

## WHAT CAUSED THE DISJUNCT DISTRIBUTIONS OF THE *LACHNAIA TRISTIGMA* SPECIES-GROUP (COLEOPTERA: CHRYSOMELIDAE) ON THE IBERIAN PENINSULA?

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### ABSTRACT

Non-overlapping distributions of closely related species can be explained by two mechanisms, either niche divergence or vicariance in the absence of niche differentiation. We assess which of these mechanisms is the most likely cause of the disjunct distributions of three closely related species of *Lachnaia* Dejean, 1836 (Coleoptera: Chrysomelidae) on the Iberian Peninsula. We estimated the three species' climatic niches, compared them using multivariate analysis, and projected their potential distributions under climatic conditions during the Last Glacial Maximum (LGM) around 20,000 years ago. *Lachnaia tristigma* (Lacordaire, 1848) and *Lachnaia pseudobarathraea* (Daniel and Daniel, 1898) hardly differ in their climatic niches. The temperature ranges are similar among the three species, but *Lachnaia gallaeca* Baselga and Ruiz-García, 2007 occupies a fraction of the environmental space with higher precipitation. The three climatic niches present a broad overlap, which does not suggest speciation events driven by niche differentiation. In turn, the projection of their climatic envelopes to the LGM conditions shows that their potential distributions are compatible with the existence of different glacial refugia for each species. Therefore, we hypothesize that the contraction of species ranges during LGM and subsequent vicariance could have been a major mechanism behind the disjunct distributions that we observe in the present.

Key Words: leaf beetles, biogeography, climatic niche, Last Glacial Maximum, Spain

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The distribution range of a species can be defined as the portion of geographical space in which one species is present and interacts in a non-ephemeral way with the ecosystem (Zunino and Zullini 2003). Knowledge of the distribution range of species and the factors that determine their shape and size is an essential tool for assessing species invasions, assessing the impact of climate, land use, and other environmental changes on species distributions, supporting conservation planning and reserve selection, and even testing biogeographical, ecological, and evolutionary hypotheses (Guisan and Thuiller 2005).

One topic intersecting the aforementioned biogeographical, ecological, and evolutionary processes is the analysis of the factors that lead sister species to have disjunct distributions. There are several mechanisms that can lead to closely related species to have non-overlapping distributions. One of them is that closely related species can have different ecological niches (Leibold and McPeck 2006). This would imply that one species could not live in the same territories as the others because the conditions in that territory are not appropriate for their life and development. In consequence, the distribution range of the species cannot overlap. Alternatively, speciation events can occur even in the absence of niche differentiation via vicariance (Wiley and Lieberman 2011). In this scenario, one

species occupies a territory and a barrier appears, so that the distribution range splits and two or more populations are now isolated. This causes independent evolution of the separated populations that eventually leads to allopatric speciation, but if selective forces are not operating on ecological niches of the vicariant populations, these may remain identical (Wiens and Graham 2005).

In this study, we aim to assess whether the disjunct distribution ranges of three closely related species of *Lachnaia* Dejean, 1836 (Coleoptera: Chrysomelidae) are associated with different climatic niches or not. The first scenario would point to a process of niche differentiation during or after speciation, while the second case would suggest a process of allopatric speciation in the absence of selection on the climatic niche of the new species. The genus *Lachnaia* is distributed in the Western Palaearctic region, especially in the western Mediterranean area (Iberian Peninsula and France), but a few species reach the northern Afrotropical region (Codina Padilla 1958). Eight species of *Lachnaia* occur on the Iberian Peninsula (Petitpierre 2000). Three of them are included in the *Lachnaia tristigma* species-group: *Lachnaia gallaeca* Baselga and Ruiz-García, *Lachnaia pseudobarathraea* Daniel and Daniel, and *Lachnaia tristigma* (Lacordaire). These three species have extremely similar external morphologies and can only be

diagnosed by the size and shape of the median lobe of the aedeagus, the size of the sperlites of the endophallus, and the size of the spermathecal duct (Baselga and Ruiz-García 2007).

