EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **122**: 210–218, 2025
doi: 10.14411/eje.2025.026
ORIGINAL ARTICLE

Distribution patterns and species richness of Notodontidae (Lepidoptera) in the Iberian Peninsula

Fernando DE JUANA[1], **João NUNES**[2] and **José Luis YELA**[3]

[1] Adriano VI, 7º-6º-izq., E-01008 Vitoria (Álava), Spain; e-mail: fdejuana@euskalnet.net

[2] Rua Eduardo Joaquim Reis Figueira, 1104 AR, P-4440-647 Valongo, Portugal; e-mail: joaomiguelfn@sapo.pt

[3] Grupo DITEG, Área de Zoología, Facultad de Ciencias Ambientales, Universidad de Castilla-La Mancha, Avda, Carlos III, s.n., Campus Real Fábrica de Armas, E-45071 Toledo, Spain; e-mail: joseluis.yela@uclm.es

Key words. Phenology, climate, temperature, Spain, Portugal

Abstract. The current spatial distribution patterns of organisms result from both historical and contemporary environmental factors, which can be challenging to identify. Previous approaches to the distribution of Palearctic and Iberian Notodontidae require revision. This study, based on the presence data of each species within 100 × 100 km UTM grid squares across the Iberian Peninsula, represents a first step in this direction. Of the 38 Notodontidae species reliably recorded from the Iberian Peninsula, 7 exhibit a Cantabrian-Pyrenean distribution pattern, 5 extend beyond this region to cover all of Galicia and northern Portugal, 7 are spread throughout the northern half of the peninsula and 11 are widely distributed. As each of these distribution patterns builds upon the previous one, the area of highest species richness is concentrated in the Cantabrian-Pyrenean zone. The number of species recorded in each grid square is influenced by the sampling effort and, to a lesser extent, by land area. However, regardless of these methodological factors, species richness correlates with two key variables: the geographical distance from the Pyrenees and the average spring-summer temperature. The decreasing gradient of species richness as one moves farther from the Pyrenees may be explained by historical southward expansions and subsequent retractions towards the continent. Additionally, the inverse correlation between species richness and average spring-summer temperature could reflect a progressive decline in species whose populations are phenologically suited to Mediterranean conditions.

INTRODUCTION

The current spatial patterns of organisms are the result of both historical and contemporary environmental factors (e.g., Whittaker et al., 2005; Bonada et al., 2009; Lomolino, 2020). However, it is difficult to pinpoint the specific variables that determine the distribution of certain species and the mechanisms involved (Parmesan et al., 1999; Galiana et al., 2023).

To explain the distribution of Palearctic notodontids, Schintlmeister (1989) first suggests that the relative scarcity of species in Europe was caused by Plesitocenic glaciations. Unlike in the eastern Palearctic, geographical barriers such as seas and mountain ranges may have hindered the retreat and subsequent expansion of many species, leading to the extinction of a significant portion of the European fauna. Furthermore, the lower species richness in the far north of the continent is attributed to climatic conditions, specifically low temperatures. Lastly, Schintlmeister posits that the low number of species in North Africa, Asia Minor, and Central Asia is likely due to the primarily forest-dwelling nature of notodontids. These regions, being sparsely forested, offer few suitable and mostly isolated habitats.

From the Iberian Peninsula, 40 species of the family Notodontidae have been reported (Vives Moreno, 2014). Of these, 37 are confirmed in this territory, while one species, *Odontosia carmelita* (Esper, 1798), is considered extinct. No reliable records were found for the remaining two species, *Clostera anastomosis* (Linnaeus, 1758) and *Notodonta torva* (Hübner, 1809) (de Juana & Nunes, 2025). Nevertheless, this number may increase in the near future due to preliminary taxonomic splits following the discovery of cryptic species (see Ortiz et al., 2023). In the central and southern parts of the peninsula, only 17 species have been recorded so far, though it should be noted that these areas have been subject to less sampling effort than the north (de Juana & Nunes, 2025). This difference in species richness between the two regions does not appear to be explained by the availability of suitable habitats, given that the main host plants of the family (genera *Salix*, *Populus*, and *Quercus*) are widely represented throughout the territory, as evidenced by the broad distribution of species like *Cerura iberica* (Templado & Ortiz, 1966) and *Harpyia milhauseri* (Fabricius, 1775). Therefore, we believe

Schintlmeister's (1989) hypotheses require more thorough verification.

This study aims to understand the distribution patterns of Iberian notodontids and to preliminarily infer the factors that influence species richness across the Iberian Peninsula.

MATERIAL AND METHODS

The faunistic and phenological information in this study is based on a compilation of bibliographic records of notodontids in the Iberian Peninsula (for more details, see de Juana & Nunes, 2025). To analyze species distribution patterns, a matrix was created to indicate the presence of each species within 100 × 100 km UTM grid squares across the peninsula. Only the 88 grid squares with more than 500 km² of land area were considered. Species richness is defined as the number of species recorded in each grid square.

Once the presence-absence matrix of the 38 Iberian species (including *Odontosia carmelita*, considered extinct) was completed for the 88 grid squares entirely or partially covering the peninsula, the Baroni-Urbani & Buser (1976) similarity index (SI) was calculated for each species pair in the matrix:

$$SI = \frac{C + \sqrt{C \times D}}{A + B + C + \sqrt{C \times D}}$$

where A and B are the numbers of grid squares where each species of a given pair is present, C is the number of grid squares where both species are present simultaneously, and D is the number of grid squares where neither species is found. Among the beta-diversity indexes, the Baroni-Urbani & Buster index is probably the simplest to interpret (e.g. Moreno, 2001).

