas of low suitability index values in coast and a wide extension of medium values in Duero and Ebro Valleys and Southern Plateau. On the contrary, the habitat suitability map performed for *T. piniperda* is very close to the probability map. *Tomicus minor* has a habitat suitability map with a non-fragmented area opposite to the probability map.

The prediction maps obtained for the three species by the two methods are quite similar, in spite of the exclusion of the

host tree data set in ENFA. Previous studies determined GAM as a robust modelling method for predicting vegetal species spatial distribution (Leathwick, 1995; Lehmann *et al.*, 2002; Zaniewski *et al.*, 2002). However this model needs a good set of true absence data, which is difficult to achieve with animal sampling. Thus, the use of ENFA may constitute an *ad hoc* way of validating the results obtained of animal data set in GAM, performed with presence/‘pseudo’ absence data (Zaniewski *et al.*, 2002).

Observed and predicted species presence

Observed and predicted mean and SD of the three species are showed in Table 5. Predicted means of *T. piniperda* are similar to the observed mean. Predicted mean of *T. destruens* by the GAM model is higher (0.753) than that observed and predicted by ENFA, according to its wide potential distribution as shown in Fig. 6. *Tomicus minor* has stronger differences between values. Predicted mean by the GAM model is the lowest of the predicted means of the three species (0.063). This result is perhaps related to the rarity of this species in the study area.

DISCUSSION

Tomicus destruens is the most frequent species in Spain, whereas *T. piniperda* occurs in an area distributed for the Northern Plateau, the Pyrenees and perhaps in the Betic Mountains, at the South. As far as *T. minor* is concerned, we found a pattern of fragmented distribution according to previous reports (Gil & Pajares, 1986; Lombardero, 1994). These three species have a good spatial segregation in the

