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Niche segregation in Iberian *Argiope* species

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Abstract. The ecological niches of the three Iberian *Argiope* species have not been studied in quantitative detail, and recently developed approaches for assessing niche overlap have rarely been applied to invertebrates. This study aimed to quantify the climatic niche differences between *Argiope bruennichi* (Scopoli, 1772), *A. lobata* (Pallas, 1772) and *A. trifasciata* (Forsskål, 1775) in the Iberian Peninsula. An extensive occurrence database for the three species was compiled from the literature, a citizen science project (Biodiversidad Virtual) and a social network (Flickr). Niche comparison and recursive partitioning analyses were used to compare and characterize the niches of these species using regional climatic information. The three *Argiope* species had different distribution patterns within the Iberian Peninsula with a clear degree of sympatry. Despite an appreciable niche overlap, the three species had significantly different climatic niches. *A. bruennichi* was present in colder and more humid environments, while *A. lobata* and *A. trifasciata* selected warmer, drier environments. *A. trifasciata* preferred areas with higher minimum temperatures than *A. lobata* and avoided continental environments that the two other species tolerated. Despite these differences, the Iberian Peninsula contained a broad range of suitable environments where more than one species co-occurred. Further studies are needed to explore these species relationships, particularly given the trend of ranges shifting north due to global warming. Considering both the results of this study and the increasingly xeric conditions in the Iberian Peninsula, *A. lobata* and *A. trifasciata* may benefit at the expense of a retraction of *A. bruennichi*.

Keywords: Distribution, climatic niche, Iberian Peninsula, segregation

Within the Araneidae family, *Argiope* Audouin, 1826 is one of the most diversified genera, with 86 recognized species (World Spider Catalog 2018). *Argiope* species are large spiders characterized by their conspicuously colorful abdomens. They weave orb-webs that typically include a stabilimentum. These webs are generally located in open areas and positioned close to the ground where they are held by low vegetation (Levi 1968, 1983; Levy 1997). The genus has a worldwide distribution, only being absent from the coldest areas (Levi 1983). Three species are known to be present in the Iberian Peninsula: *A. bruennichi* (Scopoli, 1772), *A. lobata* (Pallas, 1772) and *A. trifasciata* (Forsskål, 1775). These are also the three *Argiope* species with the widest global distributional ranges. *Argiope bruennichi* is a Palearctic species, *A. lobata* is present in southern Europe, central Asia, Africa and Australia, and *A. trifasciata* is a cosmopolitan species, originally from America, that has been introduced in many regions around the globe (World Spider Catalogue 2018).

Little detailed knowledge exists about the habitat preferences of these species in Europe (Castilla et al. 2004). *Argiope bruennichi* usually occupies natural and semi-natural habitats that are open and moist (Heimer & Nentwig 1991; Roberts 1995; Harvey et al. 2002; Bellmann 2011), although it can also be found in dry grasslands and barren habitats (Bellmann 2011). Since the first decades of the twentieth century, this species has consistently expanded its European range towards the northern latitudes (Bratli & Hansen 2004; Terhivuo et al. 2011; Fritzén et al. 2015). This expansion has been particularly evident since the 1990s, with the species reaching Sweden, Finland and Norway, much colder places than its original distribution at the beginning of the twentieth century (Kumschick et al. 2011; Krehenwinkel et al. 2015). Compared to *A. bruennichi*, *A. lobata* is a more xero-thermophilic species (Di Pompeo et al. 2011). *Argiope lobata* typically inhabits open habitats in the Mediterranean region that are hot, dry and arid (Heimer & Nentwig 1991; Bellmann 2011). In Europe, *A. trifasciata* is only known in southern Portugal, south-eastern Spain, Sicily, Sardinia, Corsica and Malta (Di Pompeo et al. 2011; Ponel et al. 2017), and its presence in these regions is likely the result of arrivals from Africa (Di Pompeo et al. 2011). Compared to the two other European species, *A. trifasciata* appears to be more of a thermophile, frequenting coastal and low altitude areas with scarce frost periods and closely associating with typical Mediterranean xerophytic vegetation (Di Pompeo et al. 2011). Nevertheless, detailed quantitative studies of the ecological niche differences among these three *Argiope* species on a regional scale are lacking.

New sources of primary biodiversity data have made possible the compilation of a significant amount of georeferenced occurrence records that have enabled the refinement of distributional range maps (Acevedo et al. 2016). In addition, the development of geographical information systems (GIS) provides easily accessible environmental information for almost any part of the globe (Acevedo et al. 2016). In general, a species will be present in those areas with environmental conditions favorable to the establishment, survival and reproduction of the individual members (Hutchinson 1957; Colwell & Rangel 2009). Thus, by cross-referencing the information provided by the biodiversity and environmental databases, one can estimate something close (or at least related) to the Grinellian niche, which is defined by the environmental conditions relevant to understanding the coarse-scale ecological and geographic properties of a species (Grinnell 1917; Soberón 2007). The development of this conceptual framework (see Peterson et al. 2011 for an extensive elaboration) has opened new research avenues in conservation, biogeography and evolution (Franklin 2009; Peterson et al. 2011; Guisan et al. 2017). Niche comparison techniques have contributed to a better understanding of the broad distribution patterns of closely related species (see Peterson et al. 2011, chapter 15).

