

Research Article

The Paths of the Galls: Differences in the Ecology and Distribution of Two European Oak Gall Wasps *Andricus dentimitratus* and *Andricus pictus*

Lola F. Multigner ¹, Diego Gil-Tapetado ¹, Jose Luis Nieves-Aldrey ²,
and José F. Gómez ¹

¹Universidad Complutense de Madrid, Facultad de Ciencias Biológicas, Departamento de Biodiversidad, Ecología y Evolución, José Antonio Novais 12, 28040 Madrid, Spain

²Museo Nacional de Ciencias Naturales (CSIC), Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain

Correspondence should be addressed to José F. Gómez; jofgomez@ucm.es

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Andricus dentimitratus (Rejtő, 1887) and *Andricus pictus* (Hartig, 1856) are two European gall wasps (*Hymenoptera*, *Cynipidae*) that induce galls on species of *Quercus*. The distribution and ecological niches of these species have not been studied in detail, though they are known to have a different distribution pattern in the Iberian Peninsula in Europe. To investigate this difference and its potential relationship with climate and host species distribution, we analysed the potential distribution of both species in the Iberian Peninsula using six algorithms and a consensus model based on 600 iterations for each species. We compared the models obtained for each species with the distribution of their host *Quercus* species. The results show that *A. dentimitratus* and *A. pictus* have a complementary distribution delimited by the Ebro valley, with *A. dentimitratus* occurring northeast of the valley and *A. pictus* southwest. The observed distribution patterns might be due to differences in the climatic requirements of each species or to the distribution of their host species given that *A. dentimitratus* is specific to *Q. humilis* and *Q. cerris* (except in the northeastern Iberian Peninsula) and *A. pictus*, to marcescent Mediterranean oaks (*Q. faginea* and *Q. pyrenaica*) and *Q. suber*. We propose two hypotheses to explain the nonoverlapping distribution of the two gall wasp species in the Iberian Peninsula: in the first scenario, *A. dentimitratus* arrived to the Iberian Peninsula from the eastern Palearctic by way of Europe and *A. pictus*, from the north coast of Africa; in the second, their distribution is a result of their speciation in different glacial refugia: *A. dentimitratus* in the Italian Peninsula and *A. pictus* in the Iberian Peninsula.

1. Introduction

Cynipidae (*Hymenoptera*: *Cynipoidea*), also known as gall wasps, includes about 1400 species worldwide, of which around 140 occur in the Iberian Peninsula [1, 2]. These wasps induce galls on specific host plant species. For instance, members of the tribe *Cynipini* are strictly associated with species within the family *Fagaceae* [2]. Two phylogenetically close species included in this tribe are *Andricus pictus* (Hartig, 1856) and *Andricus dentimitratus* (Rejtő, 1887), which both form galls on the acorn cups of deciduous

or marcescent oaks (*Quercus* L.), often causing the fruit to spoil [3]. Many species of the genus *Andricus* have an heteroecic life cycle in which the sexual generation is induced on oaks of the section *Cerris* (e.g., *Quercus cerris* L. or *Quercus suber* L.) and the parthenogenetic generation, on deciduous or marcescent oaks of the section *Quercus* (e.g., *Quercus pubescens* or *Quercus pyrenaica* Willd.) [4]. Although known to occur in *A. pictus* and *A. dentimitratus*, the sexual generation has not been found nor described in either species, and only galls produced by the parthenogenetic generation have been described to date. Molecular data has confirmed the

existence of sexual generations of *A. pictus* in the species complex *Andricus burgundus* (Giraud, 1859), which was previously considered a single species that develops exclusively on *Q. suber* [5]. The typical sexual gall of *A. burgundus* develops in inflorescences is 2.0–2.5 mm long, oval, with gall surface brown to yellowish in colour, thin-walled, and with a larval chamber filling the entire gall [2]. Regarding *A. dentimitratus*, only a few female specimens have been found that could be the sexual generation of this species, but neither the male nor the galls of this generation have been described [2, 6].

Despite the small size of these insects (about 5 mm in length), the galls induced by the parthenogenetic generation, their extended phenotype, are conspicuous and distinguishable (Figure 1). The galls of *A. pictus* are typically 1 to 2 cm in diameter (although the size is variable) and have three crowns that project from a cylindrical or conical body: a basal crown that surrounds the acorn bud, a wider middle crown, and a smaller apical crown that encircles an apical orifice connected to a single larval chamber (unilocular gall) located in the centre of the gall. The galls of *A. dentimitratus* (2.5–3.5 cm in diameter) have two crowns that project from a small central body enclosing the single larval chamber: an upper crown that is relatively flattened, and a larger bottom one that wraps around the acorn. Both galls are reddish or garnet in colour and have a very sticky surface; after maturation, they become brown or woody and less viscous [2, 7].

With respect to host-gall wasp specificity, *A. pictus* induces galls most frequently on *Q. pyrenaica*, but also on *Quercus faginea* Lam. and occasionally on *Quercus lusitana* Lam. and *Quercus canariensis* Willd. [2]. The species develops during the summer and matures in October with adults emerging in February of the following year [2]. In the Iberian Peninsula, the galls of *A. dentimitratus* develop on *Quercus humilis* Mill. and occasionally on *Quercus robur*. The species develops during the summer and matures at the end of the season with adults emerging in the spring of the following year [2].

The distributions of *A. pictus* and *A. dentimitratus* present a case of seemingly marked spatial complementarity. *Andricus pictus* is distributed in central, southern and western Iberia, and in North Africa. Though the species has also been cited in other areas, including northeastern Iberia and Iran, these records are likely misidentifications. By contrast, *A. dentimitratus* is distributed throughout southern Europe, in southern France, the Italian Peninsula, Sicily, Austria, and Hungary. In the Iberian Peninsula, this species is found only in Catalonia, in the northeast of this territory (Pujade-[8, 9]). Based on this distribution pattern, the Iberian System and the Ebro valley appear to constitute barriers separating the two cynipids.

The processes influencing the historical and current distribution and dispersion of these two species of *Cynipidae* are largely unknown. To address this question, we use species distribution models (SDM) to predict the distribution of *A. pictus* and *A. dentimitratus* and their areas of greatest habitat suitability and overlap. Considering these data and their ecology and biogeography, we develop and evaluate hypotheses about the evolutionary processes that have

shaped the distribution of these cynipids. Several recent studies have applied SDM to analyse *Cynipidae* in the Iberian Peninsula including *Cynipini* associated with *Quercus* L. host plants [10], the Asian chestnut gall wasp *Dryocosmus kuriphilus* (Yasumatsu, 1951; [11]) and species of *Diplolepis* on *Rosa* L. host plants [12]. Following this framework, this study is aimed at describing and analysing the distribution of *A. pictus* and *A. dentimitratus* using statistical models of habitat suitability based on bioclimatic variables. In addition, we discuss two phylogeographic hypotheses to approach the natural history of both species in the western Palearctic, thereby reducing the Wallacean and Hutchinsonian shortfalls [13] related to these cynipids.