### MATERIAL AND METHODS

This study is primarily based on the data published by Baselga and Ruiz-García (2007), who reviewed the collection of the Museo Nacional de Ciencias Naturales, Madrid, Spain and established the current understanding of species delimitations based on male and female genitalia. In addition, multiple leaf beetle assemblages were sampled across the Iberian Peninsula in a subsequent study (Baselga *et al.* 2015), rendering new records of *L. gallaeca* and *L. tristigma*. The sex of the collected specimens and the coordinates of their localities (Military Grid Reference System format) were recorded. Detailed information on the procedure can be found in Baselga and Ruiz-García (2007). As a result, our dataset included the taxonomic and geographical information of 292 specimens belonging to the three species of the *Lachnaia tristigma* species-group.

To reduce the geographical biases, we conducted a bibliographical review to gather additional records of *L. tristigma* in Spain. Thus, we made two estimates of the ecological niches, one with no taxonomic uncertainty but some geographical biases (hereinafter, core dataset) and another more spatially complete but with some degree of taxonomic uncertainty due to potential misidentifications of *L. tristigma* / *L. pseudobarathraea* (hereinafter, extended dataset).

Maps of the Iberian Peninsula were created in R (R Development Core Team 2016) using a combination of packages *maps* (Becker *et al.* 2016b), *mapdata* (Becker *et al.* 2016a), *maptools* (Bivand and Lewin-Koh 2017), and *scales* (Wickham 2016). Subsequently, the points where the different species were found (core and extended datasets) were superimposed using the package *rgdal* (Bivand *et al.* 2016). We estimated the climatic niche for the three species as the  $n$ -dimensional hyper-volume ( $n$  = number of variables considered) that each species occupies in the climatic hyperspace. To do this, bioclimatic data for the Iberian Peninsula were downloaded from the website wordclim.org (Hijmans *et al.* 2017a). Next, the information of six bioclimatic factors was obtained for all points where each species was recorded in the core and extended datasets: average annual temperature; maximum temperature of the warmest month; minimum temperature of the coldest month; annual precipitation; precipitation of the wettest quarter; and precipitation of the driest quarter. These six variables were submitted to a Principal Components Analysis (PCA) with varimax

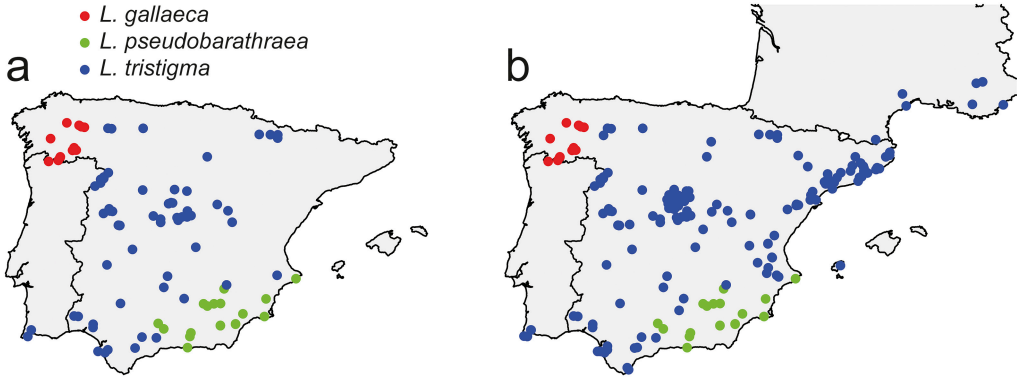
rotation (function *principal* in package *psych*, Revelle 2017) in order to represent the climatic niches in two dimensions instead of six, allowing a simpler representation of the degree of overlap of species climatic niches.

Finally, we performed two envelope models for the climatic niche of the three species, using the functions *bioclim* and *domain* (package *dismo*, Hijmans *et al.* 2017b). Both models, Bioclim (Busby 1991) and Domain (Carpenter *et al.* 1993), are strictly a presence-only method, thus allowing us to approximate the potential distributions of clades rather than their realized distributions (Jiménez-Valverde *et al.* 2008). To do this, the probabilistic model outputs were converted into presence-absence values using as the cut-off the quantile 0.05 of the presences, projecting their potential distributions under the climatic conditions of Last Glacial Maximum (LGM, around 20,000 years ago) (Braconnot *et al.* 2007).