This study characterized and quantified the environmental niche differences among *A. bruennichi*, *A. lobata* and *A. trifasciata* in the Iberian Peninsula. We expected to find statistically significant differences between the species niches, with *A. bruennichi* having the broadest and most distinct niche, while the niches of *A. lobata* and *A. trifasciata* would be the most similar. The most important climatic variables were identified along with the threshold values that discriminated occurrence records between species.

METHODS

Geographical extent of analysis.—Niche analyses require explicit geographical delimitations (Barve et al. 2011). The Iberian Peninsula, separated from north Africa by the Strait of Gibraltar and from the rest of Europe by the Pyrenees, has been described as an "almost-island" (Loidi 2017) and constitutes a unique biogeographical unit (Rueda et al. 2010; Olivero et al. 2013). The Iberian Peninsula represents a natural, neat and self-evident geographical extent for niche analyses.

Occurrence data.—A comprehensive occurrence database was compiled for the three target species (*A. bruennichi*, *A. lobata*, *A. trifasciata*) within the Iberian Peninsula, using the literature, the Biodiversidad Virtual database (BV) and Flickr (See Appendix 1 for data sources, available online at http://dx.doi.org/10.1636/JoA-S-18-054.s1). The Iberian Spider Catalogue (Morano et al. 2014) was used as a starting point, and an exhaustive literature review was performed up to 2017. Dubious records or records that could not be ascribed to a 10 × 10 km Universal Transverse Mercator (UTM) square were discarded. Additional data points were obtained from the Spanish Biodiversidad Virtual project, a scientific outreach platform based on cooperative work and citizen participation (online at http://www.biodiversidadvirtual.org). Data were accessed on 31 December 2017; all the data had been previously checked for the correct identification by experts and were referenced to a 10 × 10 km UTM grid. Finally, a collection of presence data for the three species was downloaded from the Flickr photo-sharing social network (Flickr Development Team 2014) following Barve (2014). The bdsns package (Barve 2018) for R (R Development Core Team 2018) was used to extract the data. The queries contained an exhaustive list with the scientific and common names of the species in different languages together with the geographical area of interest. The dataset was downloaded from the Flickr website on 24 March 2018. The extracted dataset was then subjected to a deep cleaning process. First, data points outside the Iberian Peninsula or without enough georeferenced precision were removed. Second, the records were reviewed to correct any misidentifications. Doubtful images that hampered accurate identification were discarded. As with the other databases, the records were referenced to a 10 × 10 km UTM grid.

At the end of the compilation procedure, 929 UTM cells out of the 6213 UTM cells that covered the Iberian Peninsula had occurrence data of at least one of the three species. For *A. bruennichi*, 100 records were obtained from the literature, 436 records from Biodiversidad Virtual, and 136 from Flickr. For *A. lobata*, 51 records were obtained from the literature, 285 records from Biodiversidad Virtual, and 79 from Flickr. In the case of *A. trifasciata*, 14 records were obtained from the literature, 163 records from Biodiversidad Virtual, and 57 from Flickr. A total of 595 unique records for *A. bruennichi*, 384 for *A. lobata* and 210 for *A. trifasciata* were available (Fig.1). More than one species were found in 260 UTM cells.

Environmental data.—For each 10 × 10 km UTM cell in the Iberian Peninsula, the mean monthly and annual climatic variables (maximum and minimum temperature and total precipitation) for the period of 1971–2000 were averaged from 1-km resolution raster climatic models provided by the Spanish Meteorological State Agency (AEMET). Then, the following seven climatic variables were extracted (following Hijmans et al. 2005): mean annual minimum temperature (TMin, in °C), mean annual maximum temperature (TMax, in °C), temperature range (TRange, in °C, calculated as the difference between the mean maximum temperature of the hottest month and the mean minimum temperature of the coldest month), isothermality (IsoTher, in percent, calculated as the mean monthly temperature range divided by TRange and multiplied by 100), mean total precipitation of the driest month (PMin, in mm.), mean total precipitation of the wettest month (PMax, in mm.) and precipitation seasonality (PSeason, in percent, calculated as the standard deviation of the mean monthly total precipitation divided by its mean value and multiplied by 100). Finally, the mean annual aridity values (Ari, calculated as the mean annual precipitation divided by the mean annual potential evapo-transpiration) for each 10 × 10 km UTM cell were obtained from the 30 arc seconds resolution CGIAR-CSI Global-Aridity and the Global-PET Database (Zomer et al. 2007, 2008; online at http://www.cgiar-csi.org) and were clipped, re-projected and averaged. Ari values classify as follows: < 0.03, hyper arid; 0.03–0.2, arid; 0.2–0.5 semi-arid; 0.5–0.65 dry sub-humid; > 0.65, humid. The correlation chart of the eight climatic variables is provided in Appendix 2 (available online at http://dx.doi.org/10.1636/JoA-S-18-054.s2). GIS analyses were conducted using the QGIS Wien Desktop version 2.8.1 (online at http://www.qgis.org).