2. Material and Methods

2.1. Data Collection. We collected all available and accessible georeferenced occurrence records of *A. pictus* and *A. dentimitratus* from the literature [1, 8, 14–31], the online repository Global Biodiversity Information Facility (GBIF, <http://www.GBIF.org>), and the citizen science platform databases Biodiversidad Virtual (<http://www.biodiversidadvirtual.org>), iNaturalist (<http://www.iNaturalist.org>) and <http://Observation.org>. In our search for occurrence records, we also considered all synonymies of both species, specifically the combinations *Andricus panteli* [31] and *Cynips panteli* (Kieffer, 1901), as synonyms of *A. pictus* (Hartig, 1856), and the combinations *Andricus viscosus* Nieves (Aldrey, 1986) and *Cynips mayri* (Kieffer, 1897) as synonyms of *A. dentimitratus* (Rejtö, 1887) [8]. Erroneous records from iNaturalist resulting from misidentifications were also corrected by validation of the georeferenced photographs. Some records from the literature mention a population or municipality, but not coordinates. In these cases, we considered the coordinates of the centroid of the locality. We obtained a total of 106 records of *A. pictus* and 210 of *A. dentimitratus*. After eliminating data with redundant coordinates, 89 records of *A. pictus* and 160 of *A. dentimitratus* were used to establish the habitable area of both species on a European scale. To model the potential distribution of both species specifically within the Iberian Peninsula and North Africa, we used only the presence points within these areas. In this case, 87 records of *A. pictus* and 103 of *A. dentimitratus* were used in the models (Supplementary Table S1). We analysed the composition of the data of both species and their accumulation over time through trend lines and linear regressions.

2.2. Variable Selection. We modelled the suitability of the territory of *A. dentimitratus* and *A. pictus* only in the Iberian Peninsula and North Africa because both species occur in these areas. Climatic data was derived from the 19 bioclimatic variables from the WorldClim database version 2.1 ([32]; <http://www.worldclim.org>) obtained at a spatial resolution of 30 seconds (1 × 1 km). Of these 19 variables, we selected those that had the most biological significance on the species of *Cynipidae* (see [12]), making sure that there was no correlation between the variables. We discarded Bio8 and Bio9 because they showed unrealistic climatic

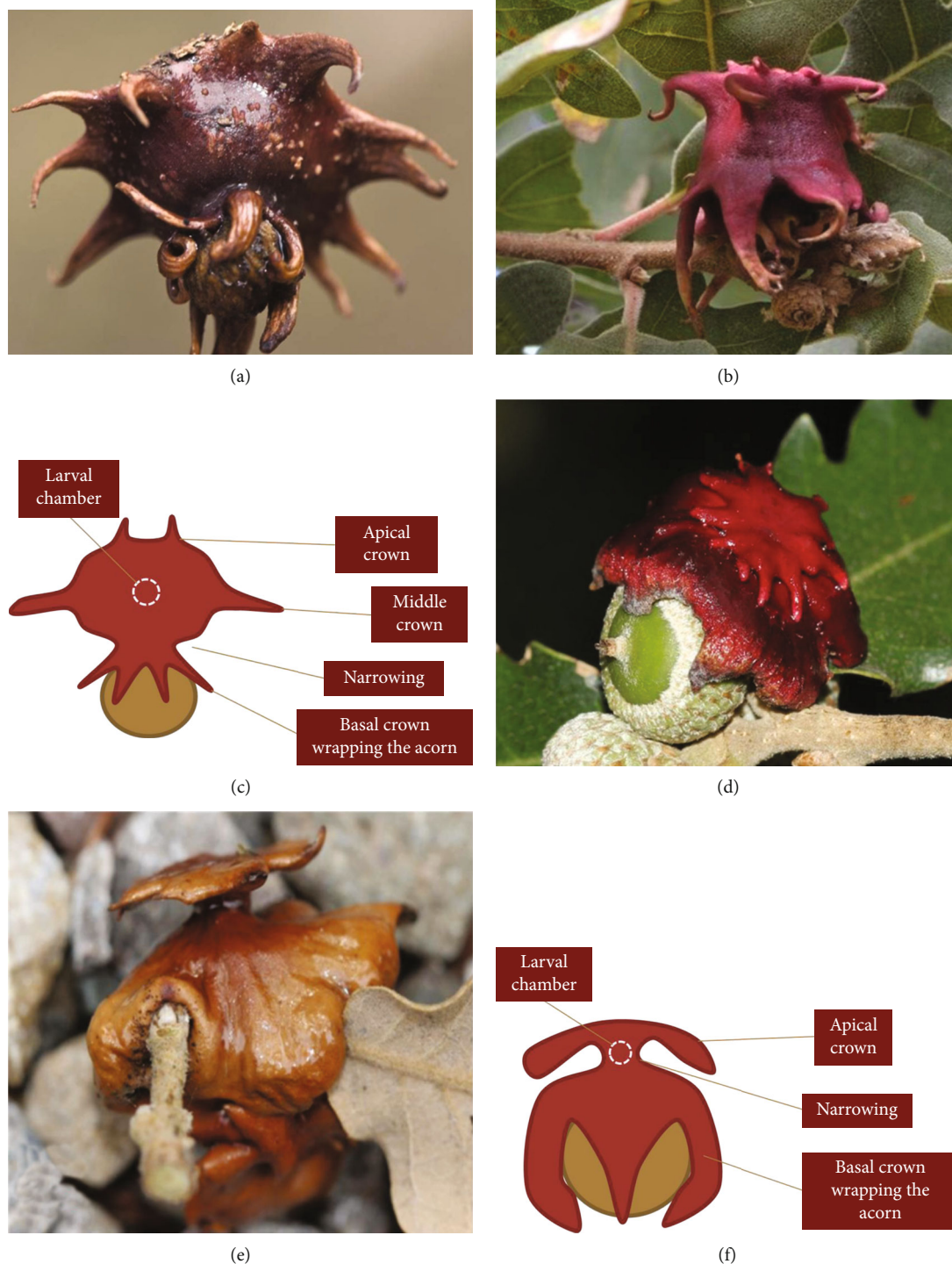


FIGURE 1: *Andricus pictus* galls on *Quercus pyrenaica* (a, b), schematic of the *A. pictus* gall (c), *Andricus dentimitratus* galls on *Quercus* sp. (d, e), and schematic of the *A. dentimitratus* gall (f).

patterns in some areas of the Iberian Peninsula, which can introduce bias in the models [33]. The other variables were analysed by a dissimilarity dendrogram using Euclidean distances (Supplementary Material, Figure S1), and we selected those above the threshold of 0.3 (i.e., those that showed less than 70% correlation). Within each cluster below the

threshold, we chose the most biologically meaningful variable according to the ecology of the species (e.g., life cycle, phenology, and gall biology). When the meaning was not clear, we selected the most derived variables, i.e., those that referred to a specific period, as they were more informative than the remaining variables. Finally, for the

TABLE 1: Data on the bioclimatic variables and altitude at the presence points of each species: mean, standard deviation (SD), and maximum (Max) and minimum (Min) values.

