Ecological niche modelling of species of the rose gall wasp *Diplolepis* (Hymenoptera: Cynipidae) on the Iberian Peninsula

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Abstract. *Diplolepis* (Hymenoptera: Cynipidae) are gall wasps that induce conspicuous galls on *Rosa* spp. (Rosaceae). These species are distributed globally and in Europe some are especially common and are founder organisms of biological communities composed of different insects. However, the ecological niches of these species have not been studied in detail. We modelled the potential distributions of these species using the locations of the galls of the four most abundant species of *Diplolepis* on the Iberian Peninsula (*Diplolepis mayri*, *Diplolepis rosae*, *Diplolepis eglanteriae* and *Diplolepis nervosa*, the galls of latter two are indistinguishable) using four different algorithms and identified the resulting consensus for the species. We compared the potential distributions of these species, considering their spatial complementarity and the distributions of their host plants. We found that *D. mayri* and *D. eglanteriae/nervosa* have complementary distributions on the Iberian Peninsula. The former species is found in the Mediterranean region, while *D. eglanteriae* and *D. nervosa* are distributed mainly in the Eurosiberian region. *Diplolepis rosae* has the widest distribution on the Iberian Peninsula. Our models constitute the first effort to identify suitable areas for species of *Diplolepis* species on the Iberian Peninsula and could be useful for understanding the evolutionary ecology of these species throughout their distribution in the western Palearctic.

INTRODUCTION

The Cynipidae family comprises approximately 1,500 species worldwide, mainly distributed in temperate areas in the Northern Hemisphere (Ronquist, 1999; Csoka et al., 2005; Melika, 2006). On the Iberian Peninsula and Balearic Islands there are 29 genera and 147 species of Cynipidae (Nieves-Aldrey, 2001a; Nieves-Aldrey et al., 2006, 2012, unpubl.). Most of the cynipids (86%) are associated with oak trees (Fagaceae), 7% induce galls on the genus *Rosa* L., and the remaining 7% are associated with different camephytic and herbaceous plants of the families Rosaceae, Asteraceae, Lamiaceae, Papaveraceae, Valerianaceae and Aceraceae (Folliot, 1964; Shorthouse, 1973; Nieves-Aldrey, 1981, 2001a). The Diplolepidini tribe is strictly associated with Rosaceae and includes two genera, *Diplolepis* Geoffroy, 1762 and *Liebelia* Kieffer, 1903, the species of which induce galls only on plants of the genus *Rosa*, but are not highly host-specific within this genus (Pujade-Villar, 1993). Among these genera, the most diverse and widespread is *Diplolepis*. A total of fifteen species of this genus are recorded in the Palearctic (Belizin, 1957; Pujade-Villar, 1993; Nieves-Aldrey, 2001a; Abe et al., 2007; Pujade-Villar et al., 2020) and thirty-one in the

Nearctic (Burks, 1979; Csóka et al., 2005). Six species of *Diplolepis* are common and widely distributed in Europe, but only five species are recorded on the Iberian Peninsula (Nieves-Aldrey, 2001a) (Fig. 1): *Diplolepis eglanteriae* (Hartig, 1840), *Diplolepis nervosa* (Curtis, 1838), *Diplolepis rosae* (Linnaeus, 1758), *Diplolepis mayri* (Schlechtendal, 1877) and *Diplolepis spinosissimae* (Giraud, 1859). In addition to the western European species, there is an additional *Diplolepis* species, *Diplolepis fructuum* (Rübsaamen, 1896), which is distributed from Ukraine to the Anatolian Peninsula and in the neighbouring regions of the Caucasus and Kazakhstan (Nieves-Aldrey, 2001a; Lotfalizadeh et al., 2006; Güçlü et al., 2008; Katılmış & Kıyak, 2010; Todorov et al., 2012). The second member of the Diplolepidini tribe, the predominantly Asian genus *Liebelia*, has only one species in Europe, *Liebelia cavarai* (Kieffer, 1895), which is restricted to the island of Sardinia (Vyrzhikovskaja, 1963).

Galls of the European *Diplolepis* may be categorized into two morphological groups according to the plant organs they attack and the shape and structure of the galls they induce, which correspond with different extant phylogenetic lineages (Zhang et al., 2019). *D. eglanteriae*, *D.*

nervosa and *D. spinosissimae* induce mainly small spherical and unilocular galls on leaves, and *D. rosae*, *D. mayri* and *D. fructuum* cause larger, multilocular galls on stems, leaves or hips.

D. eglanteriae and *D. nervosa* form a complex of cryptic galls that are morphologically indistinguishable, potentially leading to misidentification. Both species are univoltine and bisexual. On the other hand, the galls of *D. spinosissimae* are produced on the leaves, the fruits and sometimes the stems of different species of the genus *Rosa*, mainly shrubs of *Rosa pimpinellifolia* L.

The species *D. rosae* and *D. mayri* induce conspicuous and striking galls and are thus the most collected and recorded within the genus. The galls of both species develop on buds or twigs, but sometimes on leaflets or fruits. The galls of *D. mayri* (Fig. 1G) have a sparse coating of stiff spines instead of the filamentous appendix of the so-called 'rose bedeguar' galls of *D. rosae* (Fig. 1D–F). The life cycle of both species is univoltine, but their modes of reproduction vary with their geographical range, particularly on the Iberian Peninsula. While males of *D. rosae* are very scarce or virtually absent in most areas on the Iberian Peninsula, the sex ratio of this species is closer to 1 : 1 in the rest of Europe. In fact, some studies in other areas have linked latitude with the relative presence/abundance of males of *D. rosae* (Askew, 1960; Stille, 1984, 1985). Males of *D. mayri* (Fig. 1A) are not abundant in non-Iberian Europe, but other authors have discovered differences in the reproductive biology of this species on the Iberian Peninsula, where it does not undergo thelytokous parthenogenesis as it does in other countries. Instead, the Iberian *D. mayri* has a bisexual generation and a sex ratio close to 1 : 1 (Pujade-Villar, 1983; Nieves-Aldrey, 1989; Nieves-Aldrey, 2001a).

From the biogeographical and macroecological point of view, determining the potential distribution of organisms is an important tool for the ecological and biological conservation of animals (Guisan & Zimmermann, 2000; Guisan et al., 2006; Peterson, 2006). Using mathematical algorithms to model the potential distribution of species has allowed the determination of those areas where there is a greater probability of finding them. Niche models, suitability models or predictive habitat distribution models are empirical or mathematical approximations of the ecological niche of a species constructed from their presence and/ or absence records and variables that limit and define this niche (Araújo & Guisan, 2006; Austin, 2007; Peterson et al., 2011).

It is important that these niche models are based on environmental conditions in the regions studied and that the potential distribution models provide a distribution of habitat suitability for each species (Franklin, 2009; Zimmermann et al., 2010). The variable selection procedure is quite important since these variables are going to limit and define the habitat of a species. In addition, selecting appropriate predictor variables will decide if the model is essential for predicting species distributions (Guisan & Zimmermann, 2000; Jiménez-Valverde et al., 2011). Climatic variables are probably the main contributors to species niche delimitation at a large scale (Barbet-Massin et al., 2013).

Currently, there are a few cynipid ecological models, all of them related to *Fagaceae* hosts (Rodríguez et al., 2015; Gil-Tapetado et al., 2018). This paper presents, for the first time, an accurately niche suitability modelling of *Diplolepis* communities on Rosaceae hosts.

The main aim of this study is to determine potentially favourable areas for gall-inducing cynipids associated with shrubs of the family Rosaceae on the Iberian Peninsula. This objective is achieved by comparing different ecological models incorporating predictive climatic and environmental variables, *Diplolepis* records and a suitability model of host plants, which is used to limit the distribution. These favourability models are used to analyse the association of species of *Diplolepis* with biotic and abiotic variables and draw conclusions about their distribution on the Iberian Peninsula.