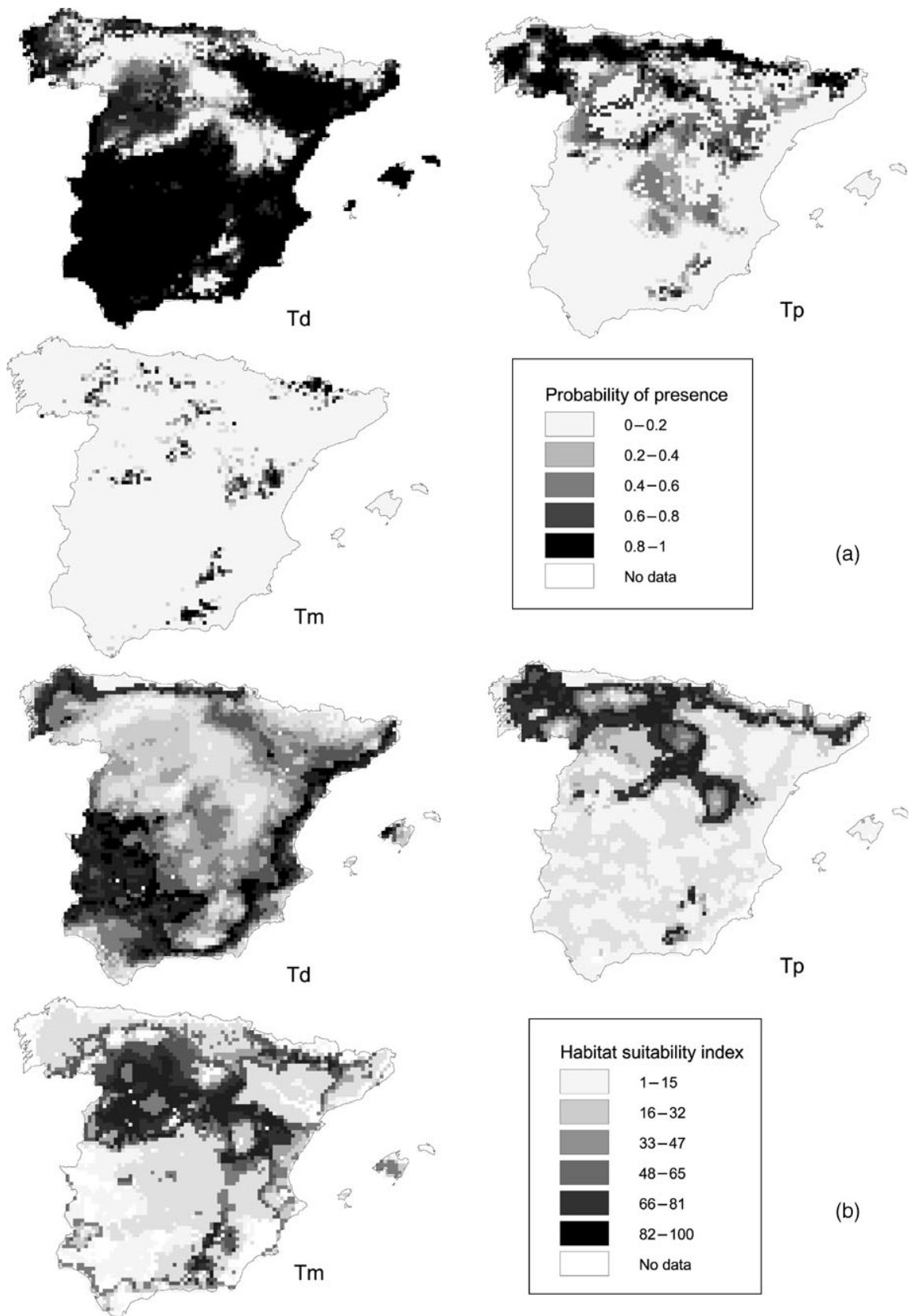


Figure 6 Spatial expressions of Generalized additive (a) and Ecological Niche Factor Analysis (b) models. Td, *Tomicus destruens*; Tp, *T. piniperda*; Tm, *T. minor*.

largest part of the study area. However, the Atlantic coasts and the Bay of Biscay coasts are a sympatric areas of *T. destruens* and *T. piniperda*. In these sites, at the end of winter and beginning of spring, both species coexist and could be caught in reproductive galleries in the same host tree. During this period, the reproductive flight of both species overlaps (Langström, 1983; Gil & Pajares, 1986; Hui, 1991; Monleón *et al.*, 1996). It is observed in 25% of the samples of the Atlantic coast and in 15.4% of the samples of the Bay of Biscay coasts. This sympatry is not detected in other areas, such as in the Iberic and Central Mountains where the species occur spatially segregated. A possible climatic explanation for it is discussed below. These results indicate that reproductive adults

Table 3 Global values of marginality, specialization and tolerance of Ecological Niche Factor Analysis models for the three species

	Marginality	Specialization	Tolerance
<i>Tomicus destruens</i>	0.73	1.27	0.79
<i>T. piniperda</i>	1.06	1.96	0.51
<i>T. minor</i>	0.82	12.5	0.08

of *T. destruens* and *T. piniperda* could be probably attracted to the same host-tree (primary attraction). The secondary attraction of both species are unknown and the possibility of an interspecific attraction, by sexual or aggregation pheromones, should not be excluded. *Tomicus destruens* and *T. piniperda* are phylogenetically very closely related as showed by Gallego & Galián (2001) and confirmed by Kerdelhué *et al.* (2002) and Kohlmayr *et al.* (2002).

The potential distribution of the three species is related to an environmental gradient that is defined by the predictive

Table 5 Comparison among mean observed probability, mean predicted probability of presence in generalized additive model and mean habitat suitability in Ecological Niche Factor Analysis models for 1000 randomly selected cells

Species	Observed	GAM	ENFA
<i>Tomicus destruens</i>	0.564 (0.018)	0.753 (0.011)	0.422 (0.007)
<i>T. piniperda</i>	0.30 (0.014)	0.258 (0.012)	0.237 (0.005)
<i>T. minor</i>	0.14 (0.008)	0.063 (0.005)	0.346 (0.008)

Values are expressed as mean (SD).

Table 4 Variance explained (in brackets) by the first four ecological factors and coefficient values of the variables used in Ecological Niche Factor Analysis models for the three species. Positive values on the marginality factor indicate that the species distribution is positively correlated with the corresponding eco-geographical variable (EGV). The signs of the specialization coefficients have no meaning

EGV	Marginality (39.4%)	Factor 2 (25.1%)	Factor 3 (15.1%)	Factor 4 (0.89%)
<i>Tomicus destruens</i>				
Alt	-0.278	0.013	0.474	0.101
Cooln	-0.456	0.562	0.288	0.339
Maxabmt	-0.106	0.061	0.543	0.041
Minabmt	0.505	0.779	0.126	0.221
Tmann	0.377	0.010	0.319	0.474
Tmseas	-0.552	0.224	0.406	0.744
Wdefann	0.048	0.153	0.339	0.215
<i>T. piniperda</i>				
	Marginality (58.1%)	Factor 2 (22.7%)	Factor 3 (6.9%)	Factor 4 (6.2%)
Alt	0.322	0.029	0.254	0.217
Cooln	0.202	0.064	0.076	0.183
Maxabmt	-0.446	0.547	0.043	0.353
Minabmt	-0.073	0.315	0.098	0.456
Tmann	-0.577	0.588	0.768	0.628
Tmseas	0.208	0.501	0.13	0.365
Wdefann	-0.524	0.016	0.559	0.245
<i>T. minor</i>				
	Marginality (9.9%)	Factor 2 (86.1%)	Factor 3 (2.9%)	Factor 4 (0.5%)
Alt	0.801	0.017	0.034	0.039
Cooln	0.351	0.302	0.184	0.139
Maxabmt	-0.092	0.185	0.422	0.422
Minabmt	-0.331	0.144	0.598	0.258
Tmann	-0.253	0.823	0.632	0.408
Tmseas	0.227	0.31	0.17	0.751
Wdefann	-0.042	0.283	0.025	0.059