Subsequently, we performed a cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA). To classify species based on their distribution patterns, we grouped clusters with a distance value of less than 1 on a scale from 0 to 3.

To determine the factors explaining species richness distribution (S) across the study area, we analyzed variables identified in the literature as likely predictors of species presence (Araújo & Guisan, 2006; Bede-Fazekas & Somodi, 2020; Yoon & Lee, 2021; Booth, 2022). The methodological variables tested were land area of the grid square within the Iberian Peninsula (Su), i.e., the UTM grid area excluding portions occupied by the sea or located outside the peninsula, and sampling effort (SE), estimated as the number of publications citing notodontids in each grid square, on a logarithmic scale. Geographical variables were latitude (Lat) and longitude (Lon) of the grid centroid; shortest distance from the grid centroid to one end of the Pyrenees (Dis); mean altitude above sea level (Alt); and altitudinal range (AR), defined as the difference between the maximum and minimum altitudes. Thermal variables were annual mean temperature (T = BIO1); spring-summer mean temperature (Tss), calculated as the average of monthly mean temperatures from April to September; and mean temperature of the warmest quarter (BIO10). Variables describing climate continentality were temperature variability index (BIO3), calculated as the ratio of mean daily range to annual range; temperature seasonality (BIO4), calculated as the standard deviation of monthly mean temperatures, expressed as a percentage of their mean; and spring-summer thermal amplitude (TAss), calculated as the difference between the highest and lowest monthly mean temperatures from April to September. Variables related with precipitation tested were annual precipitation (P = BIO12); precipitation seasonality (BIO15), calculated as the standard deviation of monthly precipitation, expressed as a percentage of the mean; and precipitation of the warmest quarter (BIO18). Last, as for variables describing Mediterranean climate, we tested the ombrothermic index for the warmest quarter (Ios3), calculated as the ratio of precipitation to the mean temperature during the warmest quarter.

Bioclimatic data, covering the period 1970–2000 at a spatial resolution of 30 s (approximately 0.6 km²), were obtained from www.worldclim.org (Fick & Hijmans, 2017). For each variable, the average value for each grid square was calculated using the raster statistics algorithm in QGIS 3.22.

To avoid multicollinearity, the correlation matrix of the variables was analyzed (Table 1), and for each pair with r > 0.5, the variable with the weaker correlation to species richness was excluded. This resulted in the selection of five independent, non-correlated variables (Su, Dis, Tss, BIO3, and SE), which were used to perform multiple linear regression, with species richness of notodontids in each grid square as the dependent variable.

Phenology was studied using records with registered dates, including those that did not specify the exact day, but only the month. To analyze the phenological plasticity of each species, the average deviation of observation dates was calculated. Both means and deviations assigned the midpoint of each month as the value for that month.

All statistical analyses were performed using the 'cluster' and 'fuzzySim' packages in R (R Core Team, 2014). Distribution

Table 1. Correlation matrix showing the relationships among independent variables and with the dependent variable (abbreviations are provided in the Materials and Methods section).

	Su	Lat	Lon	Dis	Alt	AR	T	Tss	BIO3	BIO4	TAss	BIO10	P	BIO15	BIO18	Ios3	SE
S	0.19	0.56	0.23	–0.51	0.4	0.42	–0.63	–0.65	–0.32	–0.11	–0.05	–0.64	0.45	–0.5	0.63	0.62	0.76
Su		–0.18	–0.08	0.04	0.26	0.25	–0.04	0.14	–0.04	0.4	0.38	0.18	–0.23	0.09	–0.32	–0.32	0.25
Lat			0.13	–0.65	0.27	0.07	–0.72	–0.8	–0.15	–0.28	–0.28	–0.81	0.58	–0.78	0.87	0.82	0.21
Lon				–0.78	0.32	0.38	–0.21	–0.1	–0.43	0.54	0.57	0.03	–0.39	–0.64	0.28	0.24	0.31
Dist					–0.44	–0.28	0.57	0.5	0.43	–0.33	–0.35	0.41	0.04	0.91	–0.62	–0.56	–0.34
Alt						0.57	–0.81	–0.65	–0.56	0.55	0.6	–0.49	0.03	–0.48	0.28	0.37	0.32
AR							–0.44	–0.34	–0.37	0.31	0.38	–0.25	0.02	–0.31	0.2	0.23	0.52
T								0.94	0.39	–0.08	–0.14	0.87	–0.47	0.69	–0.71	–0.77	–0.36
Tss									0.27	0.19	0.14	0.97	–0.61	0.67	–0.81	–0.87	–0.32
BIO3										–0.54	–0.56	0.13	0.13	0.33	–0.1	–0.13	–0.43
BIO4											0.97	0.37	–0.66	–0.18	–0.34	–0.32	0.1
TAss												0.33	–0.61	–0.19	–0.29	–0.26	0.17
BIO10													–0.71	0.59	–0.83	–0.87	–0.29
P														–0.09	0.69	0.71	0.16
BIO15															–0.74	–0.69	–0.27
BIO18																0.98	0.31
Ios3																	0.31