MATERIALS AND METHODS

Selection of presence data

To create the niche models, we compiled a dataset of the presence of five species of *Diplolepis* recorded in southern Europe: *D. eglanteriae/nervosa*, *D. spinosissimae*, *D. rosae* and *D. mayri* (Fig. 1). This was compiled using the published and georeferenced records of each species. All records for synonymous species names were also considered acceptable and included in the data matrix (Nieves-Aldrey, 2001a). This data was compiled from different sources up to 2017 (Table 1, Fig. 2A–D, Table S1). As species of *Diplolepis* are dependent on *Rosa* species, we used the modelled distribution of the host plant to define the limits of the cynipid distributions. Records of *Rosa*, consisting of 17,943 presences (Fig. 2E), were compiled from GBIF (Global Biodiversity Information Facility) datasets (GBIF Data Portal, 2016) and used in niche models. Both cynipid and host plant records were cleaned by eliminating geographically redundant (we included only one presence record per km^2) and low accuracy georeferenced data.

Selection of variables

Bioclimatic and environmental variables can be used to predict the presence of each species of gall wasp. In the present study, different variables were used to model cynipid-gall and host *Rosa*, because it is important to distinguish those variables that have a direct effect on cynipid biology and those that influence the wasp through its host plant (Rodriguez et al., 2015; Gil-Tapetado et al., 2018).

The WorldClim version 1.4 (Hijmans et al., 2005) variables at a resolution of 30 arc seconds were used in the niche models of *Diplolepis*. As they emerge from their galls in spring (March, April, and May), only the spring variables Bio04 (temperature seasonality), Bio08 (mean temperature in wettest quarter), Bio13 (precipitation in wettest month), Bio15 (precipitation seasonality) and Bio16 (precipitation in wettest quarter) were used in these analyses, because they directly affect adult *Diplolepis*. Galls isolate the wasps from external environmental conditions, although some variables, such as snow cover, glycerol concentration or mild winter temperatures, affect the survival of those that overwinter in galls (Somme, 1964; Shorthouse, 1980; Williams et al., 2003). The free-living stage (i.e., adult cynipid), however, is affected directly by bioclimatic conditions (Shorthouse & Rohfrisch, 1992).
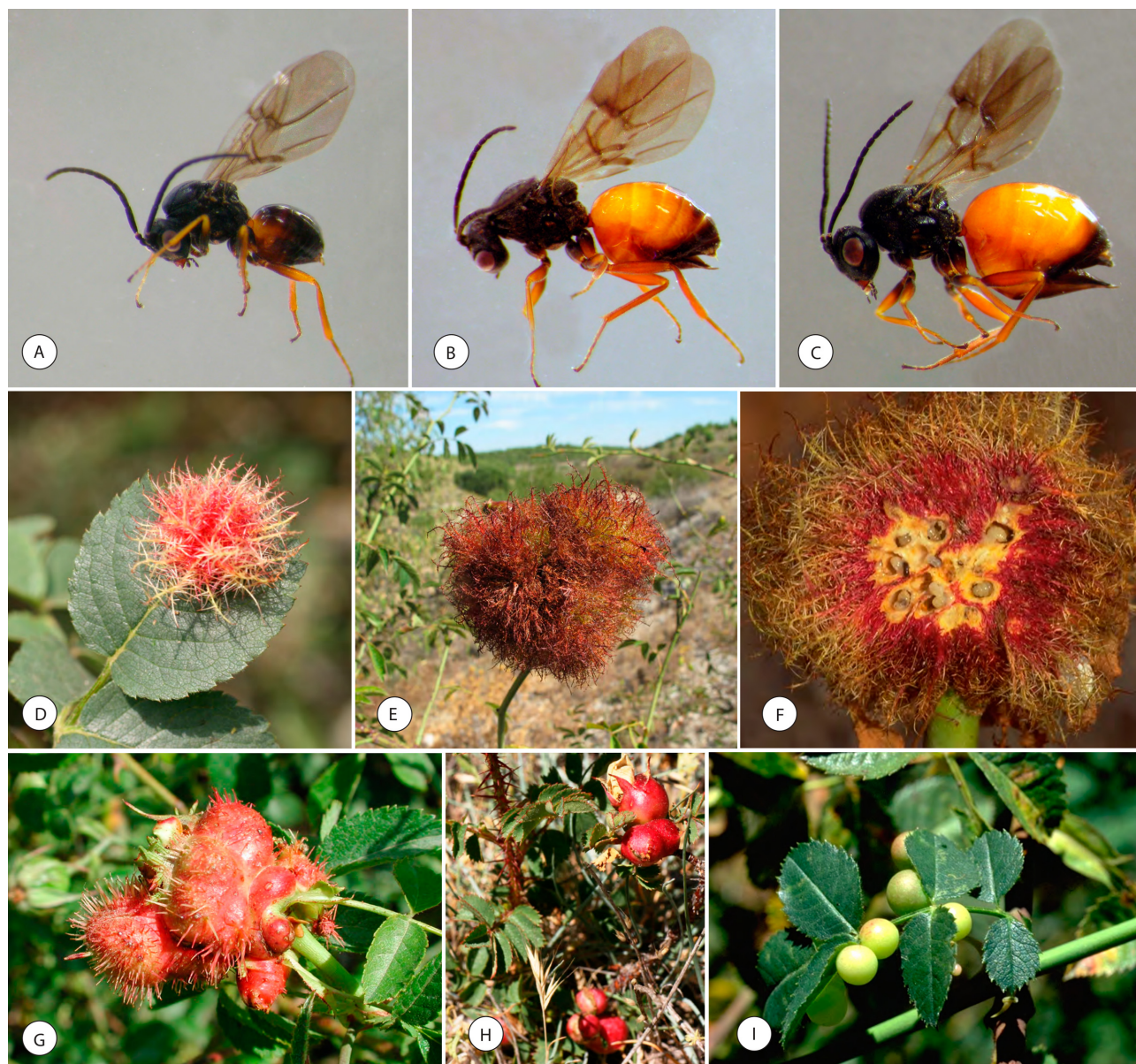
Fig. 1. Adults and galls of species of *Diplolepis*. A – adult male *Diplolepis mayri*; B – adult female *D. mayri*; C – adult female *D. rosae*; D–F – galls of *D. rosae* and a section of a gall; G – *D. mayri* gall; H – *D. spinosissimae* gall; I – galls of *D. eglanteriae/nervosa*.

We used cluster dendrogram analysis of correlation distances to identify possible correlation biases between the variables. First, we chose all the variables that exceeded a value of 0.3 (or less than 70% correlation). Second, we selected all the uncorrelated variables (those variables that did not form a cluster); finally, we chose the variable with the greatest biological significance for *Diplolepis* from the clusters of correlated variables. In cases in which a variable did not have a clear biological meaning, the most derived variable was chosen (i.e., the variable that refers to a specific period of the year). Bio16 was excluded from the modelling of *Diplolepis* due to its high correlation with the rest of the variables (Fig. 3A). In addition, we applied a forward elimination process, variance inflation factor (VIF), to the variables. VIF measures how much the variance in a regression coefficient increases when predictors are correlated. We computed the VIF of the variables using R version v 3.3.1 (R Development Core Team, 2008) and RStudio 0.99.903 (RStudio Team, 2016) in the package HH 3.1–32 (Heiberger & Holland, 2015). The threshold value of 5 was used to determine which variables were strongly corre-

lated with other factors, thereby indicating that it was appropriate to eliminate them from the analysis (Kutner et al., 2004; O'Brien, 2007; Lin et al., 2011). All the variables in the dendrogram satisfied the threshold value condition (VIF > 5) and no variable was excluded from the analysis.

The selection of environmental variables for the construction of the *Rosa* model was difficult because these plants are widely distributed and it is a group with many species (Zhang & Gandelin, 2003; Yan et al., 2005; Koopman et al., 2008). The ecological and edaphic conditions selected are general, which makes it difficult to determine those conditions that are most likely to influence its presence (Castroviejo et al., 1998). We used the modelling methods previously mentioned and selected the most general climatic variables from WorldClim (Bio01 (annual mean temperature), Bio02 (mean diurnal range), Bio03 (isothermality), Bio07 (temperature annual range) and Bio12 (annual precipitation)) and other non-climatic variables (available water capacity (ESDB, 2004), percentage of clay (ESDB, 2004), lithology (IGME, 2020), proximity to water masses (rivers, lakes, reservoirs and

Table 1. Record of presence of different species of *Diplolepis* on the Iberian Peninsula and the sources of the information (Source) from which they were compiled. N indicates the number of records per source.