Statistical analyses.—The environmental principal component analysis (PCA-env) method described by Broennimann et al. (2012) was used to characterize and compare the realized climatic niches of the three *Argiope* species, since this method has been shown to perform best compared to other techniques (Broennimann et al. 2012). First, a PCA was performed on the eight climatic variables. Second, a grid of 100 × 100 cells was laid over the ordination space delimited by the first two PCA axes, and a kernel density function was then used to create occurrence density plots for each *Argiope* species. Third, the observed overlap in the occurrence densities between each pair of species was estimated using the Schoener's D metric (D_{obs}), since this metric has been shown to perform better than other overlap indexes (Rödder & Engler 2011). The D values range from zero for niches that have no overlap to one for niches that are identical. Fourth, the niche identity test originally proposed by Warren et al. (2008) was performed. For this test, the pooled occurrences of a pair of species were randomly assigned to one or another species and the overlap (D_{sim}) of these new simulated species was calculated. Each simulated species had the same number of occurrences as the original species. For each pair of species, this procedure was repeated 100 times to obtain the D_{sim} distribution, which could be used to assess whether D_{obs} was significantly lower (niche divergence hypothesis) than random. For further details about the implementation of the PCA-env method, see Broennimann et al. (2012). The analyses were performed with the ecospat package (Broennimann et al. 2017) for R.

Recursive partitioning was performed to identify the main variables that discriminated between the occurrence records of pairs of species and to obtain a better understanding of the partitioning of the climatic niches. Classification trees (Breiman et al. 1984) were run in R using the rpart package (Therneau & Atkinson 2018a) with a three-class categorical variable as a response (first species, second species or both) and the eight environmental variables as predictors. First, a tree was built using the Gini coefficient as an impurity measure with the complexity parameter set to zero and the maximum number of surrogate splits set to seven. A 10-fold cross-validation was used to estimate the relative error. This tree was pruned using the 1-[Standard Error] criterion to obtain a final parsimonious tree (Breiman et al. 1984), and the importance of each environmental variable was measured considering the decrease in impurity both when the predictor was the primary variable and when it was a surrogate (see Therneau & Atkinson 2018b for further details).

The occurrence density curves were used to visualize the response of the species to the most important variable in each species pair. These curves were prepared using the ecospat package.

RESULTS

The three *Argiope* species had different distribution patterns within the Iberian Peninsula (Fig. 1). *Argiope bruennichi* was widely distributed throughout the Iberian Peninsula and was notably more present along the mid-northern latitudes than in the south. In contrast, *A. lobata* occurred on the mid-eastern part of the Iberian Peninsula and avoided the northern areas along the Galician massif and the Cantabrian mountains. *Argiope trifasciata* showed a coastal distribution along the south-eastern areas except for a few inland occurrence points in the central parts of the Iberian Peninsula.

The first two PCA axes accounted for 75.5% of the original variance in the climatic data (see Appendix 3, available online at http://dx.doi.org/10.1636/JoA-S-18-054.s3). Axis 1, which accounted for 46.4% of the variance, had a generally positive relationship with PMax, PMin and Ari and a negative relationship with TMax and TMin (see Appendix 3). Axis 2, which accounted for 29.1% of the variance, generally showed a negative relationship with TMin, PMax and PSeason and a positive relationship with TRange (see Appendix 3). The climatic spaces of the three species revealed a nested pattern (Fig. 2). *A. bruennichi* occupied most of the climatic conditions present in the Iberian Peninsula, although its centroid was shifted towards the positive values of axis 1 with respect to the region‘s average conditions (the central point of the diagram) (Fig. 2). The climatic space of *A. lobata* was a subset of the *A. bruennichi* space, avoiding the higher values of axis 1. Also, the centroids of both species were clearly separated along axis 1,