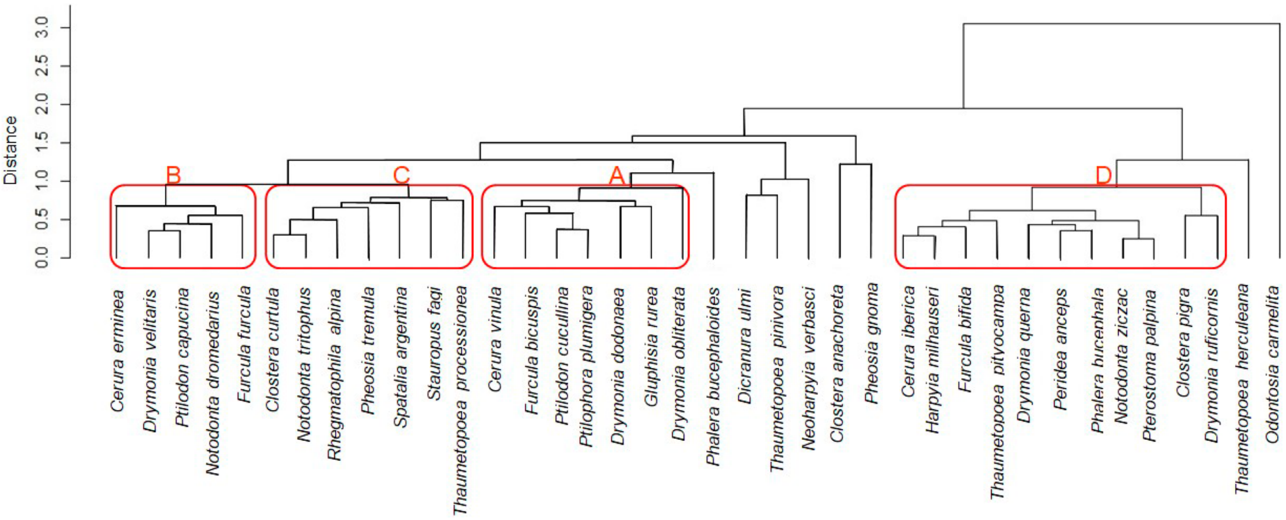

Fig. 1. Dendrogram of species similarity based on their distribution in the Iberian Peninsula and groups obtained from cluster analysis.

maps were generated using QGIS software. Species nomenclature follows de Juana & Nunes (2025).

RESULTS

At a distance value of less than 1, the dendrogram shows four clearly defined clusters of more than two species (Fig. 1). Group A includes *Cerura vinula* (Linnaeus, 1758), *Furcula bicuspis* (Borkhausen, 1790), *Ptilodon cucullina* (Denis & Schiffermüller, 1775), *Ptilophora plumigera* (Denis & Schiffermüller, 1775), *Drymonia dodonaea* (Denis & Schiffermüller, 1775), *Gluphisia rurea* (Fabricius, 1787) and *Drymonia obliterata* (Esper, 1785); group B, *Cerura erminea* (Esper, 1783), *Drymonia velitaris* (Hufnagel, 1767), *Ptilodon capucina* (Linnaeus, 1758), *Notodonta dromedarius* (Linnaeus, 1767) and *Furcula furcula* (Clerck, 1759); group C, *Clostera curtula* (Linnaeus, 1758), *Notodonta tritophus* (Denis & Schiffermüller, 1775), *Rhegmatophila alpina* (Bellier, 1880), *Pheo-*