Species	Source	N	Presence data
Diplolepis spinosissimae	Nieves-Aldrey (1986, pers. comm.)	5	8
	Pujade-Villar (1991, 1993, 1996)	3	
Diplolepis eglanteriae and *Diplolepis nervosa*	Cogolludo (1921)	4	115
	Nieves-Aldrey (1984, 1989, 1995, 2001b, pers. comm.)	36	
	Pujade-Villar (1991, 1993, 1996)	12	
	Tavares (1931a, b)	13	
	Vilarrúbia & Vilarrúbia (1933)	3	
	BiodiversidadVirtual.org	47	
Diplolepis mayri	Cogolludo (1921)	5	147
	Lázaro e Ibiza (1917)	1	
	Nieves-Aldrey (1984, 1986, 1989, 1995, 2001b, pers. comm.)	55	
	Pujade-Villar (1983, 1987, 1991, 1993, 1996)	22	
	Tavares (1931a, b)	1	
	Vilarrúbia (1933, 1936)	2	
	BiodiversidadVirtual.org	61	
Diplolepis rosae	Codina (1920)	1	282
	Cogolludo (1921)	7	
	Fernández de Gata (1901)	1	
	Lázaro e Ibiza (1917)	1	
	Nieves-Aldrey (1981, 1985, 1986, 1989, 2001b)	76	
	Pujade-Villar (1983, 1987, 1991, 1993, 1996)	40	
	Tavares (1931a, b)	16	
	Ventalló (1905)	1	
	Vilarrúbia & Vilarrúbia (1933); Vilarrúbia (1936)	2	
	BiodiversidadVirtual.org	129	
	GBIF	8	

other continental water bodies) (modified from EEA, 2009) and land uses from CORINE Land Cover 2006 (EEA, 2012) resized to 1 km². Bio2 and available water capacity were not included in the final set of variables (Fig. 3B).

Modelling the distributions of species

We used the following algorithms: generalized linear models (GLMs) (McCullagh & Nelder, 1989), generalized additive models (GAMs) (Hastie & Tibshirani, 1990, Yee & Mitchell, 1991), random forest (RF) (Breiman, 2001) and MaxEnt (Phillips et al., 2006). The first three were created using R version 3.3.1 (R Development Core Team, 2008) and RStudio version 0.99.903 (RStudio Team, 2016) in the packages dismo 1.1-1 (Hijmans et al., 2015), mgcv 1.8-12 (Wood, 2016) and randomForest 4.6-12 (Breiman et al., 2015), with 3,000 trees and a node number of 3. We used MaxEnt version 3.4.1 (Phillips & Dudik, 2008) with the default configuration, including a regularization parameter of 1 and 10 replicates.

For both the *Rosa* and *Diplolepis* models, we performed background point generation tests following and improving upon the methodology of Gil-Tapetado et al. (2018), using the maximum and minimum values of the predictor variables as parameters of habitability for each species. The sum of the resulting areas between the maximum and minimum values of each predictive variable was classified as habitable area in which to generate random background points; the excluded areas were classified as non-habitable zones in which to generate the pseudo-absences.

Four individual models (GLM, GAM, MaxEnt and RF) were developed for the host plant taxa (genus *Rosa*), *D. rosa* and *D. mayri*, and the group formed by *D. eglanteriae* and *D. nervosa*, the galls of which are not externally morphologically distinguishable. We could not develop models for *D. spinosissimae* (Fig. 1H) because of the few records for this species from the Iberian Peninsula (Fig. 2D, Table 1). With respect to host plant taxa, models were made including different species of the genus *Rosa*.

We evaluated these models using area under the curve (AUC) statistics. Finally, we selected models that had a maximum suitability value of at least 0.80 to obtain an improved estimation of the potential geographic distribution of a species. The models selected for each species were joined to create an average consensus map.

ArcGIS 10.1 software (ESRI, 2011) was used to transform highly suitable areas (i.e., areas with a suitability greater than or equal to 0.70) indicated by the host plant consensus models into buffer zones of high suitability – i.e., zones with a radius of one kilometre around the presence data for *Rosa*, which constitute possible action areas for the species. Presence data for the genus *Rosa* were also included, and corresponding buffers with a one-kilometre radius were generated around the presence points. We overlapped this mask layer with each consensus model of *Diplolepis* species to obtain the final models. These results reflect the high and low probabilities of the presence of each cynipid within their host plant areas on the Iberian Peninsula.

The complementary maps of the *Diplolepis* species were developed in ArcGIS 10.1 (ESRI, 2011) based on the most favourable areas (areas with values greater than 0.70). Finally, these maps were combined by twos. In addition, the possible associations of environmental variables Bio04 (temperature seasonality), Bio15 (precipitation seasonality) and Bio16 (precipitation in wettest quarter) from WorldClim version 1.4 (Hijmans et al., 2005) with the potential distribution areas of the *Diplolepis* species were checked using boxplots in the ggplot2 package in RStudio.

RESULTS

The results from the RF, GLM and GAM algorithms were selected for the species *D. eglanteriae/nervosa* and *D. rosae* because they had a maximum suitability of more than 0.80. In the case of *D. mayri,* only the results of the RF and GAM met this requirement. In all these cases, MaxEnt did not exceed a maximum suitability of 0.80 and we
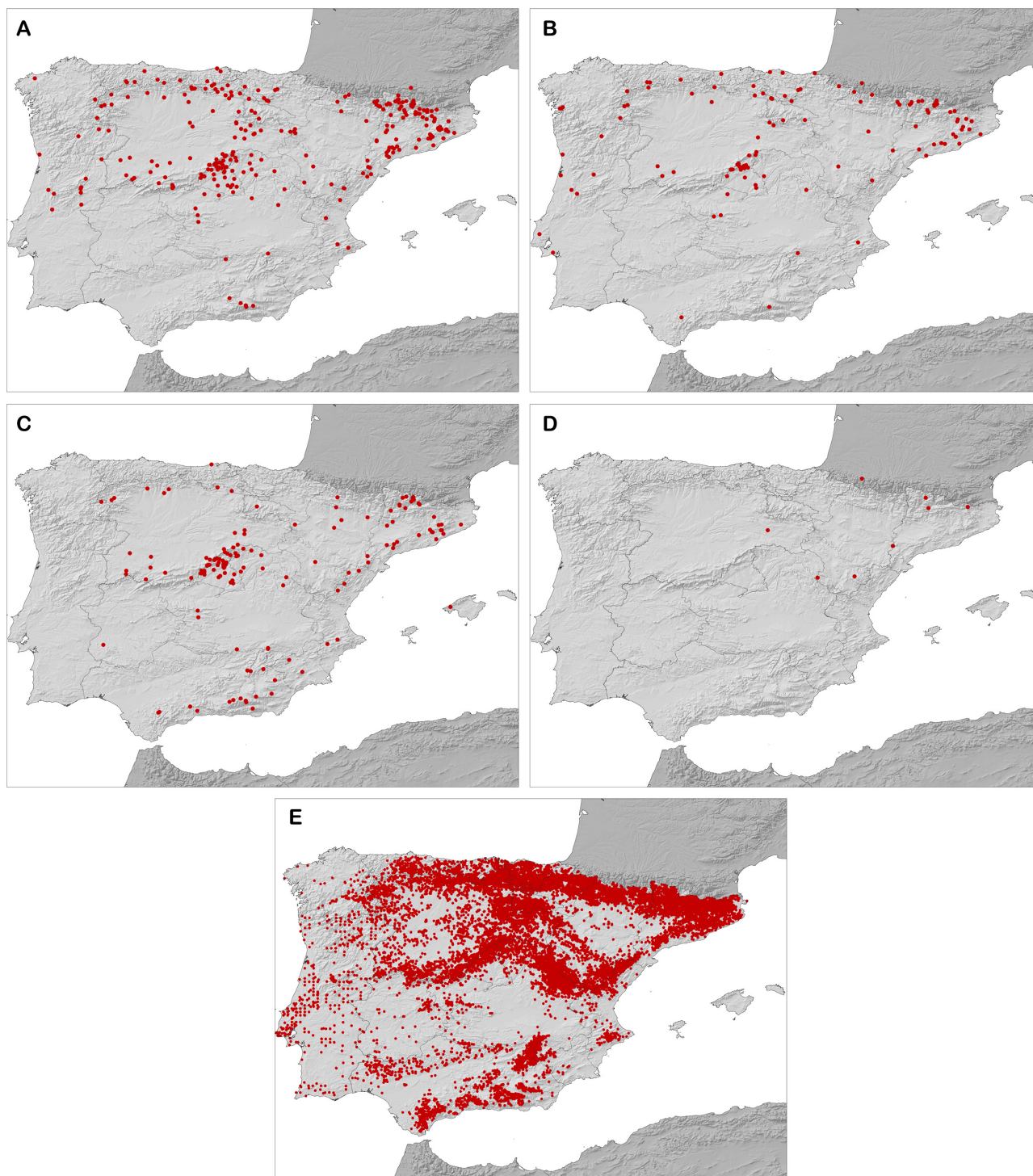
Fig. 2. Maps of the Iberian Peninsula showing the presence points for the species. A – *Diplolepis rosae*; B – *Diplolepis eglanteriae/nervosa;* C – *Diplolepis mayri*; D – *Diplolepis spinosissimae*; E – *Rosa*.

did not use this algorithm in the average consensus models. RF, GLM and GAM were selected to produce the final model for *Rosa* (Table 2).