	<i>A. dentimitratus</i>				<i>A. pictus</i>			
	Mean	SD	Max	Min	Mean	SD	Max	Min
Bio1 = annual mean temperature	12.01	2.09	16.19	4.75	12.65	2.40	17.76	7.56
Bio2 = mean diurnal range (mean of monthly (max temp–min temp))	9.23	0.94	11.03	6.11	10.35	1.49	14.38	6.55
Bio3 = isothermality (Bio2/Bio7) ($\times 100$)	35.65	2.43	41.55	26.76	37.93	2.81	44.28	32.20
Bio4 = temperature seasonality (standard deviation $\times 100$)	607.57	50.35	779.55	461.31	609.02	81.89	710.03	327.20
Bio5 = max temperature of warmest month	26.34	2.10	30.82	20.04	28.48	2.39	34.12	22.70
Bio6 = min temperature of coldest month	0.47	2.35	6.30	-6.20	1.16	3.00	8.28	-3.80
Bio7 = temperature annual range (Bio5-Bio6)	25.87	1.73	29.68	18.85	27.32	3.42	33.29	15.75
Bio8 = mean temperature of wettest quarter	12.61	3.50	19.60	1.93	8.23	2.44	13.89	1.98
Bio9 = mean temperature of driest quarter	12.98	8.26	23.73	0.18	20.02	3.58	24.81	3.30
Bio10 = mean temperature of warmest quarter	19.79	2.01	23.73	12.87	20.62	1.92	25.01	15.90
Bio11 = mean temperature of coldest quarter	5.09	2.36	10.26	-1.99	5.83	2.96	12.66	0.94
Bio12 = annual precipitation	771.43	156.28	1425.00	255.00	644.52	222.63	1388.00	380.00
Bio13 = precipitation of wettest month	95.77	21.55	189.00	31.00	90.34	38.56	212.00	44.00
Bio14 = precipitation of driest month	33.47	12.56	66.00	8.00	12.87	6.11	29.00	1.00
Bio15 = precipitation seasonality (coefficient of variation)	29.08	8.37	59.07	13.60	46.47	12.21	75.66	30.31
Bio16 = precipitation of wettest quarter	254.79	53.84	506.00	84.00	251.56	107.82	599.00	124.00
Bio17 = precipitation of driest quarter	127.96	40.41	236.00	34.00	57.51	19.64	97.00	14.00
Bio18 = precipitation of warmest quarter	165.48	52.61	251.00	43.00	62.87	21.37	130.00	22.00
Bio19 = precipitation of coldest quarter	180.26	60.40	387.00	63.00	230.21	117.15	599.00	78.00
Altitude	568.81	369.87	1955.00	4.00	832.24	387.30	1717.00	47.00

final variable selection, we applied a variance inflation factor (VIF) [34] and only chose variables with a value lower than 5. The final variables selected for the analysis were Bio3, Bio4, Bio11, Bio16, Bio17, and Bio18 for *A. dentimitratus* and Bio2, Bio3, Bio10, Bio16, and Bio7 for *A. pictus* (Table 1).

2.3. Potential Distribution Models and Phylogeographic Hypotheses. The potential distribution of each species was estimated using species distribution models (SDMs) based on suitability and climatic variables, following the methodology described by Polidori et al. [35] and Gómez true [36]. We used the following algorithms: general linear model (GLM; [37]), general additive model (GAM; [38]), artificial neural network (ANN; [39]), classification tree model (CTA; [40]), random forest (RF; [41]), and maximum entropy (MaxEnt; [42]).

To calculate pseudoabsence and background points, we first generated an environmental coverage model. This model assumes that a species can only be present in the areas where all the climatic variables are within the species tolerance range, estimated as between the maximum and the minimum value of each variable founded at the presence points of the species [11, 43]. Additionally, to assess host dependence of *Andricus* on species of *Quercus*, we combined the maps of the habitable area derived from the environmental coverage model with chorological distribution maps

of *Q. humilis* for *A. dentimitratus*, and *Q. faginea* and *Q. pyrenaica* for *A. pictus* and examined their areas of overlap. Other host tree species were not considered due to the low spatial relationship between species occurrence and host distribution in the study area. For instance, although *Q. robur* is common and abundant in northern Iberia, *A. dentimitratus* is absent in this area (see Figure 2). The chorological maps were obtained from the European Atlas of Forest Tree Species published by the European Commission in March 2016 [44]. The overlapping areas were considered the species' habitable area. Background points were generated in the regions within the habitable area, whereas pseudoabsence points were generated in the areas where the variables were outside the tolerance range and/or where the *Quercus* species were absent.

We split the presence and background data into two data sets, and we ran the models with 75% of the data in order to evaluate the final models using an external AUC (Area Under the receiver operating characteristic (ROC) Curve) evaluation procedure [45] with the remaining 25% of the data. The AUC was used to assess the discrimination capacity of the models: 0.5 indicates no discrimination, 0.6–0.8 indicates acceptable discrimination, and 0.8–0.9 indicates high discrimination [46]. We performed 100 replicates for each of the six algorithms (for a total of 600 individual models) and obtained a consensus model using the average of each individual model that passed the internal AUC evaluation (>0.7).