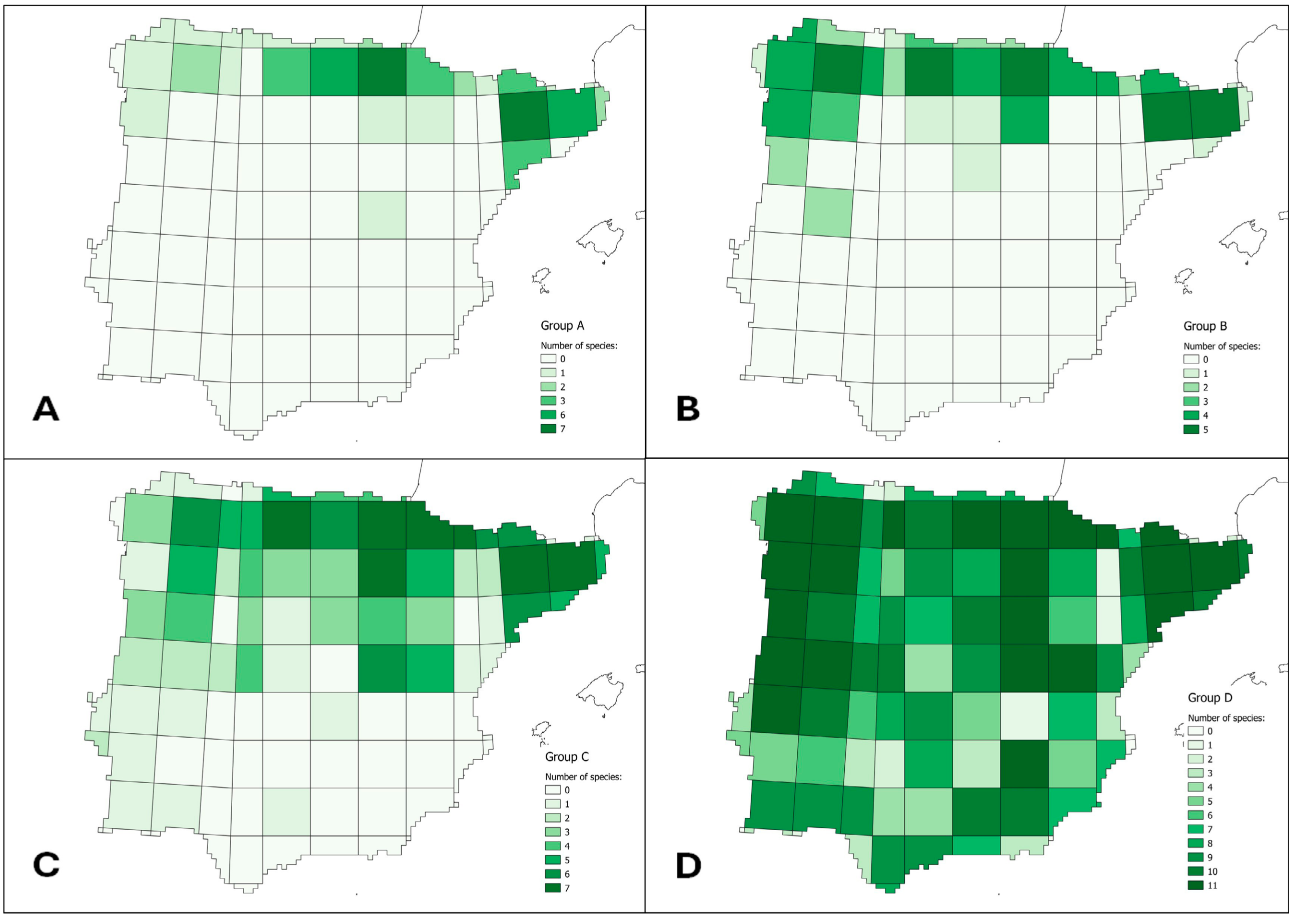

Fig. 2. Number of species recorded in each 100 × 100 km UTM grid square for each defined group.

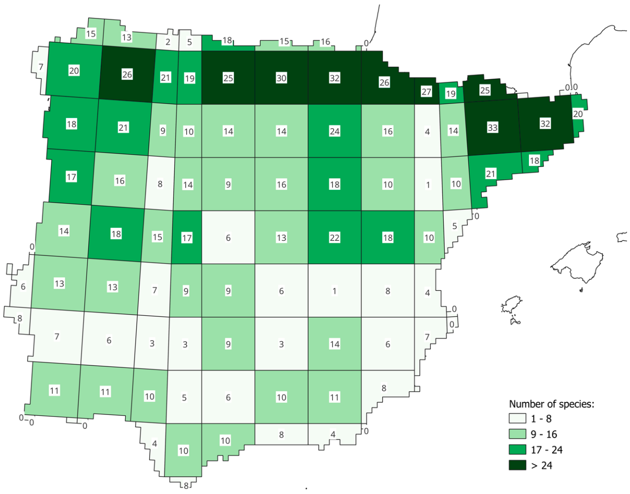

Fig. 3. Total number of notodontid species recorded in each 100 × 100 km UTM grid square (de Juana & Nunes, 2025).

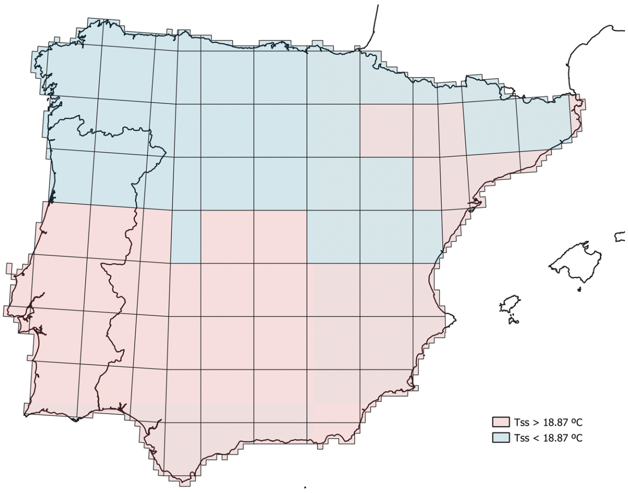

Fig. 4. Classification of the 100 × 100 km UTM grid squares of the Iberian Peninsula based on whether the Tss value for each grid square is above or below the average.

sia tremula (Clerck, 1759), *Spatalia argentina* (Denis & Schiffermüller, 1775), *Stauropus fagi* (Linnaeus, 1758) and *Thaumetopoea processionea* (Linnaeus, 1758); and finally, group D includes *Cerura iberica*, *Harpyia milhauseri*, *Furcula bifida* (Brahm, 1787), *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775), *Drymonia querna* (Denis & Schiffermüller, 1775), *Peridea anceps* (Goeze, 1781), *Phalera bucephala* (Linnaeus, 1758), *Notodonta ziczac* (Linnaeus, 1758), *Pterostoma palpina* (Clerck, 1759), *Clostera pigra* (Hufnagel, 1776) and *Drymonia ruficornis* (Hufnagel, 1766). Altogether, these four groups encompass 30 of the 38 species analyzed and represent increasing distribution ranges, with 25, 30, 56, and 88 grid squares occupied, respectively (Fig. 2).

The numbers of species from each group recorded in each grid square (Fig. 2) show no clear geographical trend; number of squares displaying particular species richness do not differ among groups (Chi2 = 7.428, d.f. = 3; p = 0.1149). On the other hand, total species richness per grid tends to decrease with greater distance from the northernmost Iberian land strip (Fig. 3).

Results of the linear regression analysis (Table 2) show that the final model is highly significant ($p < 0.001$) and explains 78.86% of the observed variance. The resulting function is: $S = 8.134 + 0.591\ (SE) + 0.120\ (BIO3) + 0.117\ (Su) - 0.434\ (Tss) - 0.147\ (Dis) + \varepsilon$. This indicates that species richness is directly proportional to sampling effort, grid square area, and temperature variability index, and inversely proportional to the distance from the Pyrenees and the mean spring-summer temperature.