### RESULTS

The geographic distributions of *L. gallaeca*, *L. pseudobarathraea*, and *L. tristigma* on the Iberian Peninsula based on the core dataset (no taxonomic uncertainty, but some spatial biases) are shown in Fig. 1a. The distribution ranges based on the extended dataset (higher spatial completeness, some degree of taxonomic uncertainty) is shown in Fig. 1b. The known distribution ranges jointly occupy almost all of the Iberian Peninsula. *Lachnaia gallaeca* is located exclusively in the inland mountains of Galicia (northwestern Spain), occupying a narrow range in the provinces of Lugo and Ourense. Some localities are extremely close to the Portuguese border, although no specimen has been yet collected in Portugal. *Lachnaia pseudobarathraea* is located in the southeastern portion of the Iberian Peninsula, in an area larger than that occupied by *L. gallaeca*. Its distribution is spindle-shaped, flanked to the south by the Mediterranean Sea and to the north by the Subbaetic and Prebaetic mountain ranges. *Lachnaia tristigma* is distributed throughout the central part of the Iberian Peninsula, reaching the Atlantic coast in the Southwest (including southern Portugal) and entering France across the Pyrenees in the Northeast.

The two axes of the climatic PCA explained 93% of the variance in the core dataset. For the extended dataset, the variance explained by two axes was 87%. Therefore, climatic niches are represented in two dimensions (Fig. 2), the first one correlated with the precipitation variables ( $r = 0.96$  with annual precipitation,  $r = 0.98$  with precipitation of the wettest quarter), the second one correlated with the temperature variables ( $r = 0.94$  with average annual temperature,  $r = 0.96$  with the minimum temperature of the coldest month). *Lachnaia gallaeca* occupies a fraction of the environmental space



**Fig. 1.** Known records for *Lachnaia gallaeca* (red dots), *Lachnaia pseudobarathraea* (green dots), and *Lachnaia tristigma* (blue dots), using the core (a) and extended (b) datasets.

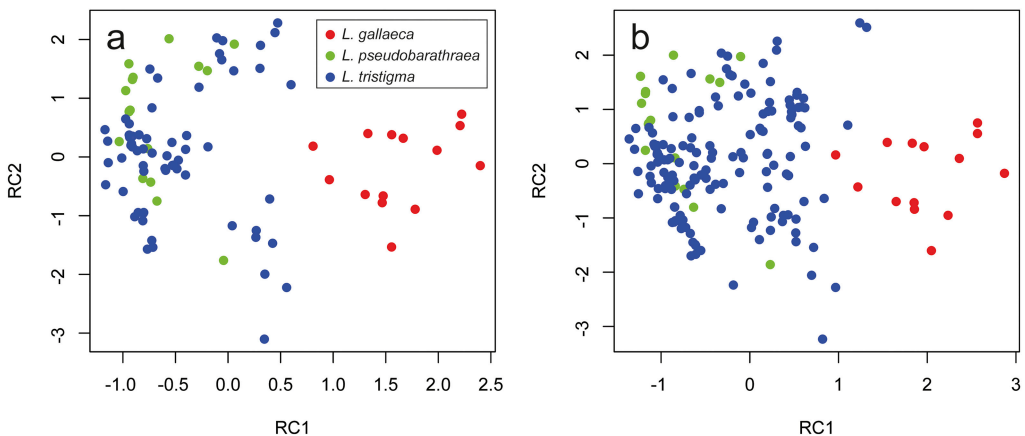
characterized by higher precipitation values than the other species. However, the temperature ranges are similar among the three species, although *L. pseudobarathraea* and especially *L. tristigma* live in a wider range of temperatures. The climatic niches of *L. tristigma* and *L. pseudobarathraea* widely overlap, although the climatic range occupied by *L. tristigma* is wider (therefore, the niche of *L. pseudobarathraea* is a subset of that of *L. tristigma*). Extreme precipitation values for *L. tristigma* overlap with the precipitation range of *L. gallaeca*, unlike their geographic distributions.

