

Lack of congruence between fundamental and realised aridity niche in a lineage of water beetles

Susana Pallarés^{1,2}  | Andrés Millán³  | Jorge M. Lobo¹  | Abraham Pérez⁴ | David Sánchez-Fernández³ 

¹Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

²Departamento de Zoología, Universidad de Sevilla, Seville, Spain

³Departamento de Ecología e Hidrología, Universidad de Murcia, Murcia, Spain

⁴Facultad de Ciencias Ambientales y Bioquímica, Universidad de Castilla-La Mancha, Campus de Toledo, Toledo, Spain

Correspondence

Susana Pallarés, Departamento de Zoología, Universidad de Sevilla, Avenida de la Reina Mercedes, 6, 41012, Seville, Spain.

Email: susana.pallares@um.es

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Abstract

1. Coping with aridity is a physiological challenge for all organisms, including freshwater ones. Aridity shapes distributions of aquatic species at fine and large geographical scales. Specifically, for aquatic beetles, the desiccation resistance of the adults is a potential constraint for the colonisation of arid regions.
2. We assessed the congruence between the fundamental and realised aridity niche in eight species of a Palearctic lineage of water beetles (subgenus *Lumetus*, genus *Enochrus*, family Hydrophilidae). We also estimated the relative explanatory capacity of aridity-related versus other environmental variables in species distributions.
3. Most of the species, even those most sensitive to desiccation stress in laboratory experiments, occur in areas with high aridity within the Palearctic region. Our results suggest a lack of association between the physiological (desiccation resistance) and environmental distance matrix (realised aridity niche), or between either of these and phylogenetic distances. Aridity-related variables had generally a similar explanatory capacity in explaining the distribution of species than non-related ones.
4. Our results indicate that desiccation resistance has not been an important physiological constraint for the colonisation of arid environments by this clade and suggest that other non-physiological factors are more important in shaping their distributions along aridity gradients. The studied beetle lineage might conserve a high basal desiccation resistance from relatively recent terrestrial ancestors, which could have provided a physiological advantage for the colonisation of arid areas. Further research could shed light on whether these unexpected results are common to other groups of aquatic insects living in arid areas or are particular to this group of beetles.

KEYWORD

aquatic insects, aridification, desiccation resistance, freshwaters, geographic distribution, inland waters, physiology, water loss rate,

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1 | INTRODUCTION

It is well known that coping with increasing aridity is a physiological challenge for all organisms (Chown et al., 2011). Aridity influences biodiversity at multiple levels, shaping species distributions at fine and large geographical scales (Craine et al., 2013; Rajpurohit et al., 2013; Watling & Braga, 2015), driving lineages diversification (Catullo & Keogh, 2014; Dorn et al., 2014; Pinceel et al., 2013; Razeng et al., 2017) and community turnover (Vander Vorste et al., 2021), and regulating ecosystem structure and function (Berdugo et al., 2020).

Aridity is a critical stressor in many freshwater ecosystems around the world (Bond et al., 2008; Woodward et al., 2010). Indeed, desiccation resistance traits have been associated with the distributions of freshwater invertebrate species along gradients of drought intensity and water availability (e.g., Céréghino et al., 2020; Perez-Quintero, 2012). For aquatic organisms with aerial dispersal, such as true water beetles (i.e., species with all life stages aquatic, Jäch & Balke, 2008), the physiological desiccation resistance capacity of the adult (dispersive) stage may limit dispersal capacity and thus could be a key determinant of distribution patterns, as demonstrated for other animal taxa prone to desiccation (e.g., amphibians—Watling & Braga, 2015—or terrestrial arthropods—Dias et al., 2013; Kellermann et al., 2012; Kellermann et al., 2020; Rajpurohit et al., 2013). In arid and semi-arid areas, where temporary inland aquatic systems are common, spatial connectivity is disrupted during droughts and many small and shallow water bodies can remain completely dry for long periods (Datry et al., 2016; Davis et al., 2018; Morán-Ordóñez et al., 2015; Murphy et al., 2015). Some aquatic invertebrates possess traits to resist desiccation *in situ*, but those that lack such traits are forced to disperse (resistance vs. resilience strategies, see Chester & Robson, 2011; Chester et al., 2015 or Strachan et al., 2015 for reviews on this topic). This is the case for water beetles, whose main mechanism to cope with desiccation consists of minimising cuticular transpiration by improving the waterproofing capacity of the cuticle (Botella-Cruz et al., 2021). Adult beetles disperse among wetted reaches recolonising dry sites when flow returns (Bilton et al., 2001; Cañedo-Argüelles et al., 2015; Velasco & Millán, 1998), experiencing dehydration during such aerial exposure (Bogan et al., 2017; Strachan et al., 2015). Consequently, their capacity to control cuticular water loss during such events could be an important physiological constraint for the occupation of aquatic habitats in arid and semi-arid regions, as well as a determinant of meta population dynamics (Cañedo-Argüelles et al., 2020; Chester et al., 2015; Razeng et al., 2016).