Spring-summer mean temperature (Tss) is, thus, an important factor correlated with the distribution of species richness. Differences in observed distribution are related to rising temperatures, which seem to be responsible for advancing the phenology of spring univoltine species (e.g., *Cerura iberica, Peridea anceps, Harpyia milhauseri, Rhegmatophila alpina, Dicranura ulmi*) and delaying the phenology of summer univoltine species (e.g., *Phalera bucephala, Thaumetopoea pityocampa, T. pinivora, T. processionea, T. herculeana*). Both groups of species are those whose flight peak occurs before or after July 31, respectively (see Table 3 and 4 for the number of records per species by month and average date of recording in zones with above-average and below-average Tss, respectively, as defined in Fig. 4; both Table 3 and Table 4 present these data only for species with more than 10 records per zone; Fig. 5 shows the overall monthly distribution of records included in this study, separated by the zones defined in Fig. 4; Fig. 6 highlights three specific cases that clearly illustrate the effects of temperature on species phenology within each zone). The average phenological amplitude of species in each chorological group (calculated as the average devia-

Table 2. Results of the linear regression analysis.

	Model coefficients	*p*	R^2	Cumulative R^2
Dis	–0.1475	0.0224 *	26.90%	26.90%
SE	0.5909	<0.001 ***	24.13%	51.03%
Tss	–0.4339	<0.001 ***	23.78%	74.81%
Su	0.1169	0.0339 *	3.72%	78.54%
BIO3	0.1202	0.0474 *	0.32%	78.86%

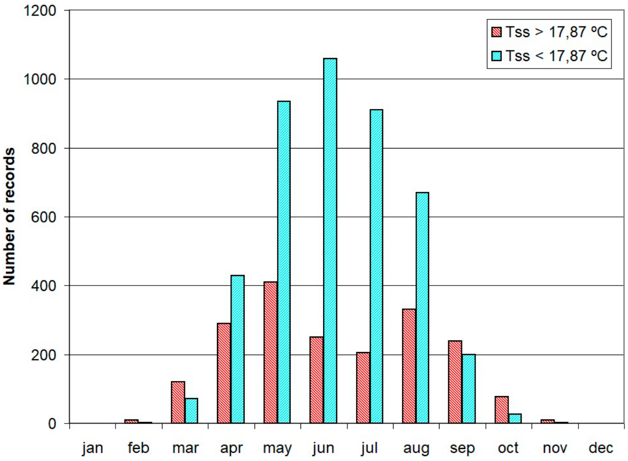

Fig. 5. Monthly distribution of adult moth observations for all analyzed species, separated by grid squares with Tss values above and below the average.

Table 3. Number of records by month for each species in grid squares with above-average (top) and below-average (bottom) Tss, considering only species with more than ten records in both zones.

Tss > 17.87°C	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec
Cerura iberica		2	32	67	63	16	5		1			
Clostera curtula		1		10	8		1	2	1			
Clostera pigra		1	1	18	12	3	7	16	2	1		
Dicranura ulmi			3	4	7							
Drymonia querna			3	19	37	36	17	31	34	9		
Drymonia ruficornis			8	16	8			3	1			
Furcula bifida			7	13	13	15	11	29	6			
Harpyia milhauseri		3	29	46	73	54	26	25	11			
Neoharpyia verbasci				1	10	4	3	4	1			
Notodonta ziczac			7	14	16	6	3	19	14	1		
Peridea anceps		2	21	53	68	4						
Phalera bucephala			1	1	7	8	22	34	28	22	5	
Pheosia tremula			1	5	5	1	4	2	3	1		
Pterostoma palpina			6	16	32	23	32	36	10			
Rhegmatophila alpina			0	3	15	18	4					
Spatalia argentina				0	22	38	26	16				
Stauropus fagi		1	2	3	7	4	6	6	3	3		
Thaumetopoea herculeana								1	30	20	3	
Thaumetopoea pinivora								8	12			
Thaumetopoea pityocampa					7	20	37	92	75	20	1	
Thaumetopoea processionea							1	7	7	1		
Total	0	10	121	289	410	250	205	331	239	78	9	0
Tss < 17.87°C	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec
Cerura iberica			10	62	100	85	11	4				
Clostera curtula			7	41	34	11	17	21	4			
Clostera pigra			6	17	12	12	31	26	16	1		
Dicranura ulmi				12	14							
Drymonia querna			3	4	31	56	97	74	12	1		
Drymonia ruficornis			17	61	60	9	3	3				
Furcula bifida			4	8	23	37	18	27	11			
Harpyia milhauseri		1	6	30	93	75	56	40	6			
Neoharpyia verbasci					17	17	6	2	3			
Notodonta ziczac			3	19	43	37	46	61	16	3		
Peridea anceps			7	80	141	59	2	1	2			
Phalera bucephala				3	22	75	119	60	11	2		
Pheosia tremula			2	30	33	24	22	59	25	1		
Pterostoma palpina			6	30	76	77	109	62	14	1		
Rhegmatophila alpina			1	22	110	268	84	6	1			
Spatalia argentina				2	81	133	89	32	3			
Stauropus fagi				7	39	51	52	28	14	3		
Thaumetopoea herculeana							1	3	16	10	1	
Thaumetopoea pinivora							5	8	2	2		
Thaumetopoea pityocampa					6	32	135	116	29	2	1	
Thaumetopoea processionea							7	37	14			
Total	0	1	72	428	935	1058	910	670	199	26	2	0

tion in observation dates) plotted against their geographical range (calculated as the total number of occupied grid squares) reveals that both variables are strongly correlated ($r^2 = 0.985$, $p < 0.01$) (Fig. 7).