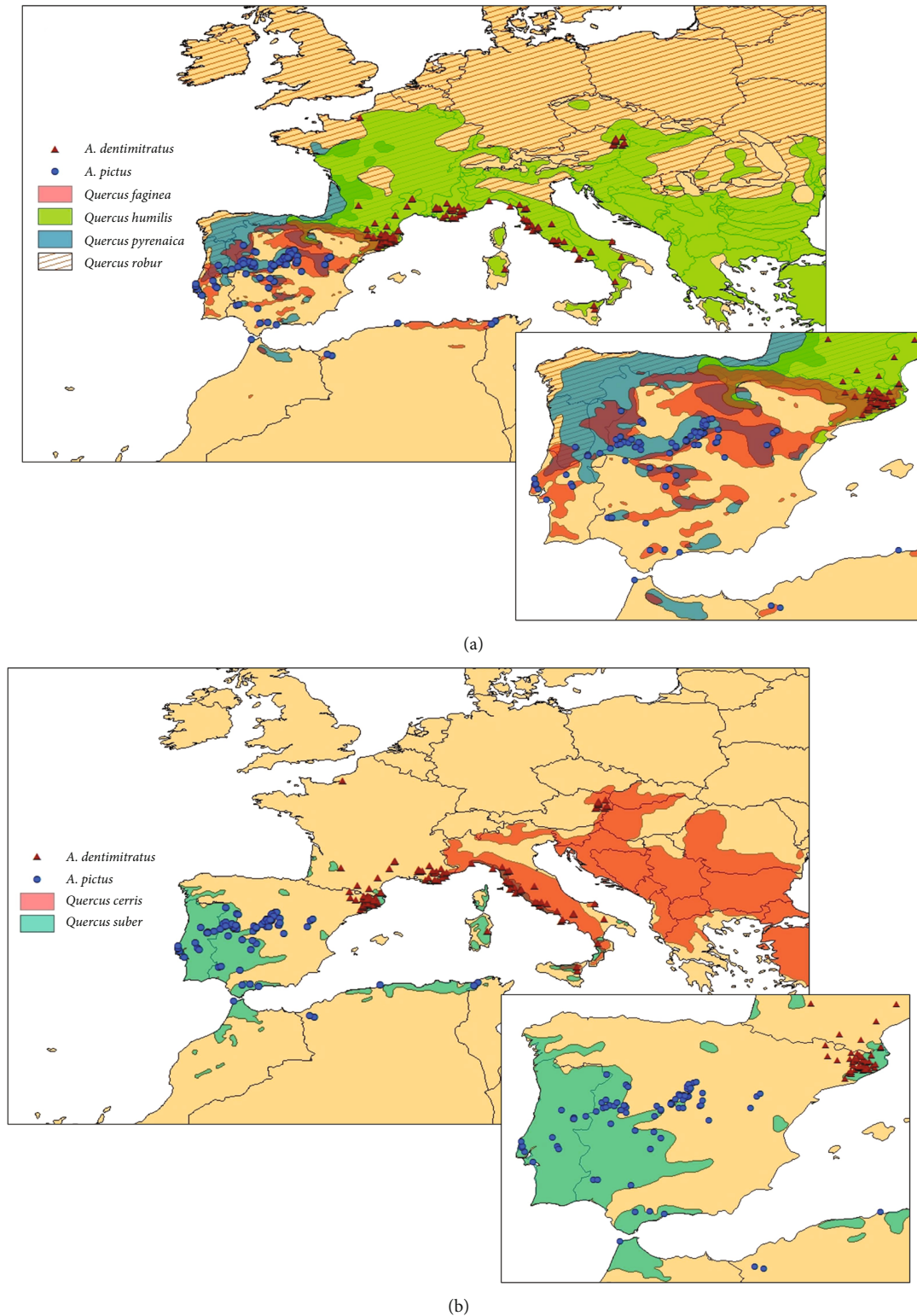


FIGURE 2: Occurrence data of *A. dentimitratus* and *A. pictus* across Europe and in the Iberian Peninsula, and the distribution of host tree species of the parthenogenetic (a) and sexual (b) generations.

We verified the relationship between the presence of each species and the values of the variable that most influences the distribution of the species. For this purpose, we used an ANOVA to compare the values of the most important variables at the presence and pseudoabsence points.

Finally, to discuss the phylogenetic context inferred from the SDMs, we made a series of maps showing the distribution of the host species of *Quercus* on which the analysed species depend: *Q. pyrenaica*, *Q. faginea*, *Q. humilis*, *Q. suber*, and *Q. cerris*.

The variable selection process, SDMs, and their evaluation and statistical analyses were all performed in R 4.0.5 [47] using RStudio 1.4.1106 [48] and the packages HH version 3.1-43 [49], biomod2 version 3.1-64 [50], raster version 2.0-12 [51], and ggplot2 [52]. The maps, environmental coverage models and background, and pseudoabsence points were generated in ArcGIS desktop 10.6.1 [53].

3. Results

3.1. Analyses of the Occurrence Data. The occurrence data for *A. dentimitratus* were obtained mostly from georeferenced databases associated with citizen science platforms, whereas those for *A. pictus* were mostly from bibliographic sources (Figure 3(a)). The data on *A. dentimitratus* are more recent than those on *A. pictus* (mean = 2008.56, SD = 13.75 vs. mean = 1984.04, SD = 32.49). For *A. dentimitratus*, the data follows two trends: one before 2008 ($R^2 = 0.8294$) indicating the accumulation of about two new records each year and another one ($R^2 = 0.8367$) indicating the accumulation of around 10 records each year (Figure 3(b)). This difference is due to the emergence of virtual citizen science platforms at the end of the 2000s, which have facilitated the acquisition of new occurrence records. According to the exponential trend of accumulated data for *A. pictus* ($R^2 = 0.8903$, calculated using data from only the last 50 years, to avoid a distortion that would be caused by the lack of records from 1912 to 1975), around two new occurrences were registered each year.

The records for *A. dentimitratus* were from throughout Europe, particularly Austria, France, Italy (including Sicily and Sardinia), and northeastern Spain (Catalonia) (Figure 2). The species has been cited in more countries; however, these records were not georeferenced and thus excluded from this study. The occurrence data for *A. pictus* were mainly restricted to Spain (except the northeast area), Portugal, and North Africa (Morocco, Algeria, and Tunisia).

3.2. SDMs of *A. dentimitratus* and *A. pictus* and Overlapping Areas. The consensus models generated for *A. dentimitratus* and *A. pictus* (Figure 4) show a complementary distribution in the Iberian Peninsula. While *A. dentimitratus* is restricted to the region north and northwest of the Ebro valley, and also in southern France, *A. pictus* is distributed across the Iberian, Central and Baetic systems, and the central and coastal region of Portugal and North Africa, especially in mountainous regions. The AUC values of the external evaluation of the consensus models were greater than 0.9 (0.997 for *A. dentimitratus* and 0.92 for *A. pictus*), indicating their high capacity to discriminate between presences and absences.

Analysis of the bioclimatic variables showed significant differences between the habitable areas of the two species (Table 1). The most important variables in the model for *A. dentimitratus* were Bio18, precipitation of warmest quarter (mean contribution = 61.28%) and Bio17, precipitation of driest quarter (mean contribution = 24.55%); in the model for *A. pictus*, Bio10, mean temperature of warmest quarter (mean contribution = 56.67%) and Bio 17, precipitation of

driest quarter (mean contribution = 37.78%) (Table 2). We also observed significant differences in these variables between high and low suitability areas (Figure 5(a)–5(c)). According to the comparison of Bio17 as a relevant variable in the models of both species, *A. pictus* prefers areas with low precipitation in the driest quarter (Figure 5(d)).

With the obtained models, we observed spatial overlap between the potential distributions of the gall wasp species and that of the *Quercus* trees upon which the parthenogenetic generation develops (Figure 2(a)). Specifically, the high suitability areas predicted for *A. dentimitratus* overlap with the distribution of *Q. humilis*, and those areas for *A. pictus*, with that of *Q. faginea* or *Q. pyrenaica*.

4. Discussion

4.1. Species Distribution Models. The most influential bioclimatic variables in the SDM for *A. dentimitratus* were precipitation of the warmest quarter (Bio18) and precipitation of the driest quarter (Bio17). This species' occurrences were associated with high values of the variables ($p < 0.0001$, see Figures 5(a), 5(b) and 5(d)), indicating that it prefers climates with less summer drought. The oak wood forests of *Q. humilis* in Catalonia (northeastern Spain) where *A. dentimitratus* is highly abundant are characterised as having a climate intermediate between Mediterranean and Atlantic, with characteristics of each climate type. For *A. pictus*, the most important variable was the mean temperature of the warmest quarter (Bio10), indicating the species prefers milder temperatures ($p < 0.0001$, see Figure 5(c)). This finding is consistent with its presence at higher altitudes and with the climate preference of its host oaks: a mountain climate with strong winter frosts and high summer temperatures (supra-Mediterranean areas) [54].