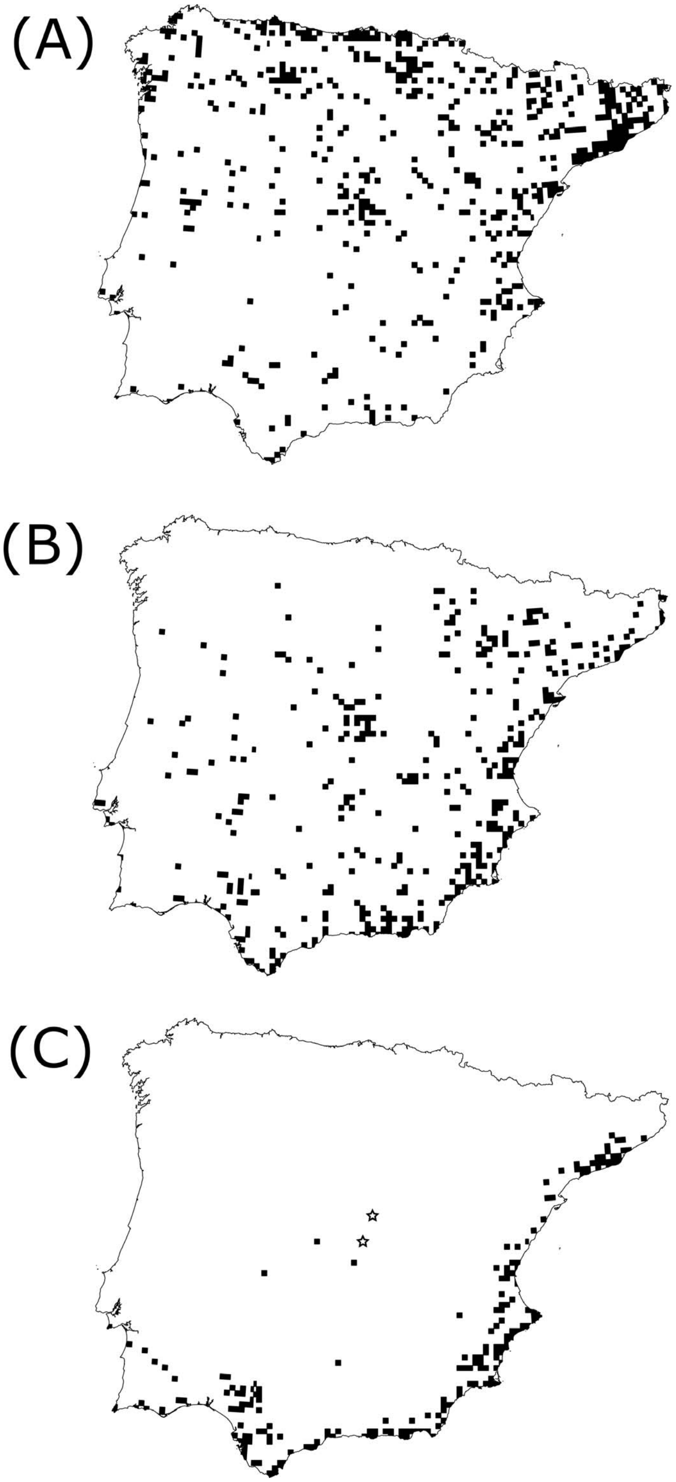

Figure 1.—The observed species occurrence for (A) *A. bruennichi*, (B) *A. lobata* and (C) *A. trifasciata* within the Iberian Peninsula. Each square corresponds to a Universal Transverse Mercator (UTM) 10×10km grid cell. In (C), empty stars correspond to new records not used in the analyses (see Discussion).

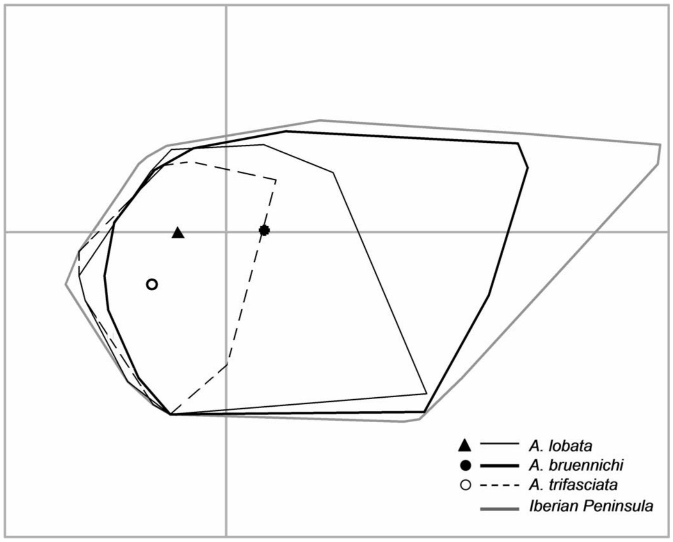

Figure 2.—The ordination space delimited by the first two principal component analysis (PCA) axes showing the contour polygons and the centroids of the point clouds for each species (*A. bruennichi*, a large polygon comprising a thick black line and a solid circle; *A. lobata*; a medium-sized polygon and a solid triangle; and *A. trifasciata*, a smaller polygon comprising a thin black line and a white circle). The environmental conditions present in the Iberian Peninsula are delimited by a convex hull in gray color.

with *A. lobata* tending to occupy lower values than *A. bruennichi* (Fig. 2). The distance between both centroids in the PCA space was 1.946. *A. trifasciata* had the narrowest climatic space, restricted to the lowest values of axis 1. Compared with the other two species, its centroid was displaced toward the negative values of axis 2 (Fig. 2). The distance between the centroids of *A. trifasciata* and *A. bruennichi* was 2.811, while between *A. trifasciata* and *A. lobata* was 1.262. The three species had significantly non-equivalent niches (Fig. 3), although the niche overlap values differed between the pairs of species: $D_{obs} = 0.32$ ($P < 0.01$) for *A. bruennichi*-*A. lobata*; $D_{obs} = 0.16$ ($P < 0.01$) for *A. bruennichi*-*A. trifasciata*; and $D_{obs} = 0.62$ ($P < 0.05$) for *A. lobata*-*A. trifasciata*.