The models indicate that southern areas of the Iberian Peninsula are more suitable for *D. mayri* (Fig. 4C) and northern areas more suitable for *D. eglanteriae/nervosa* (Fig. 4B), while *D. rosae* is a generalist, with highly suitable areas throughout the Iberian Peninsula (Fig. 4A).

Below, are the detailed results for each of the species of *Diplolepis*.

Diplolepis rosae (Figs 1C–F, 4A) is the most common species of this genus on the Iberian Peninsula. According to the presence points and areas of maximum suitability, this species occurs in areas with a mean annual temperature of approximately 11°C and annual precipitation of 700–800 mm and at an average altitude of approximately 900–1000 m a.s.l. In the areas in which *D. rosae* occurs, in
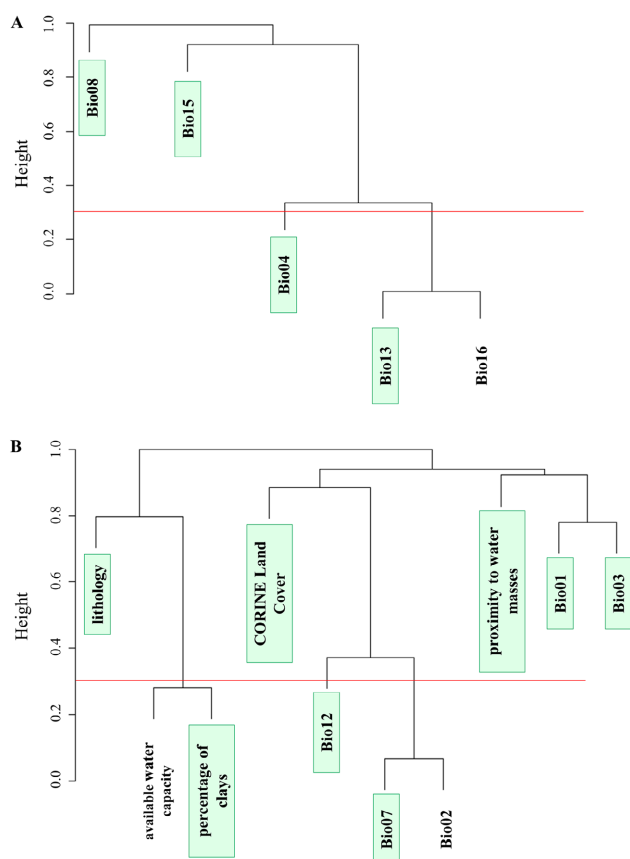
Fig. 3. Cluster dendrogram analysis based on the correlation coefficient distance for the following datasets. A – cynipid-related variables: Bio04 (temperature seasonality), Bio08 (mean temperature of wettest quarter), Bio13 (precipitation of wettest month), Bio15 (precipitation seasonality) and Bio16 (precipitation of wettest quarter); B – host plant-related variables: Bio01 (annual mean temperature), Bio02 (mean diurnal range), Bio03 (isothermality), Bio07 (temperature annual range), Bio12 (annual precipitation), available water capacity, percentage of clays, lithology, proximity to water masses and CORINE Land Cover (derived from land uses in the CORINE Land Cover 2006).

Table 2. Results of (AUC) area under the curve and the maximum suitability values of the four models used to develop each consensus model.

Species	Model	AUC	Maximum suitability value
Rosa	GAM	0.757	0.88
	RF	0.890	0.91
	GLM	0.734	0.85
	Maxent	0.623	0.59
Diplolepis eglanteriae/ nervosa	GAM	0.715	0.91
	GLM	0.721	0.84
	RF	0.931	0.88
	Maxent	0.768	0.69
Diplolepis rosae	GAM	0.794	0.85
	GLM	0.796	0.81
	RF	0.905	0.85
	Maxent	0.764	0.69
Diplolepis mayri	GAM	0.814	0.86
	RF	0.911	0.93
	GLM	0.561	0.76
	Maxent	0.787	0.70

the warmest quarter, the mean temperature was 19°C and there was approximately 160 mm of precipitation, while in the coldest quarter, the mean temperature was 4°C and there was approximately 190 mm of precipitation (Table 3). The presence areas for *D. rosae* are diverse, with suitability percentages of > 0.70 in all areas. The areas with the most suitable ecological conditions are concentrated in the region of the Catalonian Pyrenees (north eastern Iberian Peninsula) and Montes de León (north western Iberian Peninsula) (Fig. 4A).

The most favourable areas for *D. eglanteriae* and *D. nervosa* (Fig. 1I, Fig. 4B) are in mountain ranges. The results indicate that areas in the Cantabrian Mountains and Pyrenees (in the north of Iberian Peninsula), both the Central and Iberian Mountain Ranges (central Iberian Peninsula), and part of the Baetic System (in the south of Iberian Peninsula) are the most suitable areas (with suitability percent-

Table 3. Different measurements of climatic variables Worldclim and altitude in the points of presence and of high suitability for the *Diplolepis rosae*, with the average value (AV), standard deviation (SD) and minimum (MIN) and maximum (MAX) values for each.

Variable	Code	PRESENCE DATA				HIGH SUITABILITY			
		AV	SD	MIN	MAX	AV	SD	MIN	MAX
Altitude	Alt	942	409	26	2172	1009	397	24	2281
Annual mean temperature	Bio01	10.93	2.53	3.40	16.00	10.15	2.11	3.70	16.00
Mean diurnal range [Mean of monthly (max temp − min temp)]	Bio02	9.60	1.38	5.90	12.30	9.17	1.37	6.90	12.50
Isothermality [(Bio2/Bio7) × 100]	Bio03	3.63	0.24	3.00	4.50	3.61	0.29	2.90	4.30
Temperature seasonality (standard deviation × 100)	Bio04	576.52	59.51	330.80	689.30	555.38	46.12	456.10	682.00
Max temperature of warmest month	Bio05	25.83	3.40	16.20	34.10	24.37	2.35	16.60	30.90
Min temperature of coldest month	Bio06	−0.25	2.43	−7.40	6.90	−0.64	2.27	−6.40	5.80
Temperature annual range (Bio5–Bio6)	Bio07	26.08	3.02	15.70	32.80	25.01	2.54	20.20	32.90
Mean temperature of wettest quarter	Bio08	9.98	3.63	2.90	20.30	9.41	4.12	3.00	20.70
Mean temperature of driest quarter	Bio09	14.01	7.72	−2.40	24.20	11.37	7.15	−2.00	22.90
Mean temperature of warmest quarter	Bio10	18.62	2.73	10.60	24.20	17.54	2.16	11.10	23.00
Mean temperature of coldest quarter	Bio11	3.98	2.46	−3.10	10.10	3.45	2.11	−2.50	9.50
Annual precipitation	Bio12	716.61	225.09	373.00	1280.00	829.35	152.00	432.00	1260.00
Precipitation of wettest month	Bio13	85.36	26.18	44.00	178.00	96.86	15.12	53.00	139.00
Precipitation of driest month	Bio14	32.28	19.15	6.00	85.00	42.66	14.72	11.00	82.00
Precipitation seasonality (coefficient of variation)	Bio15	27.42	9.39	13.00	56.00	23.23	6.25	13.00	45.00
Precipitation of wettest quarter	Bio16	229.99	73.57	121.00	481.00	259.32	42.51	146.00	368.00
Precipitation of driest quarter	Bio17	121.39	57.80	34.00	291.00	153.23	44.44	50.00	283.00
Precipitation of warmest quarter	Bio18	139.24	70.75	34.00	294.00	175.51	55.36	50.00	298.00
Precipitation of coldest quarter	Bio19	180.88	74.33	73.00	477.00	201.13	52.50	101.00	362.00

Table 4. Different measurements of climatic variables Worldclim and altitude in the points of presence and of high suitability for the *Diplolepis eglanteriae/nervosa* gall complex, with the average value (AV), standard deviation (SD) and minimum (MIN) and maximum (MAX) values for each.