DISCUSSION

Of the four distribution patterns identified, pattern A corresponds to species generally restricted to the Cantabrian-Pyrenean region, although some also appear in Galicia and Minho, as well as in the northern Iberian System and southern Catalonia (Fig. 2A). The case of *Ptilophora plumigera*, which has been recorded in the southern Iberian System, seems anomalous, leading us to believe that this species might be more widely distributed in the Iberian Peninsula than previously known (de Juana & Nunes, 2025), and thus may not fully conform to pattern A. An alternative explanation is that a relict population remained in the central peninsula following a hypothetical contraction of its distribution toward the north during the Holocene.

Group B includes species that, in addition to the previous area, also occupy all of Galicia and northern Portugal, with some species extending into the northern Meseta and the Central System (Fig. 2B). Distribution pattern C can be termed northern, comprising species spread across the entire northern half of the Iberian Peninsula, although *Stauropus fagi* and *Thaumetopoea processionea* also appear in parts of the southern half (Fig. 2C). Finally, group D corresponds to species with a wide Iberian distribution (Fig. 2D).

The eight species not included in any of the above groups exhibit unique distribution patterns: *Clostera anachoreta* (Denis & Schiffermüller, 1775) is only known from the

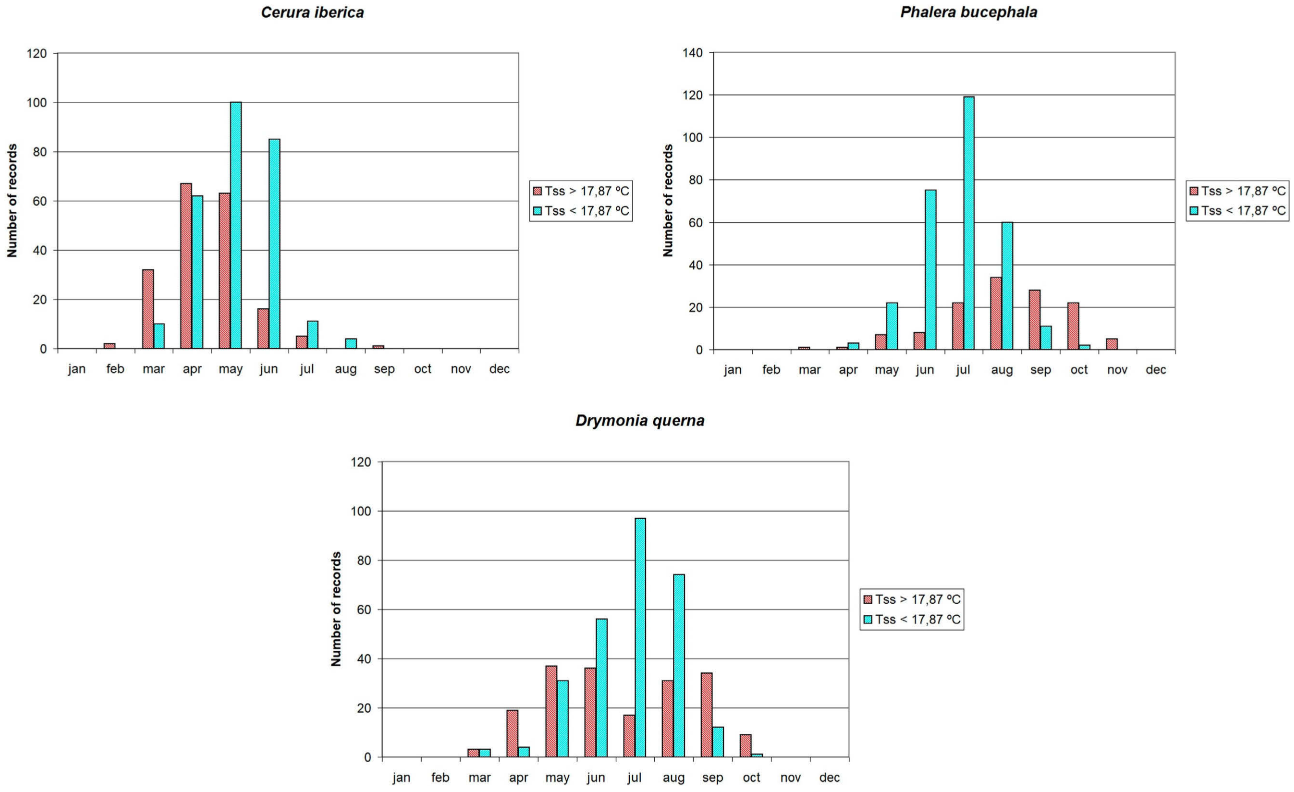

Fig. 6. Monthly distribution of adult moth observations, separating those from grid squares with Tss values above and below the average, for three species that clearly represent the effects of temperature on their respective phenologies.