The AUC of the *A. dentimitratus* model was only slightly higher than that of the *A. pictus* one (0.997 vs 0.92, see Figure 4), indicating the two models are qualitatively similar despite important differences between the characteristics of the data used for each. For instance, the occurrences of *A. dentimitratus* were more numerous and recent than those of *A. pictus* because they were mostly from virtual citizen science platforms (see Figure 3(a)), which have become enormously useful data sources for species distribution modelling studies (e.g., [12, 35, 55]). This difference is most evident in the data accumulation trend line observed for *A. dentimitratus* (see Figure 3(b)), which was very similar to that of *A. pictus* up until 2010 when the amount of data started to increase dramatically, coinciding with the growth of these platforms during the last decade. Considering the wider distribution area of *A. pictus*, one would expect that its records would also greatly increase on these platforms. A possible explanation for the higher abundance of *A. dentimitratus* records in the citizen science databases may be that the number of active users is higher in the Iberian northeast compared with the other regions. Moreover, *A. pictus* has been generally less well studied than *A. dentimitratus*, particularly in recent decades with most studies of the species having been published between 1970 and 1990, mainly by Nieves-Aldrey (e.g., [1, 17–24]). The occurrence data of *A.*

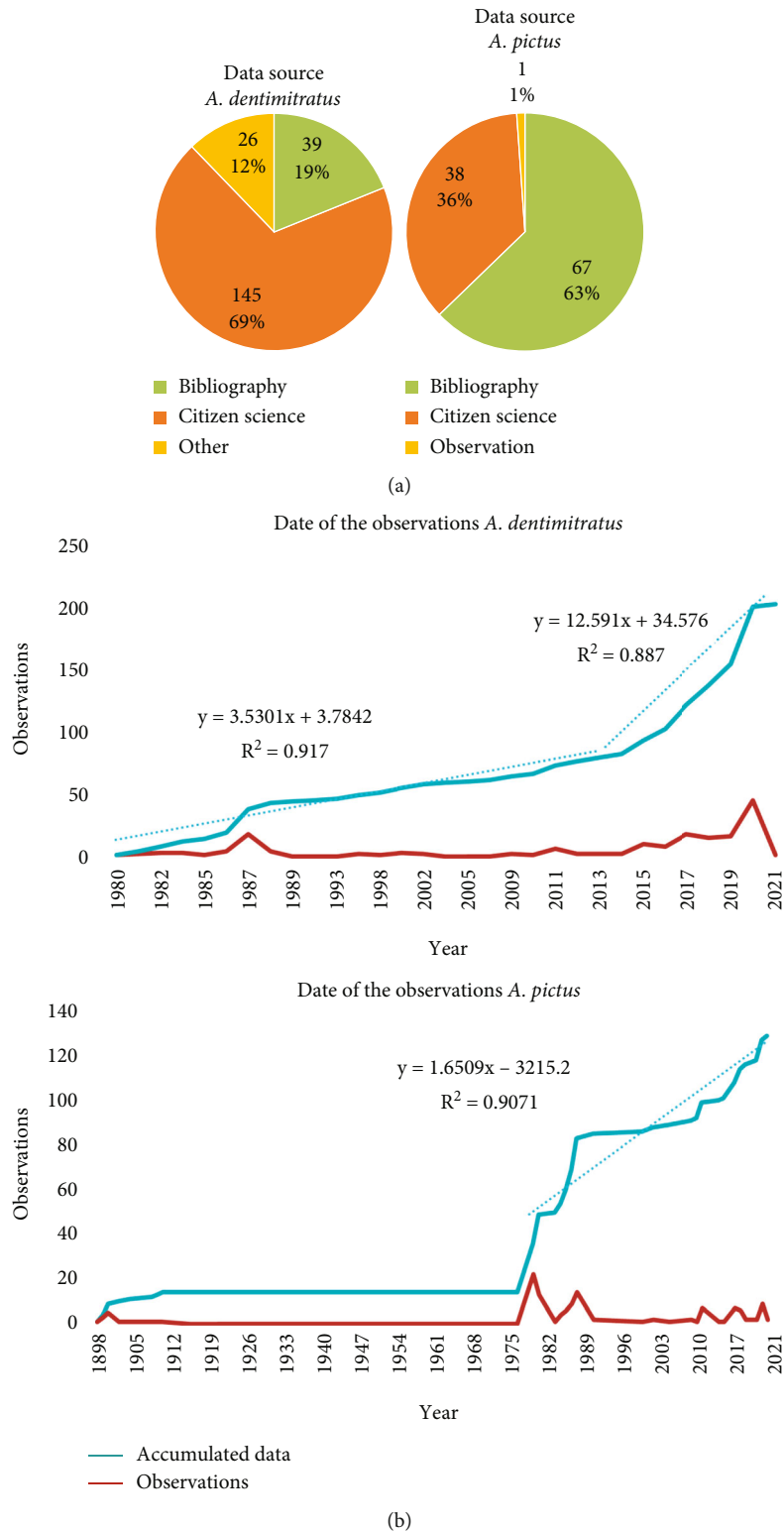


FIGURE 3: Georeferenced occurrence records according to source (a) and date (b). In (b), both yearly observations and accumulated data and associated trend lines are shown.

pictus were so scarce in both the citizen science databases and the literature that we had to rely on older records, including some observations from the early 20th century [31], that were restricted to specific territories. Data older than 50 years may be uninformative, or worse, misleading,

with respect to the bioclimatic variables as climatic conditions may have changed significantly since that time. For instance, we might have inferred the presence of the species in places where it may no longer be able to inhabit. Nevertheless, differences between the occurrence data used for