Variable	Code	PRESENCE DATA				HIGH SUITABILITY			
		AV	SD	MIN	MAX	AV	SD	MIN	MAX
Altitude	Alt	869	485	3	1951	939	432	–3	2292
Annual mean temperature	Bio01	11.13	2.82	3.50	17.10	9.97	2.44	2.50	16.40
Mean diurnal range [Mean of monthly (max temp – min temp)]	Bio02	9.29	1.51	5.90	12.10	8.74	1.18	5.80	12.20
Isothermality [(Bio2/Bio7) × 100]	Bio03	3.67	0.29	3.10	4.50	3.66	0.29	2.90	4.50
Temperature seasonality (standard deviation × 100)	Bio04	552.51	76.27	332.20	687.60	520.12	46.75	332.40	674.70
Max temperature of warmest month	Bio05	25.37	3.23	16.30	33.40	23.26	2.22	15.10	29.50
Min temperature of coldest month	Bio06	0.35	3.23	–6.70	8.40	–0.26	2.78	–7.60	7.70
Temperature annual range (Bio5–Bio6)	Bio07	25.02	3.60	15.80	32.50	23.52	2.23	15.60	32.50
Mean temperature of wettest quarter	Bio08	9.72	3.72	2.00	19.00	8.49	3.74	1.70	19.20
Mean temperature of driest quarter	Bio09	14.01	7.44	–0.90	23.60	12.56	6.79	–2.40	23.10
Mean temperature of warmest quarter	Bio10	18.48	2.72	10.60	23.60	16.86	2.26	9.60	23.30
Mean temperature of coldest quarter	Bio11	4.45	3.08	–2.80	12.00	3.65	2.64	–3.70	10.20
Annual precipitation	Bio12	787.10	255.02	389.00	1484.00	908.00	155.44	508.00	1407.00
Precipitation of wettest month	Bio13	95.48	34.10	44.00	234.00	104.69	16.84	58.00	202.00
Precipitation of driest month	Bio14	34.07	19.98	3.00	81.00	48.22	13.48	12.00	88.00
Precipitation seasonality (coefficient of variation)	Bio15	28.48	11.78	13.00	66.00	21.17	5.14	13.00	51.00
Precipitation of wettest quarter	Bio16	258.12	93.85	127.00	597.00	282.09	45.54	159.00	564.00
Precipitation of driest quarter	Bio17	127.95	60.86	25.00	269.00	172.95	40.87	58.00	299.00
Precipitation of warmest quarter	Bio18	145.77	72.40	29.00	280.00	188.97	46.69	59.00	299.00
Precipitation of coldest quarter	Bio19	212.58	101.85	75.00	580.00	232.32	56.84	102.00	564.00

Table 5. Different measurements of climatic variables Worldclim and altitude in the points of presence and of high suitability for *Diplolepis mayri*, with the average value (AV), standard deviation (SD) and minimum (MIN) and maximum (MAX) values for each.

Variable	Code	PRESENCE DATA				HIGH SUITABILITY			
		AV	SD	MIN	MAX	AV	SD	MIN	MAX
Altitude	Alt	956	406	21	2198	1110	370	10	2313
Annual mean temperature	Bio01	11.54	2.19	5.00	16.00	10.53	1.86	5.10	16.90
Mean diurnal range [Mean of monthly (max temp – min temp)]	Bio02	10.13	1.38	6.10	12.30	10.22	1.56	6.90	12.50
Isothermality [(Bio2/Bio7) × 100]	Bio03	3.61	0.21	3.00	4.00	3.62	0.23	2.90	4.20
Temperature seasonality (standard deviation × 100)	Bio04	606.60	48.93	367.00	689.30	607.78	40.56	495.30	678.80
Max temperature of warmest month	Bio05	27.40	2.75	18.20	33.50	26.42	2.37	18.60	33.20
Min temperature of coldest month	Bio06	–0.16	2.28	–5.10	6.60	–1.27	2.18	–6.00	5.60
Temperature annual range (Bio5–Bio6)	Bio07	27.57	2.86	16.20	32.80	27.69	2.89	21.80	32.80
Mean temperature of wettest quarter	Bio08	10.16	3.69	2.50	20.30	10.41	3.49	1.90	20.70
Mean temperature of driest quarter	Bio09	16.32	6.85	–0.80	23.90	13.87	7.34	–1.10	24.10
Mean temperature of warmest quarter	Bio10	19.68	2.22	12.50	24.00	18.69	1.83	12.40	24.30
Mean temperature of coldest quarter	Bio11	4.27	2.23	–1.30	9.60	3.27	1.94	–1.50	10.80
Annual precipitation	Bio12	602.94	169.22	351.00	1174.00	646.88	162.74	390.00	1139.00
Precipitation of wettest month	Bio13	73.64	19.34	47.00	129.00	79.30	16.81	47.00	137.00
Precipitation of driest month	Bio14	23.35	15.06	2.00	78.00	29.47	14.00	6.00	76.00
Precipitation seasonality (coefficient of variation)	Bio15	30.84	9.29	14.00	68.00	27.32	6.23	15.00	46.00
Precipitation of wettest quarter	Bio16	197.29	55.09	116.00	361.00	207.65	46.81	126.00	362.00
Precipitation of driest quarter	Bio17	92.82	45.93	20.00	258.00	111.28	42.62	35.00	248.00
Precipitation of warmest quarter	Bio18	107.20	62.47	24.00	278.00	129.49	56.94	35.00	291.00
Precipitation of coldest quarter	Bio19	153.56	50.28	80.00	349.00	151.89	45.18	77.00	349.00

ages > 0.70) for this species complex on the peninsula. The most suitable areas are characterized by an average mean annual temperature of 9.97°C and an annual precipitation of 908 mm (Table 4). The models indicate that the most suitable areas for these species are coastal areas in Galicia, Asturias, Cantabria, Basque Country and Catalonia and the mainland in Navarre and Aragon (northern Spain; Fig. 4B).

Diplolepis mayri (Figs 1A, B and G, 4C), like *D. rosae*, is common on the Iberian Peninsula. The mountainous areas in the central and south eastern parts of the peninsula are highly suitable for *D. mayri* (Table 5), with the Catalonian Pyrenees (north eastern Iberian Peninsula) the most

suitable. These areas are the parts of the Iberian Peninsula with a Mediterranean climate.