Regarding the recursive partitioning analyses, in the case of the *A. bruennichi*-*A. lobata* pair, a final tree with three leaves (Fig. 4A) was retained (Appendix 4, available online at http://dx.doi.org/10.1636/JoA-S-18-054.s4), resulting in a total classification error rate of 0.321, with 93.5% of the *A. bruennichi* records well-predicted, 56.1% of the *A. lobata* records well-predicted, and zero records predicted as pertaining to both species. The analysis showed that 74% of the records pertaining to both species were classified as *A. bruennichi* records. The most important variable was PMin, which was also the variable that most reduced impurity in the two splits (Figs. 4A, 5A). The tree could be interpreted as a single split tree with two leaves and a single classification rule, that is, PMin values equal to or higher than 8.4 mm. assigned occurrences to *A. bruennichi* and lower values assigned occurrences to *A. lobata*. *Argiope bruennichi* selected areas with higher PMin values than the average Iberian values, while *A. lobata* avoided those areas with the highest PMin values (Fig. 5A).

In the case of the *A. bruennichi*-*A. trifasciata* pair, a final tree with only two leaves (Fig. 4B) was retained (Appendix 4), resulting in a total classification error rate of 0.169 with 92.8% of the *A. bruennichi* records well-predicted, 87.9% of the *A. trifasciata* records well-predicted, and zero records predicted as pertaining to both species. The analysis showed that 65.2% of the records pertaining to both species were classified as *A. trifasciata* records. The most important variable was TMin; values lower than 10°C assigned occurrences to *A. bruennichi* (Figs. 4B, 5B). *Argiope trifasciata* preferentially selected areas with higher TMin values than the average Iberian values, and it avoided areas with TMin values lower than about 5°C; these lower TMin areas were tolerated by *A. bruennichi* (Fig. 5B).

In the case of the *A. lobata*-*A. trifasciata* pair, a final tree with three leaves (Fig. 4C) was retained (Appendix 4), resulting in a total classification error rate of 0.320, with 82.7% of the *A. lobata* records well-predicted, 46.8% of the *A. trifasciata* records well-predicted, and 49.5% of the records pertaining to both species well-predicted. The most important

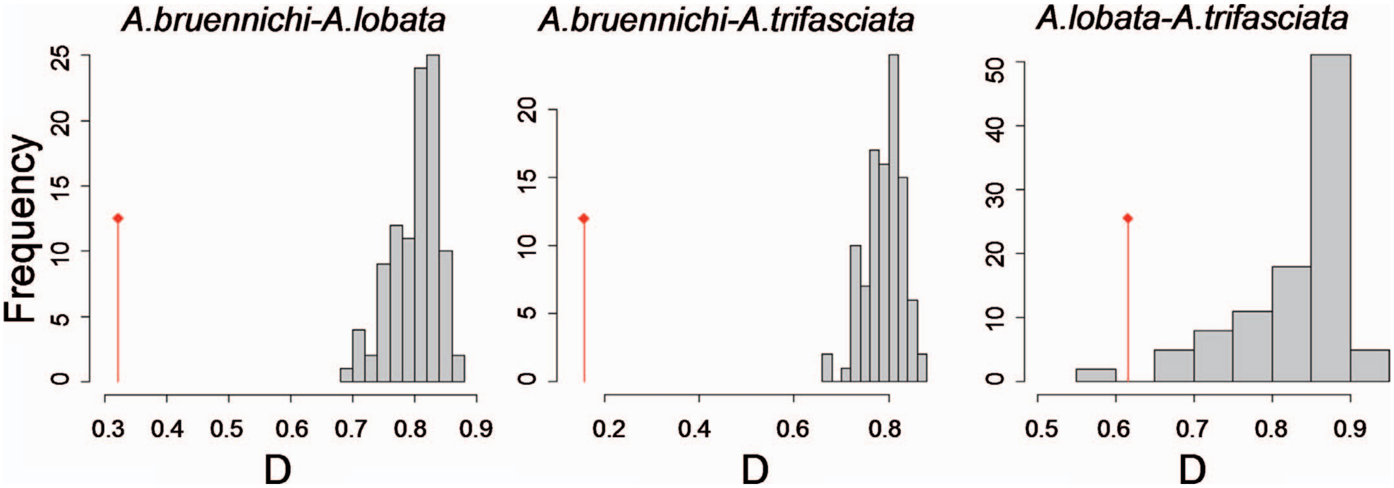

Figure 3.—The distribution of the simulated Schoener's D metric (D_{sim}, bars) from the niche identity tests for each pair of species. The observed Schoener's D metric (D_{obs}) is indicated with a dot and vertical line.