Basque-Cantabrian region, representing a distribution even more restricted than pattern A. *Dicranura ulmi* (Denis & Schiffermüller, 1775) is a species that has likely become scarcier due to the spread of Dutch elm disease and may have had a wider distribution in the past. *Neoharpyia verbasci* (Fabricius, 1798) shows a fragmented distribution, seemingly associated with enclaves of the major river valleys and their tributaries, though de Juana & Nunes (2025) suggest that existing bibliographic information may be insufficient to obtain a reliable representation of the species' actual distribution. *Odontosia carmelita* (Esper, 1799) is known from only one old record, and de Juana & Nunes (2025) consider it extinct in the Iberian Peninsula. *Phalera bucephaloides* (Ochsenheimer, 1810) appears restricted to the northeastern quadrant of the Iberian Peninsula, although its resemblance to *P. bucephala* may have caused it to go unnoticed in other regions. *Pheosia gnoma* (Fabricius, 1776) is linked to birch groves, which may not have been adequately surveyed. Its recent discovery in the

Table 4. Average date of records for each species in grid squares with above-average and below-average Tss, and the difference in days between the two, arranged in descending order of this difference. Only species with more than ten records in each zone are considered.

	Tss<17.87°C	Tss>17.87°C	Difference
Cerura iberica	19-may.	27-apr.	21.7
Clostera pigra	2-jul.	11-jun.	20.9
Peridea anceps	13-may	25-apr.	17.9
Clostera curtula	30-may	14-may	16.9
Harpyia milhauseri	12-jun.	28-may.	15.6
Pheosia tremula	3-jul.	19-jun.	14.6
Notodonta ziczac	3-jul.	23-jun.	10.0
Rhegmatophila alpina	11-jun.	1-jun.	9.4
Dicranura ulmi	1-may	23-apr.	7.8
Furcula bifida	27-jun.	23-jun.	4.1
Drymonia querna	10-jul.	6-jul.	4.0
Stauropus fagi	1-jul.	28-jun.	3.2
Drymonia ruficornis	1-may	29-apr.	1.9
Pterostoma palpina	24-jun.	25-jun.	–0.1
Neoharpyia verbasci	16-jun.	17-jun.	–1.3
Spatalia argentina	21-jun.	25-jun.	–3.9
Thaumetopoea herculeana	21-sep.	28-sep.	–7.3
Thaumetopoea processionea	18-aug.	30-aug.	–11.7
Thaumetopoea pinivora	16-aug.	2-sep.	–16.9
Thaumetopoea pityocampa	28-jul.	17-aug.	–19.9
Phalera bucephala	11-jul.	19-aug.	–39.4

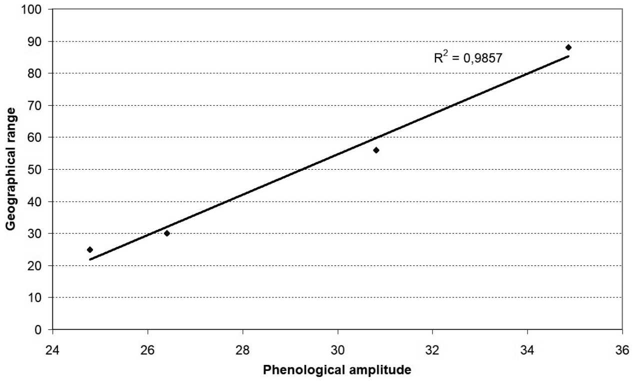

Fig. 7. Relationship between the average phenological amplitude of species in each faunistic group, calculated as the average deviation in observation dates, and their geographical range, calculated as the total number of occupied 100 × 100 km UTM grid squares.

Basque Country by one of the authors (unpubl. record) suggests a broader distribution in the Cantabrian-Pyrenean zone. *Thaumetopoea herculeana* (Rambur, 1837) differs from the rest of the species in the family because it spans throughout the south, center, and west of the Iberian Peninsula, while it appears to be absent from much of Galicia, the Cantabrian area, and the northeastern quadrant. Finally, *Thaumetopoea pinivora* (Treitschke, 1834) also has a fragmented distribution, apparently restricted to native pine forests (Hódar et al., 2016). Since each of the described distribution patterns encompasses the previous one, the zone of greatest species richness coincides with the area occupied by the species in group A.

According to the results of the multiple linear regression analysis, the number of species recorded in each grid cell is influenced primarily by sampling effort (SE), and to a lesser extent by land area covered by grid (Su). However, given equal sampling effort and land area, species richness is largely explained by a geographic variable, the distance to Pyrenees (Dis), and a climatic one, the summer-spring mean temperature (Tss). Temperature variability (BIO3) contributes little to the model.

The negative gradient in species richness from the Pyrenees to more distant areas has been observed in other groups of Iberian Lepidoptera, such as Papilionoidea, Hesperioidea and Zygaenidae (Martín & Gurrea, 1990, 2003). This has been attributed to the so-called "peninsula effect", which posits a decline in species richness from the isthmus to the farthest reaches of the peninsula due to higher extinction rates and lower immigration rates from the continent (Simpson, 1964). This theory assumes that most species in these taxa arrived in the Iberian Peninsula via the Eurasian route (Martín & Gurrea, 1990, 2003).

In the case of Notodontidae, Schintlmeister (1989) suggests that, aside from Atlantic-Mediterranean endemics such as *Cerura iberica* and *Neoharpyia verbasci*, most species reached the Iberian Peninsula from glacial refuges in the Pontic-Mediterranean and Adriatic-Mediterranean regions, or, to a lesser extent, from Western Siberia, Mongolia, or other parts of Asia, with the main route of entry being the peninsula's isthmus. However, we currently lack evidence to test this hypothesis, and it is also possible that some species occupied the Iberian region and other potential refugia in South Europe during the last glaciation and subsequently reduced their range by shifting northward during the postglacial period (see e.g. Dapporto et al., 2024). Postglacial range shifts in Iberia, especially northward, have been well-documented in other organisms, both through fossil records and molecular data (see Marabuto et al., 2023, and references therein). This challenges that the peninsula effect is associated with the arrival of most species to the Iberian Peninsula by the Eurasian route, as suggested by Schintlmeister (1989). The postglacial displacement of the distribution areas to the European continent could better explain it.