Regarding the bioclimatic variables in the highly suitable areas for each species of *Diplolepis* (Tables 3, 4 and 5), *D. mayri* is the species which can occur at higher altitudes (956 m a.s.l. on average) and *D. eglanteriae/nervosa* in areas with the highest rainfall (787.1 mm on average). Moreover, combining the potential distribution maps revealed suitable areas for all of the species of *Diplolepis*. There is a clear separation in the highly suitable areas for *D. eglanteriae/nervosa* and *D. mayri* (Fig. 5A), with those of the former mainly in the northern parts and the latter
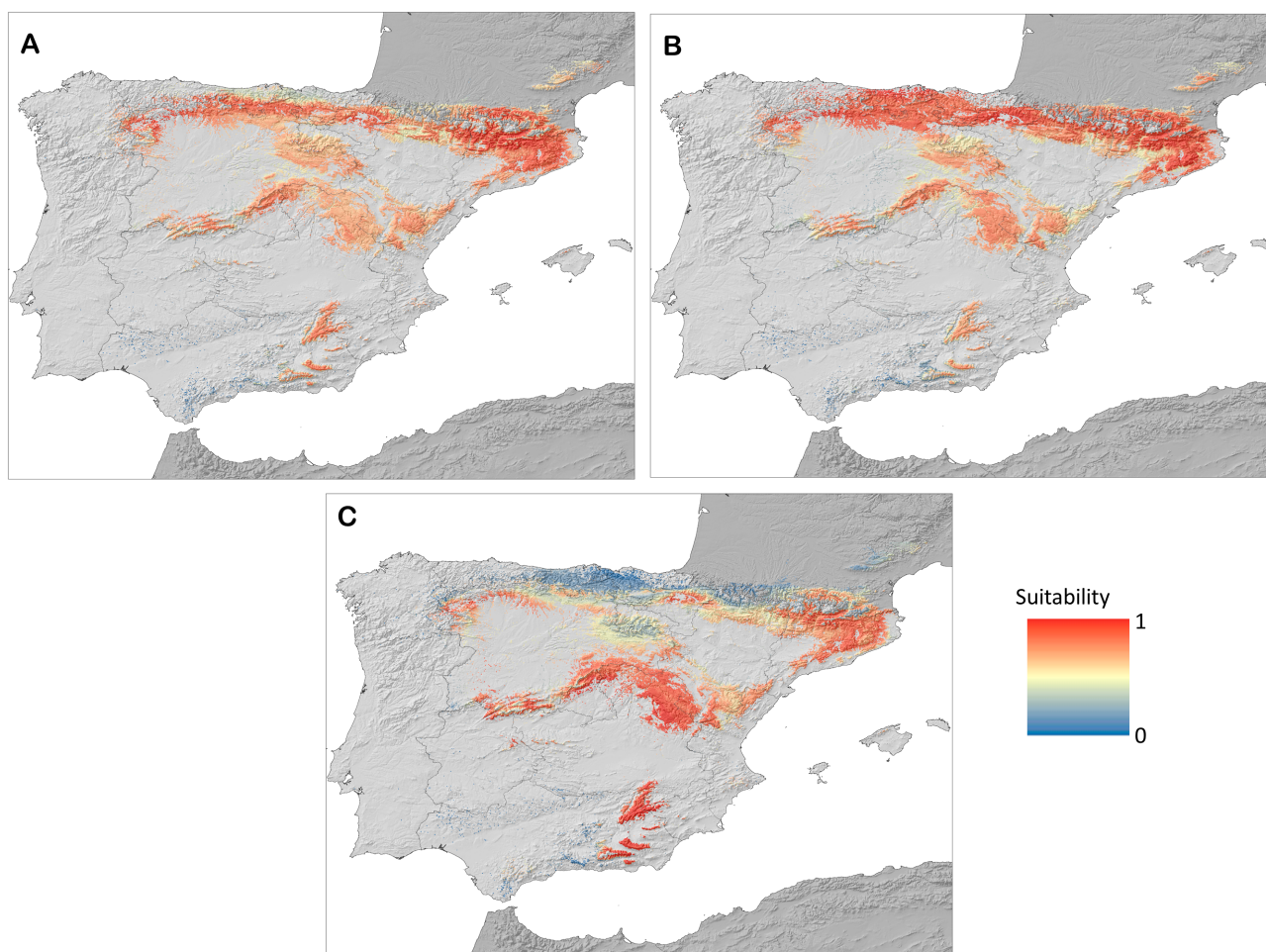
Fig. 4. Map of the suitable areas on the Iberian Peninsula for the species studied. A – *Diplolepis rosae*; B – *Diplolepis eglanteriae/nervosa*; C – *Diplolepis mayri*.

in of the central and southern parts of the Iberian Peninsula. The central mountain ranges are of low suitability for *D. eglanteriae/nervosa* and *D. rosae*, whereas the mountainous areas in the northern part of the Iberian Peninsula are the most favourable for them (Fig. 5B). The species *D. rosae* and *D. mayri* share the same potential distribution, with a small area in northern Catalonia region (north eastern Iberian Peninsula) with highest suitability for both species (Fig. 5C).

The distributions of species of *Diplolepis* seem to be associated with particular climatic variables (Fig. 6). The boxplots provide a visual approximation of the predictions of the models: areas highly suitable for *D. mayri* are in areas with higher temperatures and lower rainfall than those highly suitable for the other species of *Diplolepis*. It is also noted that *D. eglanteriae/nervosa* has the highest tolerance range for rainfall and *D. rosae* is the most generalist of the species (Fig. 6).

DISCUSSION

Suitability models for the different species of *Diplolepis*

The presence data indicate a greater occurrence of all the species of *Diplolepis* studied in the northern than in the southern part of the peninsula (Fig. 2). This may be because cynipids have been sampled less in southern Spain than in central and northern Spain (Nieves-Aldrey, 2001a). However, more recent samples collected from 2017 to 2019 by Nieves-Aldrey (unpubl. data) confirm that *D. rosae* is absent or less abundant in the southern part of the Iberian Peninsula. In addition, it is noteworthy that the records obtained from the citizen science platform Biodiversidad Virtual (BVdb, 2016), which were collected by many observers and make up ~ 50% of the total records for species of *Diplolepis* (Table 1), few of these records are for the southern Iberian Peninsula. Moreover, many galls are striking structures that are specific to the inducer wasp, which makes them easily identifiable and photographic evidence of their presence at a particular place. Such georeferenced data can be used along with previously published records in biogeographical studies of the Iberian Peninsula (Goula et al., 2013; Jiménez-Valverde et al., 2019). Based on this information and that *D. rosae* is the most common species on the Iberian Peninsula, it is possible that the data truly reflect a latitudinal gradient in the abundance of these species on this Peninsula.

On the other hand, an important aspect of these models is the environmental conditions selected and their effects on the distribution of the species analysed. The insects studied are obligatorily dependent on their *Rosa* hosts, on
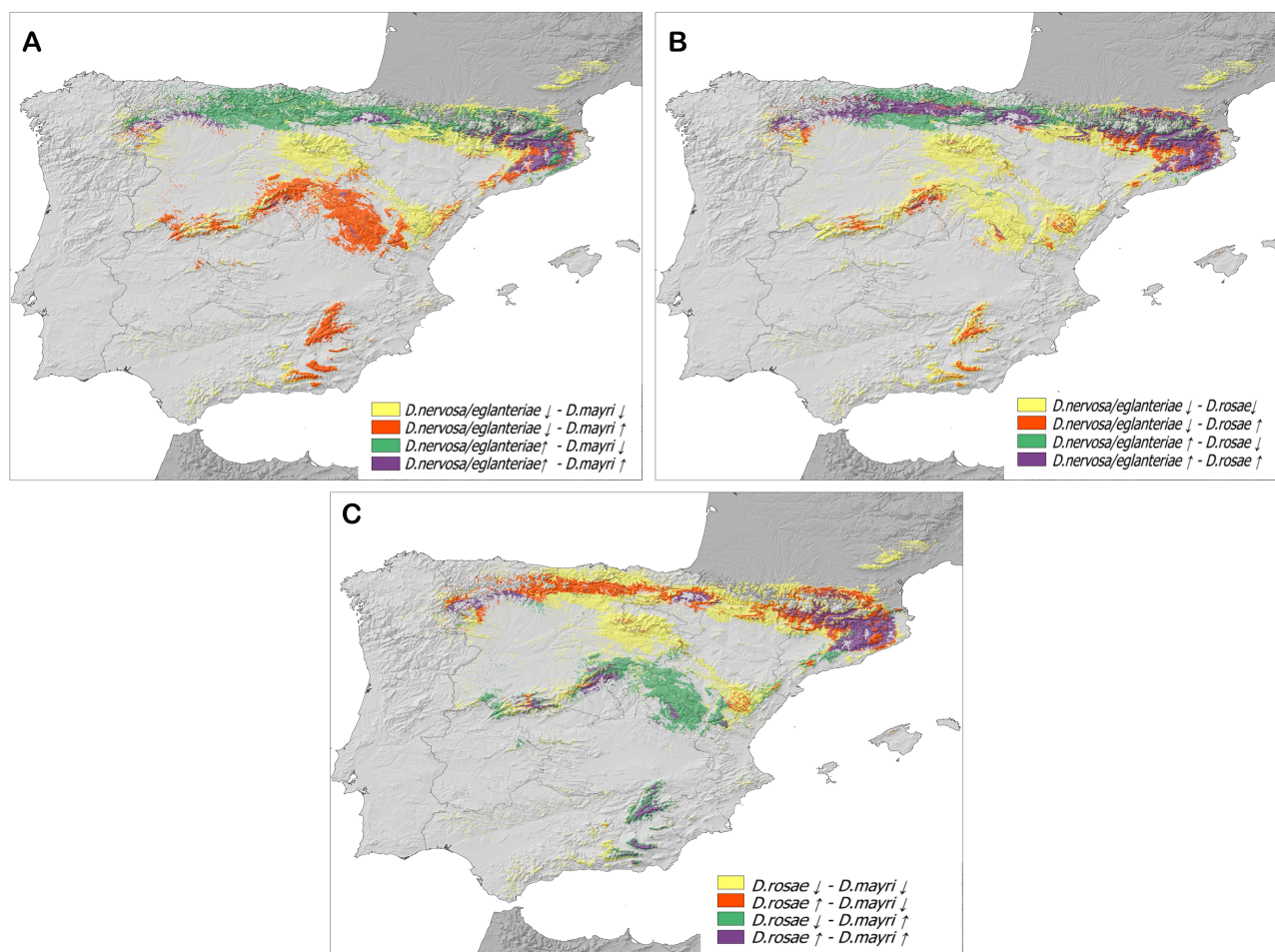
Fig. 5. Maps of the potential distributions of low (↓) and high (↑) suitable areas in the region studied for: A – the *Diplolepis eglanteriae/ nervosa* complex and *Diplolepis mayri*; B – *Diplolepis eglanteriae/nervosa* and *Diplolepis rosae*; C – *Diplolepis rosae* and *Diplolepis mayri*.