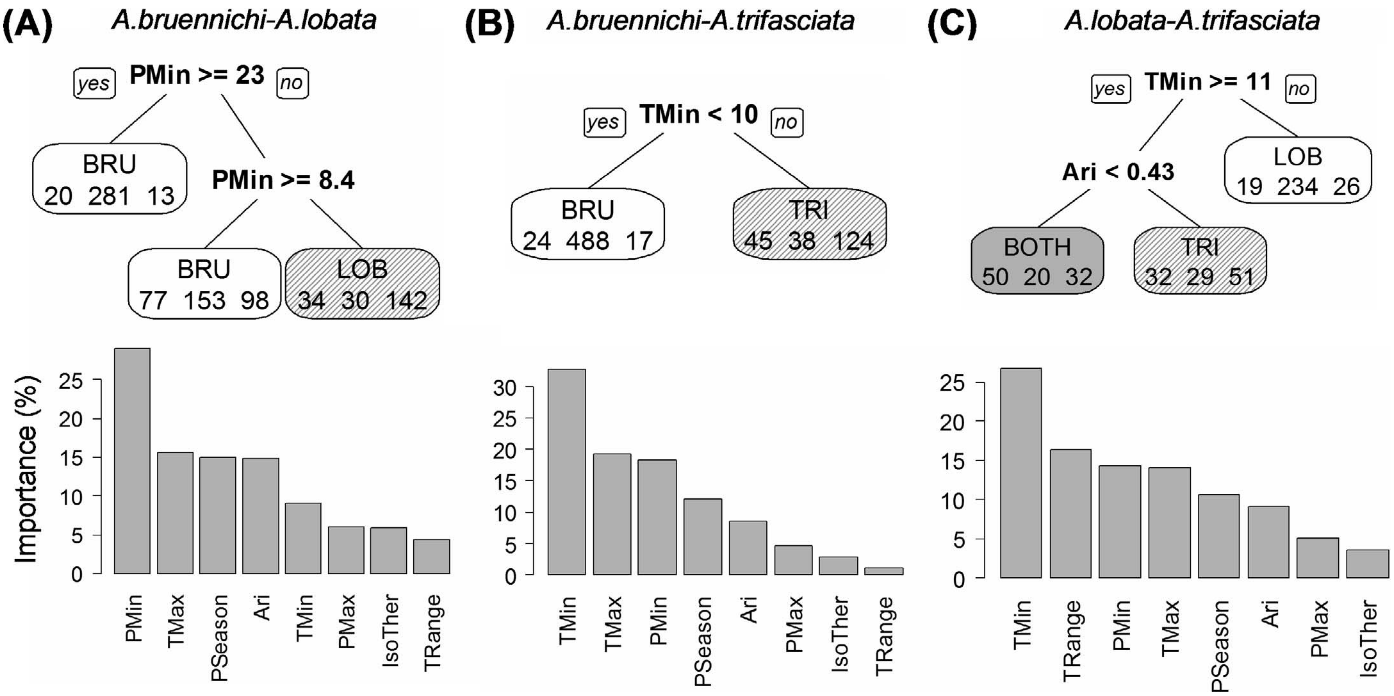

Figure 4.—The classifications trees for each pair of *Argiope* species: (A) *A. bruennichi* (BRU)-*A. lobata* (LOB); (B) *A. bruennichi* (BRU)-*A. trifasciata* (TRI); and (C) *A. lobata* (LOB)-*A. trifasciata* (TRI). In each tree split, the variable that decreased impurity the most is indicated together with its threshold value. Acronyms in each leaf indicate the species to which the cases are assigned. Cases assigned to each leaf are indicated with three numbers: left, occurrence of both species; middle, occurrence of species one; right, occurrence of species two. The bar plots represent the importance (%) of each variable: mean annual minimum temperature (TMin), mean annual maximum temperature (TMax), temperature range (TRange), isothermality (IsoTher), mean total precipitation of the driest month (PMin), mean total precipitation of the wettest month (PMax), precipitation seasonality (PSeason) and mean annual aridity (Ari).

variable was TMin, which was the variable that most reduced the impurity in the first split. TMin values lower than 11°C assigned occurrences to *A. lobata* (Figs. 4C, 5C). In the second split, the variable that reduced impurity the most was Ari; values higher than 0.43 assigned occurrences to A. *trifasciata*, while lower values classified occurrences as records for both species. Contrary to *A. bruennichi*, *A. lobata* avoided Iberian regions with lower TMin values (Fig. 5C).

DISCUSSION

In this study, the three *Argiope* species had broad overlapping ranges in the Iberian Peninsula. Occurrences for more than one species were found in 260 10 × 10 km UTM cells. At the geographic scale considered in this study, the three spider species showed a degree of sympatry. A range overlap between *A. bruennichi* and *A. lobata* has been pointed out by Levy (1997) in Israel and by Castilla et al. (2004) in the Columbretes Islands. Castilla et al. (2005) reported the co-occurrence of both species in 10 m^2 plots in the Columbretes, although they also observed a negative relationship in the abundances of the species. Regarding *A. bruennichi* and *A. trifasciata*, although Levi (1968) wrote that both species exclude one another, Levy (1997) reported some degree of sympatry in Israel, with *A. bruennichi* being the only species present at high altitudes. The apparent allopatry reported by Levi (1968) was likely the product of misidentifications of *A. trifasciata* as *A. bruennichi*. In fact, misidentification of *A. trifasciata* was pointed out by Levi (1968) as a factor that may have caused the underestimation of the species distribution range (see also Di Pompeo et al. 2011). Misidentification may also be the reason that *A. trifasciata* was not recorded in the Iberian Peninsula until 1985 (Morano & Ferrández 1985), while the first record for *A. bruennichi* dates to the second half of the nineteenth century (Bolivar de Urrutia 1875). Despite the possibility of the co-occurrence of different *Argiope* species, even at such fine scales as those reported by Castilla et al. (2005), the three species had distinct ranges and unique presence areas where neither of the other two species were found, suggesting distinct climatic optima.