The potential distributions of the three *Lachnaia* species under LGM climatic conditions are shown in Fig. 3. This projection shows that *L. gallaeca* was likely restricted to glacial refuge in western Iberian Peninsula, completely isolated from the other two

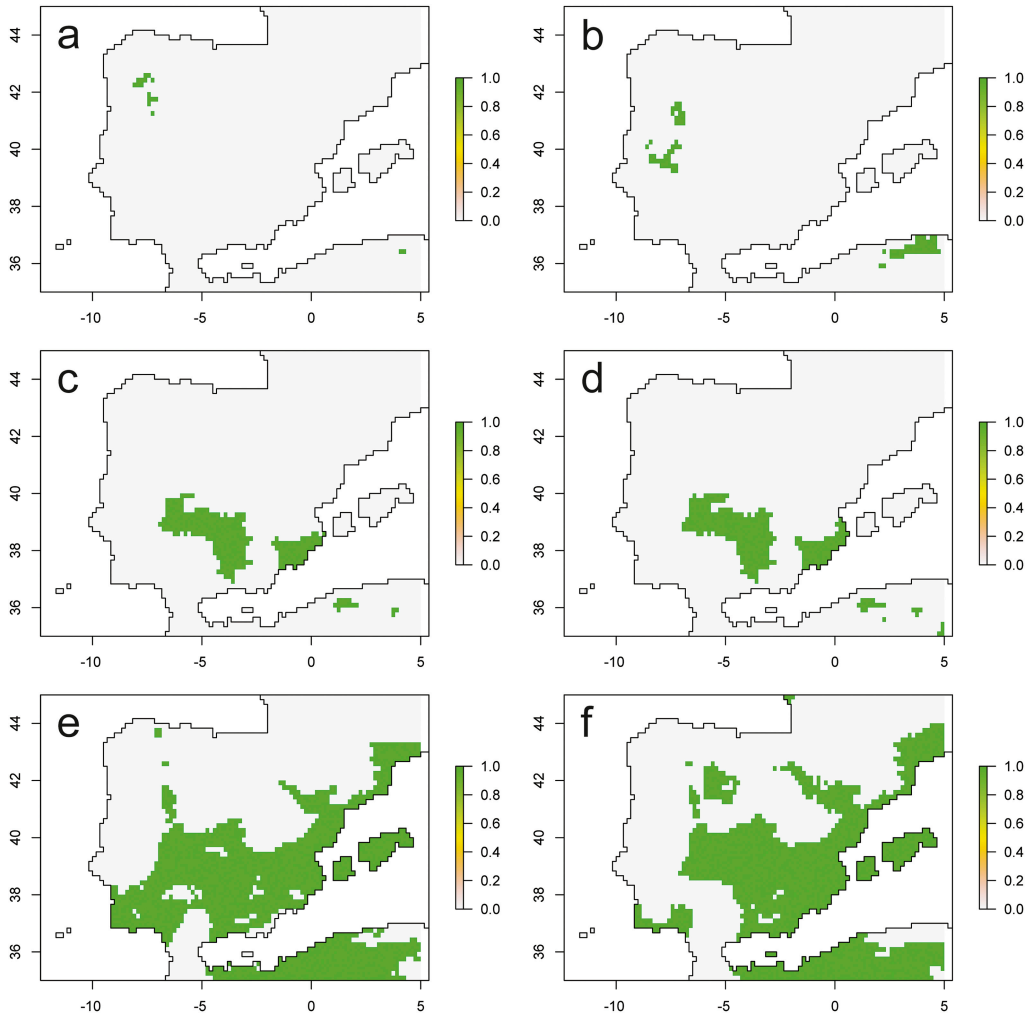
species. The potential distributions *L. tristigma* and *L. pseudobarathraea* during the LGM overlap in some regions of southern Spain, but the projected distribution range of *L. tristigma* was much wider.