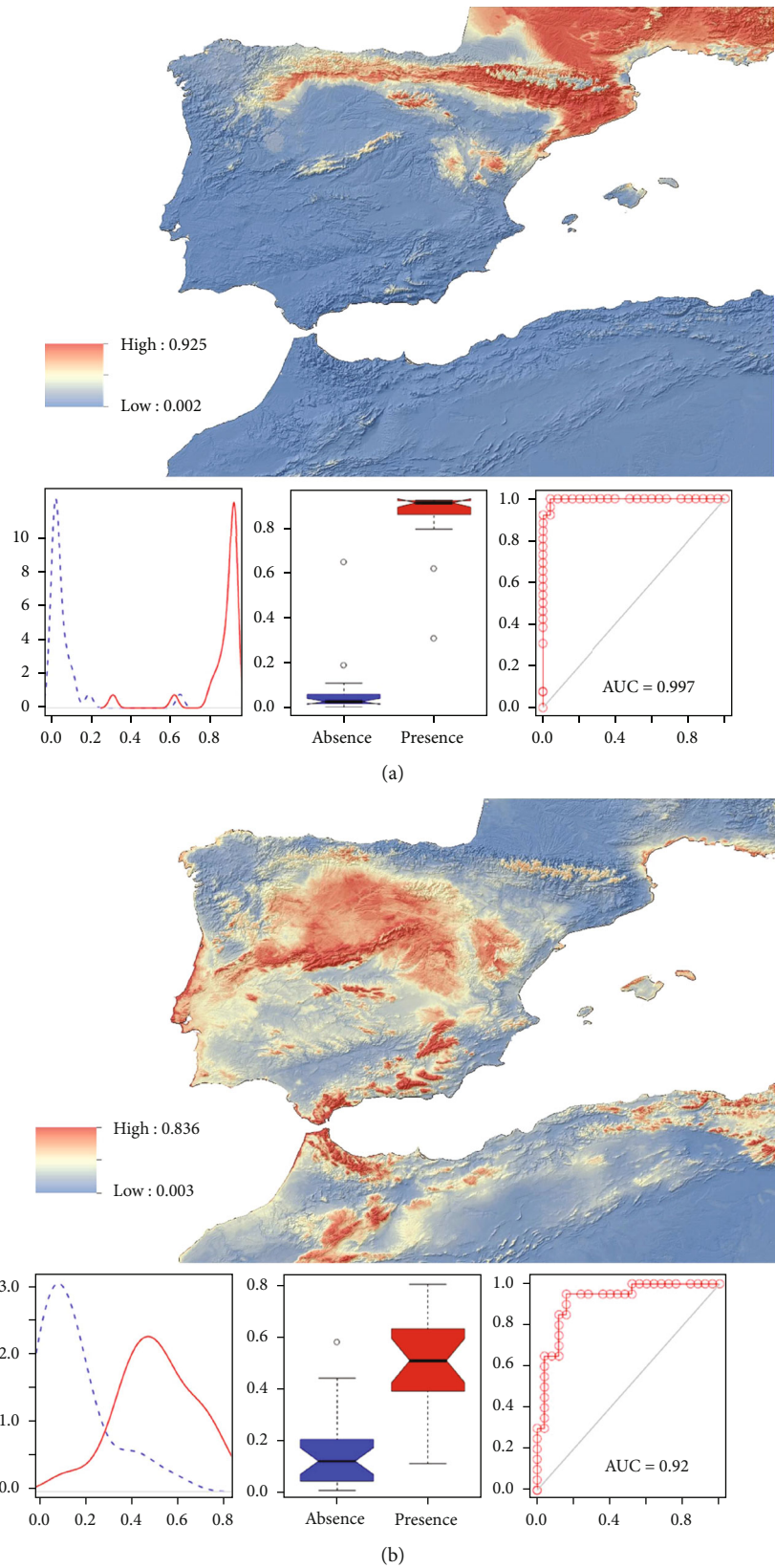


FIGURE 4: Habitat suitability models for *A. dentimitratus* (a) and *A. pictus* (b). Under each map: a graph showing the number of occurrences (red line) and pseudoabsences (blue-dashed line) according to the habitat suitability predicted by the consensus model (left), a boxplot of presence (red) and pseudoabsence (blue) according to the habitat suitability (centre), and a representation of the AUC of the consensus model (right).

TABLE 2: Contribution of each of the selected variables to the final distribution models.

	<i>A. dentimitratus</i>						<i>A. pictus</i>				
	Bio3	Bio4	Bio11	Bio16	Bio17	Bio18	Bio2	Bio3	Bio10	Bio16	Bio17
GLM	0.85	0.14	0.33	5.90	0.00	97.77	0.22	15.93	98.55	0.11	35.30
ANN	2.19	10.29	2.09	14.93	21.86	70.51	6.46	12.17	20.11	58.08	71.33
CTA	0.00	20.83	0.00	4.47	69.94	15.16	0.48	5.71	64.17	9.72	32.56
RF	0.70	3.97	1.12	5.40	12.48	16.15	11.91	20.87	24.43	10.66	20.47
MAXENT	4.19	8.89	9.82	12.18	21.62	81.43	11.11	27.70	42.31	10.10	28.76
GAM	18.70	9.10	12.45	33.49	21.42	86.67	5.13	15.24	72.48	22.73	38.27
Mean	4.44	8.87	4.30	12.73	24.56	61.28	5.89	16.27	53.67	18.57	37.78

Values are represented as percentages. Variable abbreviations: Bio2: mean diurnal range; Bio3: isothermality; Bio4: temperature seasonality; Bio10: mean temperature of warmest quarter; Bio11: mean temperature of coldest quarter; Bio16: precipitation of wettest quarter; Bio17: precipitation of driest quarter; and Bio 18: precipitation of warmest quarter.

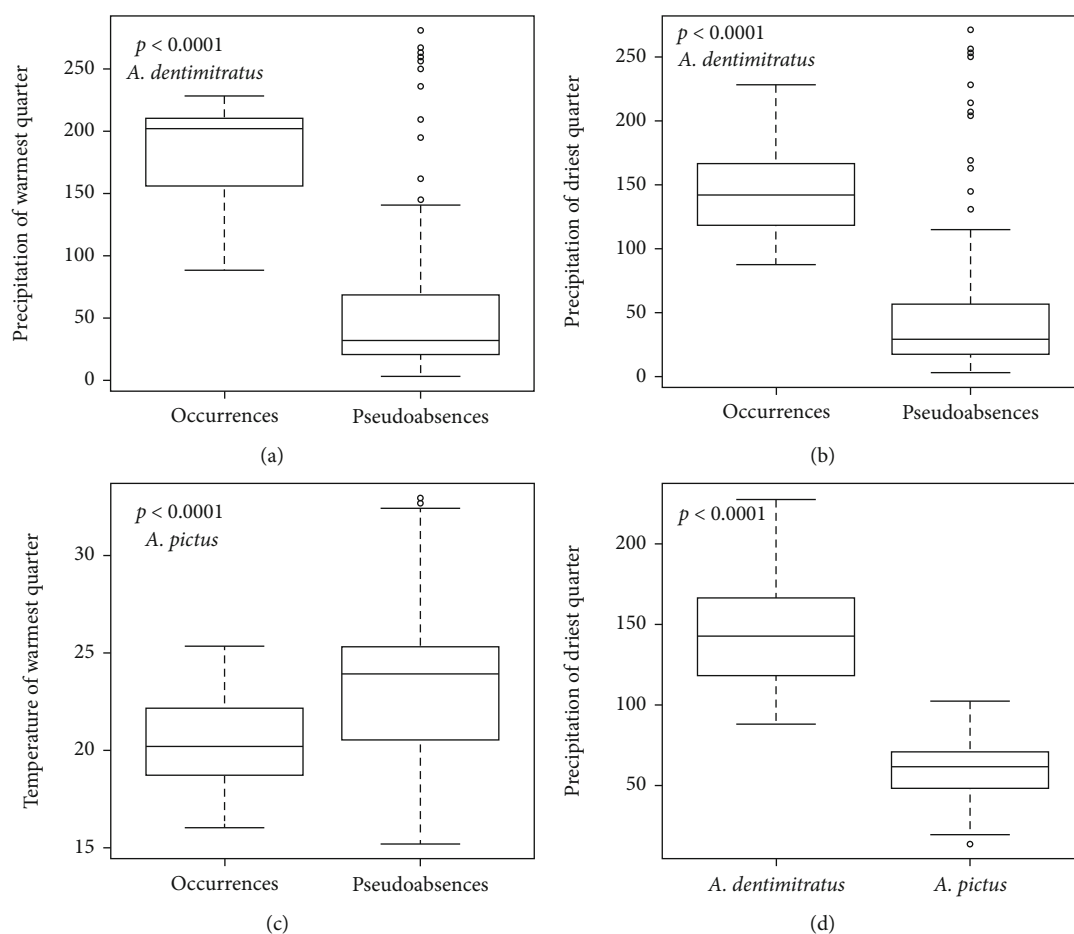


FIGURE 5: Differences in the values of the most important variables for the two species according to the degree of habitat suitability: high (occurrences) and low (pseudoabsences). (a) Bio18 (precipitation of the warmest quarter), *A. dentimitratus*; (b) Bio17 (precipitation of the driest quarter), *A. dentimitratus*; (c) Bio10 (mean temperature of the warmest quarter), *A. pictus*; (d) difference in the values of Bio17 (precipitation of the driest quarter) between the presence points of *A. dentimitratus* and *A. pictus*.