As for climate's influence on the number of species recorded in each grid cell, the most significant variable is the average spring-summer temperature (Tss), which alone explains almost 24% of the observed variance. This parameter is related to the climate's Mediterranean characteristics and the region's orography, peaking in the Guadalquivir Valley and reaching its lowest levels in higher-altitude areas. The period from April to September corresponds to the time when most Iberian Notodontidae species are in the egg, larva, or adult stage, while during the rest of the year, almost all are in diapause as pupae (e.g., Forster & Wohlfahrt, 1960; de Freina & Witt, 1987) and are thus less sensitive to temperature fluctuations (Hodek & Hodkova, 1988; Chen et al., 2014).

Of the 38 Iberian Notodontidae species, 29 are classified as Eurasian, Eurosiberian, or European, four as Palearctic, and five as Mediterranean or Atlantic-Mediterranean (de Juana & Nunes, 2025). Therefore, the predominant climates in their global ranges are continental or temperate, both of which have lower spring-summer temperatures compared to the Mediterranean climate. Temperature variability is linked to continentality, being highest in the interior of the Iberian Peninsula and lowest along the Atlantic coast. Its positive correlation with species richness may be interpreted as a preference for continental climates among these species.

The monthly distribution of adult sightings is bimodal in grid cells with above-average spring-summer temperatures and unimodal in the rest (see Fig. 5). This corresponds to the so-called "bioclimatic law" of Hopkins (1920) which states that in the temperate zones of the Northern Hemisphere, comparable seasonal events occur both before and after the summer zenith, with earlier occurrences and later delays depending on the length of the summer in a given location. This pattern has also been observed in other Lepidopteran groups, such as Noctuidae (e.g., Yela, 1992). According to Yela & Herrera (1993), the harshness of the summer drought could explain why in Mediterranean climates, adults of this family tend to emerge before or immediately after the summer, thereby "avoiding" flight during the hottest period.

This difference in observed temporal distribution is due, on the one hand, to the fact that rising temperatures advance the phenology of spring univoltine species (e.g., *Cerura iberica*, *Peridea anceps*, *Harpyia milhauseri*, *Rhegmatophila alpina*, *Dicranura ulmi*) and delay that of summer univoltine species (e.g., *Phalera bucephala*, *Thaumetopoea pityocampa*, *T. pinivora*, *T. processionea*, *T. herculeana*), with these species being those whose flight peak occurs before or after July 31, respectively (Table 4). On the other hand, some species appear to behave as univoltine in colder regions and as bivoltine or partially bivoltine in warmer ones (*Drymonia querna*, *Stauropus fagi*, *Drymonia ruficornis*, *Pterostoma palpina*, *Neoharpyia verbasci*), though in some cases the number of records is insufficient to test this hypothesis. Schintlmeister (2008) notes that some univoltine species in Central Europe, such as *Drymonia dodonaea*, *D. querna* or *Stauropus fagi*, register a partial second generation in the southern part of the continent, while other bivoltine species in the center and south, such as *Furcula furcula*, *F. bifida*, *Notodonta* *tritophus*, *N. ziczac*, *Pheosia tremula*, *Ptilodon capucina*, *Clostera curtula* or *C. anachoreta*, behave as univoltine in more northern latitudes. The monthly distribution of imago observations for three species, clearly reflecting each of the previously mentioned effects is shown in Fig. 6.

It is well-known that species adjust their annual life cycles to environmental conditions, either through a plastic response of their phenology to variables such as temperature or photoperiod, or through genetic differentiation of populations in response to these factors (Chuine, 2010). In the case of moths, Valtonen et al. (2014) found that temperature controlled the phenology of the imago stage in approximately two-thirds of the 183 species they studied in Finland. Based on the results presented in this study (Table 2), it seems that temperature also plays a significant role in determining the flight periods of Iberian Notodontidae.

According to Chuine (2010), phenology is likely the most important factor in explaining species distribution. It influences a species' ability to exploit variable resources, dictates the timing and duration of growth and reproductive phases, and is crucial for both reproductive success and individual survival. For Iberian Notodontidae, there appears to be a close relationship between the average phenological plasticity of species within each biogeographic group and the extent of their distribution (as shown in Fig. 7). However, this correlation does not imply causality, since the phenology of species and populations, as well as their respective distributions, are mutually dependent. The degree of phenological plasticity in species positively influences the breadth of their current distribution (Chuine, 2010). At the same time, a historically broader distribution of a species increases the likelihood that different populations will adjust their phenology to diverse climatic conditions. The inverse correlation between species richness and the average spring-summer temperature could be interpreted as a progressive reduction in the number of species with populations phenologically suited to Mediterranean conditions. Nonetheless, the potential influence of other variables not assessed in this study, such as the presence or selective pressure of natural enemies, cannot be ruled out (Crawley, 2009; Abrahamson & Weis, 2020).

ACKNOWLEDGEMENTS. This paper has benefited from grants Fauna Ibérica: Noctuoidea I (MICINN: PGC2018-095851-B-C63) and II (MICINN: PID2023-149039NB-I00).

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Received October 31, 2024; revised and accepted August 4, 2025