As hypothesized, the three species had significantly different climatic niches. *A. bruennichi* had broad climatic tolerances, occupying most of the available conditions in the Iberian Peninsula, although it showed a tendency to prefer more humid and cold environments than the existing average conditions in the region. *A. lobata* did not occupy areas that were as cold and humid as those occupied by *A. bruennichi*, and it preferred warmer, drier environments than the average existing conditions in the region. Finally, *A. trifasciata* had a narrower niche with respect to precipitation and temperature, generally avoiding areas that were colder and more humid than the average existing conditions in the Iberian Peninsula. It also tended to avoid continental environments that the other two species tolerated. These general tendencies were in accordance with the observations reported in the literature (Heimer & Nentwig 1991; Roberts 1995; Harvey et al. 2002; Bellmann 2011; Di Pompeo et al. 2011).

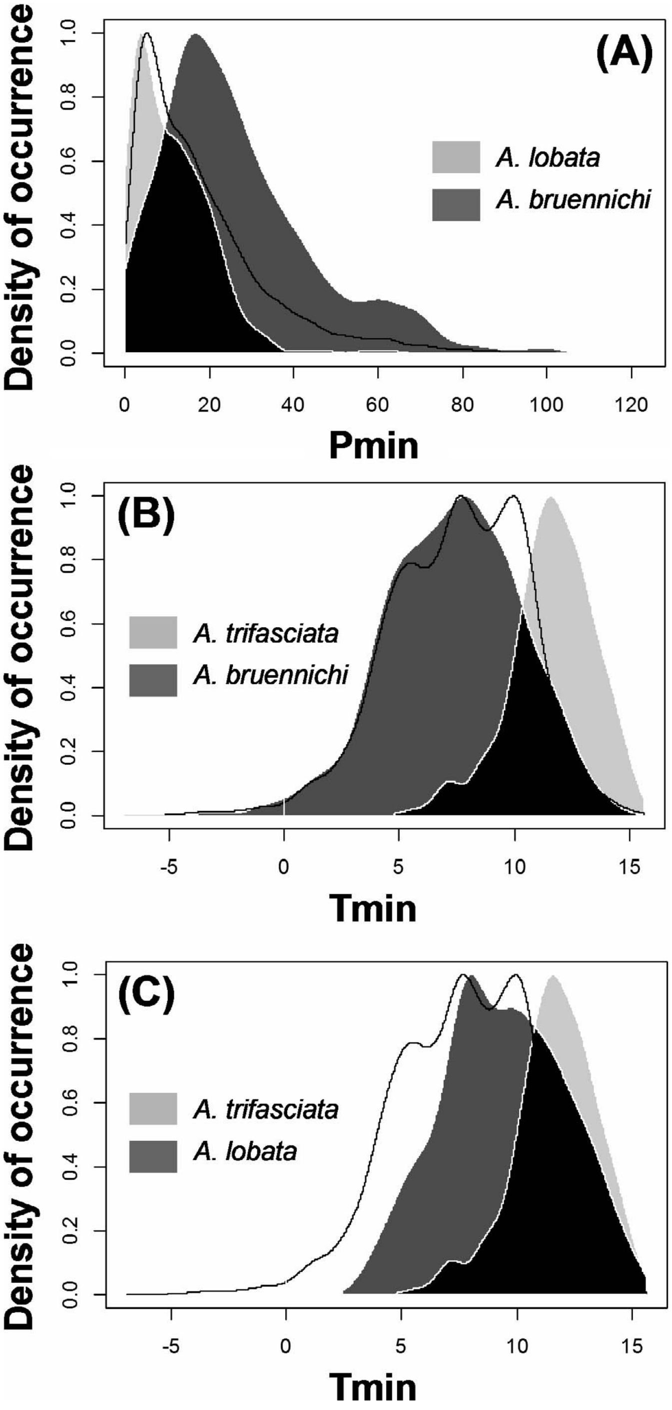

Figure 5.—The occurrence density curves for the most important variable segregating the species in each comparison pair identified in the recursive partitioning analysis (see Fig. 4). (A) *A. bruennichi* (dark gray) - *A. lobata* (light gray); (B) *A. bruennichi* (dark gray) - *A. trifasciata* (light gray); and (C) *A. lobata* (dark gray) - *A. trifasciata* (light gray). The overlap between the curves is marked in black. Black lines indicate available conditions in the Iberian Peninsula. TMin, mean annual minimum temperature; PMin, mean total precipitation of the driest month.

As expected, the most similar niches identified in this study were those of *A. lobata* and *A. trifasciata*, with the highest overlap value ($D_{obs} = 0.62$) and the shortest distance between centroids (1.262). Both species have been reported to inhabit arid regions in the Iberian Peninsula (Morano & Ferrández 1985; Morano 2017). The results of this study suggest that *A. trifasciata* preferentially selects areas with higher annual minimum temperatures than *A. lobata*. In consonance with the coastal distribution of *A. trifasciata*, once temperature has been considered, this species has a tendency to occupy less arid places than *A. lobata*, which tolerates harsher xeric continental environments. However, as expected from their geographic distributions, there was a considerable niche overlap of both species, especially in relatively warm (annual minimum temperatures higher than 11°C) and arid (aridity index lower than 0.43) areas. *Argiope trifasciata* has different physiological, morphological and behavioral adaptations to extremely hot environments, such as resistance to heat overloading, the presence of silver bands across its body, and the ability to minimize the impact of sun rays by web positioning (Tolbert 1979). The silver-colored *A. lobata* is expected to show at least the same degree of physiological and behavioral adaptation to heat as its congener.