each model did not seem to affect the quality of the model, as both were equally robust according to the AUC.

Previous studies of *A. dentimitratus* have suggested that its galls can be induced on *Q. robur* [2, 8, 25]; however, our results support the idea that the species develops its parthenogenetic generation exclusively on *Q. humilis*, not only in

the Iberian Peninsula but throughout the rest of Europe. According to our findings, the species is absent in regions of the Cantabrian coast and the Pyrenean foothills where climatic conditions are favourable for the species and where *Q. robur* is abundant, (see Figure 2(a)) but *Q. humilis* is rarely found [56, 57]. All records of the species on *Q. robur* are

from a region in Catalonia where this tree is scarce and where hybridizations of *Q. humilis* are extraordinarily frequent [54], making its identification difficult. At present, we cannot validate the accuracy of these observations to determine if these hosts really occur in this area, indicating a potential host–gall wasp interaction, or if these records represent misidentifications. New surveys of the region, combined with accurate identification (e.g., molecular-based analyses), would be needed to address this open question.

Interestingly, the host specificity of *A. pictus* appears to be much wider than that of *A. dentimitratus*. Besides *Q. faginea* and *Q. pyrenaica*, *A. pictus* can develop on other marcescent oaks, including *Q. lusitanica* and *Q. canariensis* ([2]; unpublished observations). These observations are scarce and could be similar to the case of *A. dentimitratus* and *Q. robur*. However, *Q. lusitanica* and *Q. canariensis* are taxonomically complex species, and their distributions have not been completely or accurately described, therefore, we cannot discard a possible relationship between these oak species and *A. pictus*. Regardless, our scarce records of *A. pictus* in the southern Iberian Peninsula coincide with the distribution of *Q. faginea*.

The distribution maps of *Q. faginea*, *Q. pyrenaica*, and *Q. humilis* show the presence of these species along the coast of the Cantabrian Sea, though at low abundances and with a very scattered distribution pattern (*Spanish Forestry Map*, [58]). This pattern may explain the absence of records of *A. dentimitratus* and *A. pictus* in the northern and north-western parts of the Iberian Peninsula to date. In this region, Atlantic deciduous oaks dominate (*Q. robur* and, less frequently, *Q. petraea*), and when a rare marcescent oak is sighted, it is often found in isolation. The scarcity of oaks in the central area of Castilla y León in Spain [56] might also explain the lack of occurrences of the two gall wasps in this region.

A limitation of this study is the lack of knowledge about the full life cycle of both *A. dentimitratus* and *A. pictus*, which could distort some of the results and conclusions. Since the bisexual (sexual) generations of these gall wasps have not yet been described, it is possible that the variables selected for modelling do not adequately reflect the factors most influential on their distribution as half of their life cycle is not considered. Of the two *Quercus* species on which bisexual generations of *Andricus* develop, only *Q. suber* is found in the Iberian Peninsula, as well as in North Africa, Corsica, Sardinia, Sicily, and the western coast of Italy, where it coexists with the other host species, *Q. cerris* (see Figure 2(b)). In the eastern part of Europe, only *Q. cerris* is found. The distributions of these *Quercus* species and the cynipids suggest that the bisexual generations of *A. dentimitratus* and *A. pictus* develop on, respectively, *Q. cerris* and *Q. suber* (as previously proposed by [5]). Populations of *A. dentimitratus* in the Catalan region would represent an exception as their bisexual generation can develop on only *Q. suber* as *Q. cerris* is not found in this region (see Figures 2(b) and 4). Due to this host difference, future research should focus on investigating the extent to which Catalan populations of *A. dentimitratus* may differ from

other European ones. Given the cooccurrence of *Q. suber* and *Q. cerris* in Italy (see Figure 2), the Italian populations of *A. dentimitratus* should also be studied in greater detail to confirm on which species their bisexual generations develop.

In summary, our results indicate that the distribution of both species is conditioned more by the distribution of host trees than by climatic variables. Species of the tribe *Cynipini* frequently display host specificity, developing exclusively on a specific section of the *Quercus* genus, which is known to be an important factor in their evolution and speciation [59]. Furthermore, the models obtained in this study confirm that the two gall wasp species show a complementary distribution, with the Ebro valley acting as a border that they do not cross due to the absence of their specific host plants. The valley's unfavourable climatic conditions (very dry and continental) [60] also likely limit the distribution of both gall wasps. Finally, as previously mentioned, the predicted presence of these species along the Cantabrian coast is not plausible due to the absence of marcescent oaks in this area.

4.2. Phylogeographic Hypotheses. We propose two hypotheses to explain the observed vicariant distribution of the two studied gall wasps from an evolutionary perspective (Figure 6).

- (1) Arrival of the lineage of *A. pictus* to the Iberian Peninsula through Africa and that of *A. dentimitratus*, through Europe

The genus *Quercus* appeared during the Pliocene, and the evolutionary radiation of the *Cynipidae* occurred later, around 20 million years ago, during the Oligocene–Miocene transition, followed by their dispersion throughout eastern (Asia) and western (Europe) Eurasia [61]. The fossil record suggests that *Quercus* could have been continuously present along the southern coast of the Mediterranean Sea in the past, when the climate of this area was wetter [62]. Thus, it is possible that the *A. pictus* lineage arrived in the Iberian Peninsula via the southern Mediterranean coast and the Strait of Gibraltar from North Africa (Figure 6(a)). Under this scenario, as the climate became drier during the Oligocene and Miocene, the distribution area of *A. pictus* became restricted to the mountainous areas west of the Mediterranean Sea, specifically in the Atlas Mountains and the mountain ranges in the central and southern Iberian Peninsula. In the case of the *A. dentimitratus* lineage, it would have arrived to the Iberian Peninsula through Europe. Subsequent to their arrival, the Ebro valley acted as a border for both species due to the absence of their respective oak hosts, thereby halting their expansion to other regions. As a result, the *A. pictus* lineage adapted to the Mediterranean marcescent oaks *Q. faginea* and *Q. pyrenaica* and to *Q. suber*, while the *A. dentimitratus* lineage adapted to oaks found in intermediate Mediterranean–Atlantic climates, namely, *Q. humilis* and Central European *Q. cerris*. Following this hypothesis, the host specificity of the bisexual generations of *A. dentimitratus* on *Q. suber* in Catalonia (northeastern Iberia) would represent a secondary adaptation