models and habitat suitability maps. The potential distribution of *T. destruens* in Spain is predicted in areas with low altitude, below 1000 m, without *P. sylvestris* and *P. radiata*. *Tomicus piniperda* occurs in areas with high water availability, presence of *P. sylvestris* and minimum mean annual temperature above 0 °C. *Tomicus minor* has an opposite behaviour respect to the altitude, preferring areas over 1000 m, continental, with presence of *P. pinaster* and *P. nigra* and absence of *P. halepensis*. These areas have a relatively high environmental humidity but never becoming dried. The habitat suitability maps show the preferences of high altitude and wet areas for *T. piniperda* and high altitude and cold areas for *T. minor*. *Tomicus destruens* habitat suitability shows areas with low altitude and warm. The high negative eigenvalue of continentality index is in accordance with the low habitat suitability index at the coast band and Guadalquivir Valley. It is probably related to the low frequency of caught since the ENFA model describes how suitable a habitat may be for a species, by using only presence data (Hirzel *et al.*, 2002).

We have not found influence of extreme temperatures, as it was reported for other bark beetle species as *D. frontalis*. Ungerer *et al.* (1999) proposed a lower lethal air temperature of -16 °C for this species, as the northern limit of its distribution. Bakke (1968) estimated -18.4 °C as a lethal temperature for *T. piniperda*. These extreme temperatures do not occur frequently in the Iberian Peninsula. The reported value of lowest average minimum absolute temperature is -14 °C. So that, this lowest lethal temperature does not occur at least at the scale of this study in the Iberian Peninsula. If we worked with other climatic modulators, as the orientation, wind or coldness that act at a finer scale, these lower lethal temperature could be found, but it would always be a local process (Bolstad *et al.*, 1988).

Apparently, the pattern of the *Tomicus* distribution in the study area is defined by the gradients of temperature, altitude and water availability. *Tomicus minor* occupies the areas of the cold and high altitude extreme in a fragmented distribution, and the pair *T. destruens*/*T. piniperda* occurs in the rest of the gradient, where they separate their distribution by the availability of water gradient. The fragmented distribution of *T. minor* in high altitude and cold areas suggest the hypothesis of a relict distribution in glacial refuges that could be answered by phylogeographic studies. Ritzlerow *et al.* (2004), proposed the Iberian Peninsula as a glacial refuge for *T. piniperda*. Apparently, the segregation of *T. destruens* and *T. piniperda* by water availability defines the lower limit of distribution of *T. piniperda* and the upper limit of *T. destruens*. In South-western Galicia and the Eastern Cantabric Coast, where the pair *T. destruens*/*T. piniperda* occur in sympatry, the stronger gradients of water deficit of Spain are found. We can relate these gradients with the co-occurrences of both species, so that the slope of the gradient generates the overlapping of the range of distribution of *T. destruens* and *T. piniperda*. Both species are able to attack the Mediterranean host *P. pinaster*, where they have been collected more frequently. This fact indicates that the range of distributions of both species cannot be explained only with the

distributions of Mediterranean and European species of host pines. The models indicate that there are two host pine species that can never be attacked by both *Tomicus* species, that is, *P. sylvestris* will be never attacked by *T. destruens* and *P. halepensis* will never be infested by *T. piniperda*.

How could the environmental water availability influence the distribution of a bark beetle? First of all, the distributions are related to the distribution of its host tree that is influenced by the water availability. The models only relate *T. piniperda* to the presence of *P. sylvestris* whereas relate *T. destruens* to its absence. Both species are polyphagous and attack several species of *Pinus* (*P. halepensis*, *P. pinaster*, *P. nigra*, *P. radiata* and *P. pinea* for *T. destruens*, and *P. pinaster*, *P. radiata* and *P. sylvestris* for *T. piniperda*) so that the actual influence of the host tree cannot be ascertained. Secondly, the physiology of the host tree is related to water limitations. The availability of the nutrients for the bark beetles during the shoot-feeding and the sexual-maturation depends on the osmotic pressure on the shoot. Probably, *T. piniperda* would need high pressures in the shoot, whereas *T. destruens* would mature with less osmotic pressure.

Finally, we found clear patterns of distribution range of the three *Tomicus* species in Spain. We have related these distribution ranges with the three kinds of variables used, the altitude, temperature, water availability and distribution of two host tree species, *P. sylvestris* and *P. halepensis*. The overlap of the distribution ranges are very reduced and geographically located, which allows establishing maps of theoretical distribution as a tool of forest pest management.

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