Argiope bruennichi had a low niche overlap with *A. lobata* ($D_{obs} = 0.32$) and a particularly small overlap with *A. trifasciata* ($D_{obs} = 0.16$), a pattern that was also reflected in the distances between centroids (1.946 between *A. bruennichi* and *A. lobata*, and 2.811 between *A. bruennichi* and *A. trifasciata*). With respect to *A. trifasciata*, the annual minimum temperature was again the most relevant factor differentiating the climatic niches, with *A. trifasciata* preferentially selecting areas with higher annual minimum temperatures than *A. bruennichi.* The threshold value of 10°C was similar to the 11°C estimated for the segregation of *A. trifasciata* and *A. lobata*. Regarding *A. bruennichi* and *A. lobata*, the most important variable segregating the species was the total precipitation of the driest month, with *A. lobata* avoiding the most humid regions in favor of *A. bruennichi*, which selected them preferentially.

In summary, *A. bruennichi* selected areas with dry periods that were wetter than the average existing Iberian conditions. Those areas with the highest precipitation values in the driest annual period were avoided by *A. lobata*. *Argiope trifasciata* selected areas with minimum temperatures that were higher than the average existing Iberian conditions. Although *A. lobata* tolerated those conditions, it did not preferentially select that environment, as it is capable of living in colder and more continental environments than *A. trifasciata*, although not as cold as *A. bruennichi*. Despite these broad-scale differences, considerable niche overlap was observed between the species. While *A. lobata* and *A. trifasciata* have been claimed to inhabit arid environments in the Iberian Peninsula (Morano & Ferrández 1985; Morano 2017), *A. bruennichi* has been reported to frequent riverbanks (Morano & Sánchez 2010). Further microhabitat segregation is expected to occur with respect to temperature and humidity, which could explain, at least in part, the broad overlap observed when considering the coarse spatial resolution used in this study. Yet, if conditions are suitable for both species in terms of habitat and resources, co-occurrence can happen even at fine resolutions (e.g., Castilla et al. 2004, 2005). Under such circumstances, further segregation could occur in other non-climatic dimensions of the niche, such as in the height at which the webs are placed, the activity period, or the type of prey that are consumed (Enders 1974). For instance, vertical segregation between *A. lobata* and *A. bruennichi* could reduce food competition, as suggested by Castilla et al. (2005). Phenological segregation does not appear to be an important factor in the Iberian Peninsula since the three species broadly overlap in their activity periods, although small shifts could be enough to alleviate competition. Further ecological studies are necessary to explore this co-occurrence issue.

The *Argiope* species have a high dispersive capacity through their ballooning capabilities (Ramírez & Haakonsen 1999; Walter et al. 2005). Likely, this behavior is responsible for the relatively fast poleward range expansion of *A. bruennichi* that has been observed in recent decades (Walter et al. 2005). Kumschick et al. (2011) suggested that the northern range limit is expanding either because *A. bruennichi* is not in equilibrium with its climatic niche (i.e., the species contracted its range due to past climatic events and has not yet been able to re-colonize all suitable locations) or because it has developed cold tolerance. This last hypothesis has been supported by Krehenwinkel & Tautz (2013) and Krehenwinkel et al. (2015) who suggested that the poleward movement has been caused by an increased potential to tolerate cold temperatures due to an admixture of different lineages, favored by an increase in global trade. Similarly, the fact that *A. trifasciata* was not recorded in the Iberian Peninsula until 1985 could either mean that it was unnoticed, as discussed above, or that it is a relatively recent introduction from Africa (Di Pompeo et al. 2011) and is expanding its distribution. The isolated innermost Iberian records only date from 2011–2016. During the writing of this manuscript, we were made aware of two new records of *A. trifasciata* from the center of the Iberian Peninsula, one from 2016 in Fresno de Torote, Madrid (Fernando Molina Sánchez, pers. comm.) and the other from 2017 in Mar de Ontígola, Madrid (Jose Antonio Gómez, pers. comm.) (see Fig. 1). Given the dynamism of the *Argiope* species ranges, two important consequences should be considered. First, the results presented in this study represent a species snapshot and will need to be reevaluated in the future. Second, climate warming is likely enhancing range shifts to the north (Krehenwinkel & Tautz 2013). In some instances, the range shifts of the *Argiope* species could have been facilitated by the expansion of open anthropogenized habitats (Sacher & Bliss 1989,1990) that can even act as corridors (Ramírez & Haakonsen 1999). If this is the case, then the forecasted aridification of the Iberian Peninsula (Gao & Giorgi 2008; Sánchez et al. 2011) is expected to benefit *A. lobata* and *A. trifasciata*, perhaps at the expense of *A. bruennichi*.

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