The study of the factors that shape species distributions has been typically addressed by correlative approaches relying on distributional data (e.g., species distribution modelling; SDM) and has often focused on realised rather than fundamental niches (Hutchinson, 1957; Jiménez & Soberón, 2022). Biogeographical studies of water beetles relating their thermal tolerance (Calosi et al., 2008; Hidalgo-Galiana et al., 2014), dispersal ability (Arribas et al., 2012), or lithology (Abellán et al., 2012) to distribution patterns have also shown that physiologically determined variables are

important constraints on the global distribution of some water beetle clades. However, the role of aridity and desiccation resistance in shaping the distribution of aquatic insects has been less explored (but see Carey et al., 2021; Céréghino et al., 2020; Davis et al., 2013; Perez-Quintero, 2012).

The degree of congruence between fundamental and realised niches is a central issue in biogeography and evolutionary ecology (Araújo & Pearson, 2005; Soberón & Arroyo-Peña, 2017). Exploring the relationship between climate, physiological constraints, and species distributions requires studying aspects of both the fundamental and realised niches (Kearney, 2006; Soberón, 2007). While physiological data can be used to estimate the fundamental niche, the area currently occupied by a species can only provide partial environmental information on the full spectrum of abiotic conditions under which a species can potentially survive and reproduce (Colwell & Rangel, 2009; Sánchez-Fernández et al., 2011). The degree of congruence between such aspects is linked to the extent to which species are at equilibrium with current climate and to the relative role of physiology versus other contingent factors (e.g., historical factors, biotic interactions or dispersal limitations) in shaping distributions (Bozinovic et al., 2011; Helaouët & Beaugrand, 2009; Sánchez-Fernández et al., 2012). In water beetles, estimates of thermal limits derived from laboratory experiments (proxies of the fundamental thermal niche) and from species' occurrences (realised thermal niche) have shown limited agreement (Sánchez-Fernández et al., 2012). Such a relationship has not been explored in terms of aridity, at least in freshwater ecosystems, so the question remains as to what extent the aridity conditions at which the species are currently exposed (realised aridity niche) are associated with the degree of desiccation that they can physiologically tolerate (i.e., the fundamental aridity niche). Understanding the influence of physiological constraints on species distributions is fundamental for predicting the impact of climate change and increasing aridification on biodiversity (Craine et al., 2013).

One limitation for exploring aspects of the fundamental niche is the unavailability of physiological data for most species. However, detailed examinations of a few carefully studied cases can be of great value in dissecting the nature of the underlying processes by which environmental conditions constrain species distributions (Kearney et al., 2018). Physiological desiccation resistance has been well studied for a few lineages of water beetles, such as the subgenus *Lumetus* within the genus *Enochrus* (fam. Hydrophilidae) (Botella-Cruz et al., 2017, 2019; Pallarés, Arribas, et al., 2017; Pallarés et al., 2016). This information, together with distribution and climatic data and a well-resolved molecular phylogeny of a set of representative Palearctic species of this clade, distributed across a large aridity gradient, provides an excellent study case to explore the relationship between the fundamental and realised aridity niche within an evolutionary framework. In this clade of beetles, reconstruction of the evolution of desiccation and salinity tolerance suggested that improved desiccation resistance provided a physiological basis to develop salinity tolerance and colonise highly saline waters, which are naturally stressful habitats