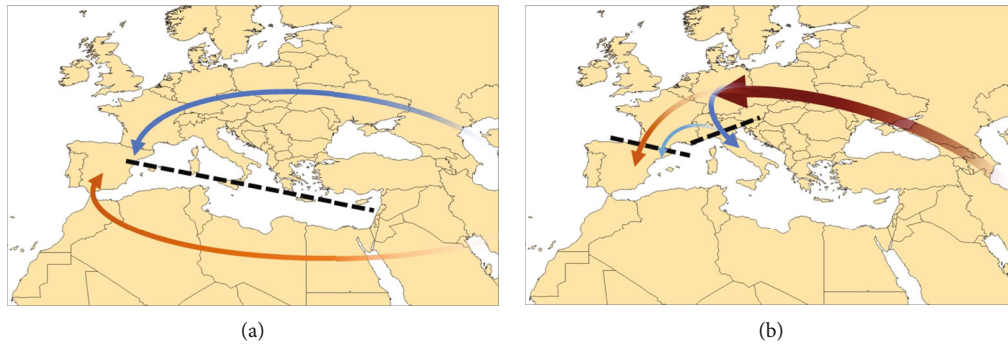


FIGURE 6: Phylogeographic hypotheses on the speciation and distribution of *A. dentimitratus* (blue arrow) and *A. pictus* (orange arrow). Black discontinuous lines indicate the putative geographic barriers separating the two lineages. (a) Arrival to the Iberian Peninsula through Europe (*A. dentimitratus*) or through North Africa (*A. pictus*). (b) Speciation in glacial refugia in the Italian Peninsula (*A. dentimitratus*) or the Iberian Peninsula (*A. pictus*). The red arrow represents the lineage containing *A. dentimitratus* and *A. pictus*. The small light blue arrow indicates the posterior colonisation of the lineage of *A. dentimitratus* to the northeast of the Iberian Peninsula.

(2) Speciation in glacial refugia

In the second hypothesis, the lineage leading to both *A. dentimitratus* and *A. pictus* expanded through Europe during the Oligocene. Subsequently, Quaternary glaciations that restricted many European lineages to lower latitudes [63, 64] also affected *Cynipini* populations, which, together with their plant hosts, became confined to different peninsulas in southern Europe and in areas of North Africa and eastern Europe [3]. The two lineages then arose by speciation while in different glacial refugia during the Pleistocene, with the *A. pictus* lineage staying in the Iberian Peninsula and associating with *Q. faginea*, *Q. pyrenaica*, and *Q. suber*, and the *A. dentimitratus* lineage staying in the Italian Peninsula and associating with *Q. humilis*, *Q. cerris*, and *Q. suber* (Figure 6(b)). After the glaciations, the lineages were then able to recolonize other areas, expanding towards their current distributions. *Andricus dentimitratus* could have expanded towards the west to reach the Iberian Peninsula (the Catalan region) through the eastern Pyrenees. In the case of *A. pictus*, the lineage could not expand north of the Ebro valley, restricting its distribution to the more southern regions of the Iberian Peninsula, though it was still able to expand towards North Africa. Expansion of their respective host plants would have accompanied those of the gall wasp lineages

At the time of writing this article, a complete phylogenetic framework and an accurate estimate of the time of divergence between these two lineages are lacking. In the article of Stone et al. [61], the divergence of the clade which contains *A. pictus* and *A. dentimitratus* is dated to 5.25 Ma ago, coinciding with the Miocene-Pliocene boundary (end of the Messinian). Following this, the diversification between these two species should have been later than this time. Before the Miocene-Pliocene boundary, the Mediterranean Sea dried up and flooded intermittently [65], supporting the hypothesis of the arrival of the lineage of *A. pictus* from the south to the Iberian Peninsula and their presence in North Africa. In this period (also known as the Zanclean flood), the last terrestrial isolation between Europe and Africa took place [66], determining the current scenario with

A. pictus on both sides of the Mediterranean Sea. Also, Rokas et al. [3] discussed about *Andricus quercustozae* (Bosc, 1792), a species phylogenetically close to *A. pictus* and *A. dentimitratus*, and the importance of glaciations during the Quaternary which determined the formation of glacial refugia in the southern European peninsulas. This coincides with our second proposed hypothesis and the isolation of each lineage in different geographical areas.

As mentioned above, the bisexual generation of *A. dentimitratus* appears to develop exclusively on *Q. cerris*, with the notable exception of populations in Catalonia (where *Q. cerris* is absent), which appear to develop on *Q. suber*. The glacial refugium hypothesis could explain why *A. dentimitratus* develops on both host species, as they were both in the Italian Peninsula. However, we cannot dismiss the possibility that the Catalan population represents a different biological entity or species, as has been observed in the case of *Andricus kollari* (Hartig, 1843) and *Andricus hispanicus* (Hartig, 1856). These two heteroecic species were previously considered a single one (*A. kollari*) and have the same host oak species difference as the populations of *A. dentimitratus* from both sides of the Pyrenees. Currently, they are considered as sister species that show differences in their distribution and host species: *A. kollari* develops on *Q. cerris* and *A. hispanicus* develops on *Q. suber* [67]. Similar to our scenario, separation and speciation in different glacial refugia followed by expansion has been proposed to explain host plant differences between *A. kollari* and *A. hispanicus* [68].

Phylogeographic studies of these species, greater knowledge on gall wasp–host specificity and a comprehensive study of the historical distributions of the host plants are needed to determine which of our two hypotheses is most plausible and for a deeper discussion of their relationship with the niche models. Although climatic niche data is relevant, knowing the actual association between specific gall wasps and host plants is indispensable, as these hosts are the limiting resource of these resource-dependent species. In conclusion, the SDMs presented in this study not only improve our biogeographic knowledge of *A. pictus* and *A. dentimitratus* by estimating high suitability areas in which

to search for these *Cynipidae* species but also the study of gall wasp and parasitoid communities.

Data Availability

All data used to perform the analyses in this study are included in the article or in the supplementary materials.

Conflicts of Interest

The authors declare they have no competing interests.

Authors' Contributions

DGT and JFG conceived and designed the work. LFM and DGT performed the experiments and analysed the data. LFM, DGT, and JLNA contributed the materials/analysis tools. LFM, DGT, JFG, and JLNA wrote the paper.

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Supplementary Materials

Supplementary 1. Figure S1: dissimilarity dendrograms obtained from the variable selection cluster. The red line represents the chosen threshold (0.3, correlation >70%). The variables selected for the models for *A. dentimitratus* (A) and the *A. pictus* (B) are shown in green; those discarded after applying the VIF are shown in red.

Supplementary 2. Table S1: records of *A. dentimitratus* and *A. pictus* used in the models, with its coordinates, year of observation, and source.

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