which they induce galls (Nieves-Aldrey, 2001a). Thus, the limiting variable is the distribution of their host plant. The suitability models developed for *Rosa* were constructed using all the data for wild rose plants, without considering host specificity or preference of each species of *Diplolepis*. Although there is currently no evidence of species of *Diplolepis* being host specific (Stille, 1984; Kohnen et al., 2011), except in the case of *D. spinosissimae* for *R. pimpinellifolia*, it is possible that the distributions of specific species of *Rosa* may be a factor affecting the distributions of these cynipids. There are 27 species of the genus *Rosa* on the Iberian Peninsula, which are highly polymorphic and hybrids are also present, making their identification by non-specialists difficult (Castroviejo, 1998; Cueto & Giménez, 2009; Calvo & Ross-Nadié, 2016; Tomljenović & Pejić, 2018). For this reason, and in addition to the fact that there are no reliable data on the distributions of species of *Rosa*, all the plant data used were at the genus rather than the species level.

Other variables not considered were the effects of habitat fragmentation due to natural and anthropogenic causes and the microhabitat or microtopographic conditions. Increasing land use intensity and habitat fragmentation are important threats to global biodiversity, especially in agricultural landscapes. Some studies report that landscape diversity has little or no effect on the species richness of *Diplolepis* (Looney & Eigenbrode, 2010) and that the homogenization of the landscape provides a perfect habitat for gall inducers and their community members (László et al., 2018). On the other hand, microtopographic conditions can mask temperature differences along altitudinal or latitudinal gradients over small scales. The interaction between microtopography, plant cover and solar radiation result in microhabitat conditions that are not represented by climatic variables (Scherrer & Körner, 2010, 2011; Scherrer et al., 2011).

Diplolepis rosae has a wider potential distribution than the rest of the species. For this reason, this species is found in most rose bushes on the Iberian Peninsula (Fig. 4A). Most of the *D. rosae* data used in the present article do not specify the sex of the galler or the composition and abundance of its parasitoid communities. However, in the summer of 2017, Nieves-Aldrey (unpubl. data) found a single male specimen of *D. rosae* in the Aracena Mountains in south western Iberian Peninsula (Nieves-Aldrey, 2001a). This observation matches those of other authors, which indicate the possibility of a latitudinal gradient (from south to north) in the sex ratio of this species. For example, Askew (1960) and Hoffmeyer (1925) suggest that there is a higher abundance of male *D. rosae* in the northern parts of the peninsula. However, some authors (Rizzo & Massa, 2006;
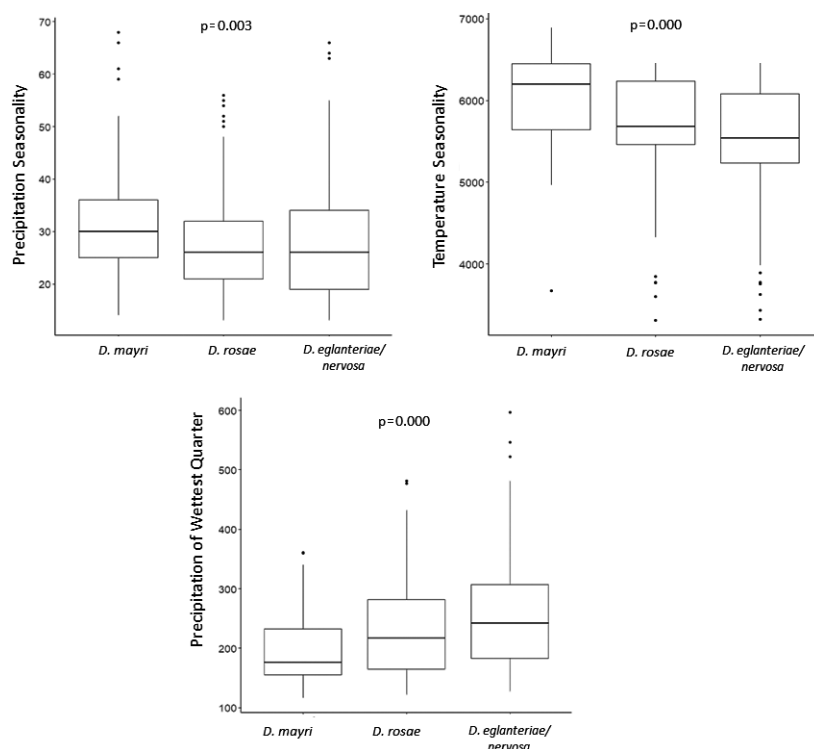
Fig. 6. Boxplots showing the associations between highly suitable areas (> 0.70) for the species of *Diplolepis* and three bioclimatic variables: precipitation seasonality (Bio15), temperature seasonality (Bio04) and precipitation in the wettest quarter (Bio16).

László & Tóthmèrèsz, 2011; Todorov et al., 2012) report the lack of a latitudinal gradient and that the presence of *D. rosae* males depends on more complicated factors, and also that the endosymbiotic bacteria *Wolbachia* affect the sex ratio of this species (Schilthuizen & Stouthamer, 1998; Rizzo & Massa, 2006). The record of a male of *D. rosae* on the Iberian Peninsula indicates the presence of males in southern Europe, although at a low abundance. However, to determine the actual sex ratio of *D. rosae,* more intensive sampling is needed in southern Europe.

The *D. eglanteriae/nervosa* model (Fig. 4B) reveals that the presence data and the maximum suitability for these two species occur in mountain forest areas and they avoid river-valleys (Table 4). In addition, *D. eglanteriae* and *D. nervosa* are also abundant in areas near the northern coast of the Iberian Peninsula. It is possible that in mountainous areas, species of *Rosa* have local characteristics, e. g. separation of vegetation patches, shrub size, or distance to the soil, that are lacking in riverbanks, and that these conditions are favourable for both cynipid species. An example is provided by Mifsud (2016), who reports that in mountainous areas, where wild roses grow in the shade of conifer trees, they do not flower and galls are not recorded. On the other hand, mountainous areas, particularly mountain forests, are favourable in many other ways; for example, the spatial configuration of trees favours optimal radiation, temperature and precipitation conditions. The conditions found in mountainous areas, together with being isolated from other areas, may have resulted in there being more or different species of *Rosa*, which could be specific or more suitable hosts for *D. eglanteriae* and *D. nervosa*, than at lower altitudes. However, the host preference of these spe-

cies of *Diplolepis* has not been determined due to the taxonomic difficulties of identifying each species of wild rose, among other reasons.