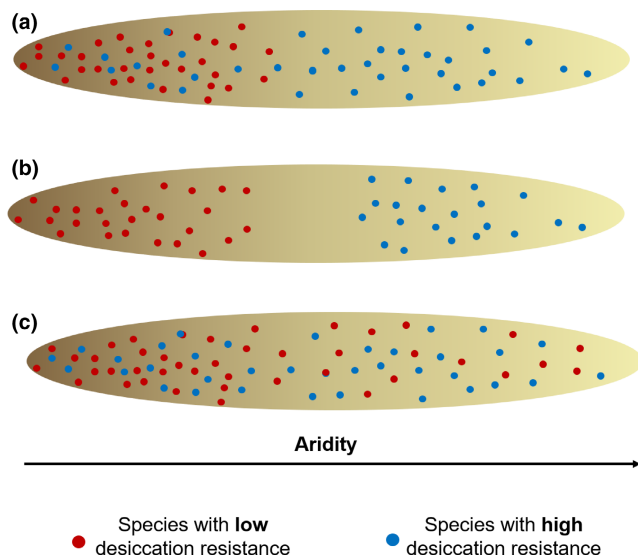


FIGURE 1 Conceptual scheme of the relationship between the fundamental (physiological desiccation resistance) and realised aridity niche (species niche position and breadth along an aridity gradient), representing different hypothetical scenarios in which species distributions along the aridity gradient are: (a) mainly shaped by physiological constraints; (b) shaped by physiological constraints and other factors (e.g., biotic interactions); or (c) not shaped by physiological constraints

located in arid and semiarid areas (Arribas et al., 2014; Pallarés, Arribas, et al., 2017). Accordingly, it could be hypothesised that physiological desiccation resistance might have been pivotal for the occupation of extreme environments in general, not only in terms of salinity, but also within an aridity gradient.

Here, we explore the association between experimentally measured desiccation resistance (as a proxy of the fundamental aridity niche) and the realised niche (i.e., climatic conditions in which the species are present, focusing on aridity-related climatic variables) in *Lumetus* species, accounting for the phylogenetic relationships among the species. Additionally, we use an SDM technique to explore the extent to which aridity-related variables are able to explain the geographical distribution of these species. If species distributions along aridity gradients are mainly shaped by physiological constraints (desiccation resistance), species with lower desiccation resistance should be restricted to wetter climates, showing narrow realised niches, whilst species with higher desiccation resistance would be potentially able to occupy the full spectrum of the aridity gradient, having wider realised niches (Figure 1a). Under this scenario, aridity-related environmental variables should have a higher contribution in explaining the distribution of those species with lower desiccation resistance. Alternatively, if factors other than physiological constraints (e.g., biotic interactions or dispersal limitations) are also important in shaping species distributions, a lack of relationship between desiccation resistance and realised niches would be expected. For example, desiccation-resistant species could be outcompeted in mesic areas—where their competitors may show higher fitness as a

lower investment in specific adaptations to cope with desiccation stress is needed—and therefore they would be restricted to arid areas, showing narrow realised niches as well (Figure 1b). In this case, the contribution of aridity-related environmental variables in explaining species distributions should be relatively high for all species independently of their physiologically determined desiccation resistance. Finally, if desiccation resistance is not an important physiological constraint for the occupation of arid areas, realised niche breadth, the species niche position along the aridity gradient and the contribution of aridity variables would be unrelated to their desiccation resistance (Figure 1c).

2 | MATERIAL AND METHODS

2.1 | Study group

Our study is based on the dataset used by Pallarés, Arribas, et al. (2017), comprising eight species of the subgenus *Lumetus* (genus *Enochrus*) from which experimental data on physiological desiccation resistance were obtained: *Enochrus ochropterus* (Marsham 1802), *Enochrus salomonis* (J. Sahlberg, 1900), *Enochrus halophilus* (Bedel, 1878), *Enochrus testaceus* (Fabricius, 1801), *Enochrus fuscipennis* (Thomson, 1884)–*Enochrus quadripunctatus* (Herbst, 1797),¹ *Enochrus politus* (Küster, 1849), *Enochrus bicolor* (Fabricius, 1792), and *Enochrus jesuarribasi* Arribas & Millán, 2013. These species represent the main Palearctic clades of *Lumetus* according to the updated phylogeny of the group published in Pallarés, Arribas, et al. (2017). They do not show any resistant trait to cope with desiccation in situ at any stage of their life cycle. Therefore, the capacity to prevent cuticular and respiratory water loss (desiccation resistance hereafter) in the adults (the flying dispersive stage) is likely to be a key trait to cope with desiccation stress. These beetles are crawling species typically found in the shallow margins of lotic (running) or lentic (standing) water bodies. The eight species studied represent a wide gradient of salinity tolerance, from poor osmoregulator species living in freshwater to good osmoregulators found in hypersaline water (Pallarés et al., 2015). Larvae are carnivorous and adults are herbivorous, feeding on aquatic plants and algae (Yee & Kehl, 2015).