## DISCUSSION

The geographic ranges of *L. gallaeca*, *L. pseudobarathraea*, and *L. tristigma* occupy distinctly defined regions of the Iberian Peninsula and show no overlap. One hypothesis to explain the three disjunct distributions could be that the species occupy different climatic niches. This would imply that each species could not live in the same territories as the others because the conditions in that territory are not appropriate for their development.



**Fig. 2.** Climatic niches of *Lachnaia gallaeca* (red dots), *Lachnaia pseudobarathraea* (green dots), and *Lachnaia tristigma* (blue dots), as represented in two Principal Components Analysis axes (first axis (RC1) is correlated with precipitation; second axis (RC2) is correlated with temperature) for the core (a) and extended (b) datasets.



**Fig. 3.** Potential distributions of *Lachnaia gallaeca* (a, b), *Lachnaia pseudobarathraea* (c, d), and *Lachnaia tristigma* (e, f) during the Last Glacial Maximum as estimated from Bioclim (a, c, e) and Domain (b, d, f) models.

Fig. 2 shows that *L. tristigma* and *L. pseudobarathraea* have very similar climatic niches (the latter being a subset of the former). *Lachnaia gallaeca* occupies a different part of the climatic space, characterized by higher precipitation values (although still with some overlap with *L. tristigma*) but the same range of temperatures as for the other two species. Based on this, the broad overlap among the three climatic niches does not support the idea of a speciation event linked to niche differentiation.

The alternative hypothesis is a speciation process via vicariance, with no niche differentiation involved. According to this hypothesis, several populations of an ancestral species would have been isolated in different locations and started a speciation process

resulting in the species that can be delimited today. Range fragmentation can be caused by multiple processes of different nature, including topographic barriers. In the the Iberian Peninsula, a plausible explanation would be the extreme climatic changes that occurred during the Pleistocene glaciations (from 2.5 million years to 10,000 years ago) (Pisias and Moore 1981). Those cooling episodes could have caused the contraction of a species' population distributions and, eventually, the fragmentation of ranges in different refugia (Hewitt 2000). This episode of contraction would be analogous to that described by Wiens (2004) and Baselga *et al.* (2011), but with fragmentation occurring in the lowlands during cold periods. In the case of the

*Lachnaia tristigma* species-group, separate populations of an ancestral species residing on the Iberian Peninsula would have remained in different glacial refugia during these episodes (Provan and Bennett 2008). Therefore, these populations would have been isolated, and, eventually, they would have undergone a process of allopatric speciation, resulting in the three species that we know now. This hypothesis is supported by our projection of the three potential distributions under LGM climatic conditions (Fig. 3), which are compatible with the existence of separated refugia: one in the northwest; another in the southeastern portion of the peninsula; and one in the central plateau or even the northeastern Iberian Mediterranean coast.

For *L. gallaeca*, the potential distribution during the LGM is close to the species' present distribution. Although the overlap is slight, it is plausible that *L. gallaeca* was isolated in northern Portugal during LGM, and the species began to expand its geographic distribution when the climatic conditions became warmer, arriving in northwestern Spain. It is even possible that the species will be detected in Portugal in the future, matching its LGM distribution from where the species could have expanded towards the Galician mountain ranges. The potential distribution of *L. pseudobarathraea* during the LGM occupies part of southern and southeastern Iberian Peninsula. The present distribution range of this species is located in southeastern Spain, broadly overlapping the potential distribution in the LGM. The same occurs for *L. tristigma*; its present distribution and potential distribution in the LGM broadly overlap.

Taken together, these results support the allopatric speciation hypothesis and suggest that the present-day disjunct distributions of *L. gallaeca*, *L. pseudobarathraea*, and *L. tristigma* are largely the consequence of speciation via fragmentation during Pleistocene glacial episodes. Once the last glaciation had retracted and the climatic conditions were favorable for the species, there was no longer a barrier that prevented their dispersion. Thus, each of the three differentiated evolutionary lineages could colonize adjacent territories (Stewart *et al.* 2009). The present-day distributions do not show evidence of this, as they remain disjunct despite the broad niche overlap, suggesting that dispersal is limited in these species, despite their flying ability.

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