Diplolepis mayri occurs in the western Palearctic in areas of north Africa and Asia Minor (Nieves-Aldrey, 2001a). The distribution model for this species (Fig. 4C) revealed that the areas with the highest suitability were mainly in mountainous regions in the Mediterranean area of the Iberian Peninsula. Unlike *D. rosae* and *D. eglanteriae/nervosa*, there is an area of high suitability for *D. mayri* in the southern third of the Iberian Peninsula. This species is distributed in areas with relatively more precipitation seasonality and temperature seasonality, and relatively less rain (Fig. 6, Table 5). This might indicate that *D. mayri* is adapted to the Mediterranean climatic conditions in the southern Iberian Peninsula, unlike the rest of the species of *Diplolepis* studied.

Habitat complementarity

A comparison of the potential distributions of *D. eglanteriae/nervosa* and *D. mayri* revealed that they occur in complementary areas, e.g., areas on Iberian Peninsula with highly suitable environmental conditions for *D. eglanteriae* and *D. nervosa* are of low suitability for *D. mayri* and *vice versa* (Fig. 5A). This phenomenon occurs between species in other genera, such as *Copris hispanus* (Linnaeus, 1758) and *Copris lunaris* (Linnaeus, 1758) (Coleoptera: Scarabaeidae) (Chefaoui et al., 2004), different species of the red-striped oil beetle of the genus *Berberomeloe* Bologna, 1989 (Coleoptera: Meloidae) (Sánchez-Vialas et al., 2020) and among species that compete for resources (De Smedt et al., 2016).

It is possible that the species of *Diplolepis* studied are allopatric. The areas of high suitability for *D. eglanteriae* and *D. nervosa* occur in the north of the Iberian Peninsula (Euro Siberian areas) and those for *D. mayri* in central and southern parts of the Iberian Peninsula (Mediterranean areas). These zones are separated by the northern plateau of the Iberian Peninsula where host plants are either absent or scarce. Studies on the structure and genetic diversity of these species are likely to reveal significant genetic differentiation between them, possibly due to this physical barrier. The molecular characteristics of the cytochrome b and 12S genes and different character states ('number of larval chambers per gall', 'organ bearing the gall' and 'surface area of the gall') of species of the *Diplolepis* reveals that the species included in our study form two species groups: the *D. eglanteriae* group (including *D. eglanteriae* and *D. nervosa*) and the *D. rosae* group (including *D. rosae*, *D. fructuum*, *D. mayri* and *D. spinosissimae*) (Plantard et al., 1997). Recently, Zhang et al. (2019) published a phylogeny of *Diplolepis* and *Periclisttus* based on COI (cytochrome c oxidase subunit I) that divides the genus *Diplolepis* into two major monophyletic clades, the 'flanged femur' clade and 'leaf galler' clade, the latter of which includes three subclades: the Nearctic leaf galler subclade, the Palearctic multichambered subclade and a mixed leaf gall subclade. The Palearctic multichambered subclade includes the *D. rosae* group (*D. fructuum*, *D. mayri* and *D. rosae*), *D. spinosissimae* and two undescribed species. Finally, the rest of the species included in our study are classified in the mixed leaf gall subclade, which distinguishes between the *D. eglanteriae* Palearctic group (*D. japonica* and *D. eglanteriae*) and the *D. eglanteriae* Nearctic group and *D. nervosa*. The different lineages of the subclades that contain *D. mayri* and *D. rosae* (Palaearctic multichambered subclade) and *D. eglanteriae* and *D. nervosa* (mixed leaf gall subclade) could partially explain the observed habitat complementarity between *D. mayri* and *D. eglanteriae/nervosa*.

There is an overlap in the most suitable areas for *Diplolepis eglanteriae/nervosa* and *D. rosae* in the northern mountain ranges (Fig. 5B); therefore, there could potentialy be interspecific competition between these species in this area. However, *D. rosae* and *D. eglanteriae/nervosa* exploit their host plants in different ways. *Diplolepis eglanteriae/nervosa* induce galls on the petioles or undersides of leaves and *D. rosae* on the buds of the stems, leaflets or fruits (Nieves-Aldrey, 2001a). It is possible that if two different species have overlapping distributions, they might use different parts of the same resource or develop strategies that allow them to exploit the same resource without competing. For example, the distributions of other Hymenoptera [*Apis mellifera* (Linnaeus, 1758) and *Bombus terrestris* (Linnaeus, 1758)] also largely overlap with respect to the plants they pollinate; however, their pollination activities have different schedules (Perez, 2013). For the two species with most records (*D. rosae* and *D. mayri*), the most suitable areas occur in the north eastern and central parts of the Iberian Peninsula (Fig. 5C) where they overlap the suitable habitat for *D. eglanteriae/nervosa*, as mentioned above.

An overview of the distribution of *Diplolepis* in Europe

Focusing on the western Palearctic, the glaciation events in the Quaternary/Pleistocene are considered to be a key determinant of the distribution of plants and therefore that of cynipids (Taberlet et al., 1998; Hewitt 1999; Rokas et al., 2003; Stone et al., 2001; Güçlü et al., 2008). Like the Iberian Peninsula, the Anatolian Peninsula was also a glacial refugium during the European glaciations and have a rich fauna, including cynipids of the genus *Diplolepis*. Therefore, a comparative study of these two peninsulas, with either similar or parallel scenarios, can be used to define the evolutionary history of this group in the western Palearctic. In addition, the Anatolian Peninsula is the transition point between the continents of Europe, Asia and Africa, and has a great variety of natural habitats, ranging from Mediterranean, Aegean and Black Sea beaches to towering coastal and interior mountains, including deeply incised valleys, expansive steppes and fertile alluvial plains along with arid, rocky slopes. Ronquist & Liljeblad (2001) report that many of the ancestral cynipid relationships occur in the eastern Mediterranean and Turano-Eremial region, indicating that this area was possibly the centre of speciation for cynipid gallers (Mete & Demirsoy, 2012).

The absence of *D. fructuum* from the Iberian Peninsula (the only other species of western Palearctic *Diplolepis* missing in this territory) and the presence of all the European species of this genus on the Anatolian Peninsula seem to indicate an east-west gradient in the richness of species of cynipids. In the past, *D. fructuum* was considered a geographic race of *D. mayri*, but molecular techniques confirm they are different species (Plantard et al., 1997; Güçlü et al., 2008; Zhang et al., 2019). It is possible that *Diplolepis* spread from eastern Europe to the west; in this case, the Iberian Peninsula is the western limit to the distribution of this genus, with greater species richness in the Nearctic and eastern Palearctic regions.

In the case of the suitable areas for *D. eglanteriae* and *D. nervosa* there are similarities between the Anatolian and Iberian peninsulas. The most suitable areas on the Iberian Peninsula for *Diplolepis eglanteriae/nervosa* are around high-altitude large mountain ranges. This is also the case on the Anatolian Peninsula, where *D. eglanteriae* and *D. nervosa* occur in provinces enclosed by mountain ranges at altitudes greater than 2,000 m (Güçlü et al., 2008; Katılmış & Kıyak, 2010; Mete & Demirsoy, 2012). This supports the hypothesis that both the Iberian and Anatolian Peninsulas were Pleistocene glacial refugia of these species. In addition, *D. eglanteriae* and *D. nervosa* spread from western Asia into Europe along major mountain ranges, such as the Carpathians in Romania, Serbia and the Ukraine (Melika, 2006; Marković, 2015; Prázsmári et al., 2017), Malta (Mifsud, 2016) and the Scandinavian Mountains at their northern latitudinal limit (Bergqvist, 2010). Based on these facts and our distribution models, which indicate that *D. eglanteriae* and *D. nervosa* occur in the Eurosiberian

region, it is likely that glaciation events may have limited the distributions of these species, which were able to adapt to cold and high-altitude conditions (Fig. 6, Table 4). On the other hand, *D. rosae* seems to have been able to spread and adapt to different temperate conditions (Table 3), although the scarcity of this species in the southern parts of the Iberian Peninsula seems to indicate it has a Euro Siberian distribution. *Diplolepis mayri* seems to have an affinity for Mediterranean conditions as the highly suitable areas for this species are on the southern plateau of the Iberian Peninsula and complementary to those of *D. rosae* and *Diplolepis eglanteriae/nervosa*.

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Supplementary file:
Table S1 (http://www.eje.cz/2021/004/S01.xlsx). Georeferenced records of species of *Diplolepis*.