2.2 | Physiological data on desiccation resistance

As an estimate of the fundamental aridity niche, we used three physiological variables obtained by Pallarés, Arribas, et al. (2017), measured for a single population of each species in a laboratory experiment. Briefly, groups of 20–35 adult beetles from each species were individually exposed to desiccation in test tubes

¹A specific name is not assigned because *Enochrus fuscipennis* and *E. quadripunctatus* belong to a cryptic species complex, so these species are difficult to distinguish and identify correctly.

TABLE 1 Environmental variables used in the analyses

| Variables | Units | Source |
|---|----------|-----------|
| Annual mean temperature | °C | WorldClim |
| Mean diurnal range | °C | WorldClim |
| Isothermality | % | WorldClim |
| Temperature seasonality | SD (°C) | WorldClim |
| Max temperature of warmest month | °C | WorldClim |
| Min temperature of coldest month | °C | WorldClim |
| Temperature annual range | °C | WorldClim |
| Mean temperature of wettest quarter | °C | WorldClim |
| Mean temperature of driest quarter | °C | WorldClim |
| Mean temperature of warmest quarter | °C | WorldClim |
| Mean temperature of coldest quarter | °C | WorldClim |
| Annual precipitation | mm | WorldClim |
| Precipitation of wettest month | mm | WorldClim |
| Precipitation of driest month* | mm | WorldClim |
| Precipitation seasonality | cv | WorldClim |
| Precipitation of wettest quarter | mm | WorldClim |
| Precipitation of driest quarter* | mm | WorldClim |
| Precipitation of warmest quarter | mm | WorldClim |
| Precipitation of coldest quarter | mm | WorldClim |
| Elevation | masl | ENVIREM |
| Aridity index* | - | ENVIREM |
| Climatic moisture index* | - | ENVIREM |
| Potential evapotranspiration of driest quarter* | mm/month | ENVIREM |

Aridity-related variables are indicated with an asterisk

placed in a climatic chamber (CLIMACELL-404, MMM Medcenter Einrichtungen GmbH, Germany) at 40% relative humidity and 20°C, for 6 hr, and then allowed to recover at freshwater conditions for 24 hr. Water loss rate was gravimetrically estimated as the percentage of water lost (i.e., the difference between body mass before and after the desiccation exposure) per time relative to initial wet mass (% mass loss/hr). Total body water content was estimated as the difference between wet and dry mass relative to initial wet mass (% wet mass) and the percentage survival after recovery from the desiccation stress was recorded (Table S1, Pallarés, Arribas, et al., 2017). Water loss rate and body water content account for the capacity to avoid desiccation, while survival after recovery reflects the capacity to tolerate the loss of body water (Chown & Nicolson, 2004; Edney, 1977).

2.3 | Distribution and environmental data

Occurrence data for each species were obtained from the GBIF (Global Biodiversity Information Facility, www.gbif.net) and CKmap (<http://www.faunaitalia.it/ckmap/>) databases, an exhaustive bibliographic revision (Appendix S1), and our own unpublished records. All occurrences were checked for inconsistencies and duplicates were removed.

Twenty-three environmental variables were used to estimate the most relevant ones in explaining the distribution of the species, including elevation and several climatic variables, five of which are indicative of aridity (precipitation of the driest month, precipitation of the driest quarter, potential evapotranspiration of the driest quarter, aridity index, and climatic moisture index; Table 1). These variables were downloaded from WorldClim version 2.1 (<http://www.worldclim.org>; Fick & Hijmans, 2017) for recent decades (1970–2000) at 2.5' resolution (c. 4.5 × 4.5 km at the Equator) and from the ENVIREM database (<https://envirem.github.io/>; Title & Bemmels, 2018), at the same spatial resolution.

2.4 | Fundamental and realised aridity niches

Potential causal relationships between two or more variables can be expressed in terms of pairwise distances between samples (Castellano & Balleto, 2002). We explored the correlation between the fundamental and realised aridity niches of the species, estimated from physiologically derived and environmentally-based variables, respectively. This correlation was assessed by examining the relationship between a physiological distance matrix and several environmental distance matrices through Mantel permutation tests (Mantel, 1967; $n = 9,999$ permutations). In these analyses, we do not

assume that aridity is the main factor responsible for explaining the distribution of the studied species. Instead, we aim to address to what extent desiccation resistance could be a constraint for the colonisation of arid environments. To control for the non-phylogenetic independence among species, we also explored the correlations between all these distances and the phylogenetic distances among species.

The mean values of the three physiological measures of desiccation resistance mentioned above (Table S1) were used to calculate a between-species physiological triangular matrix representing their physiological dissimilarity or distance. To do this, the scale invariant Mahalanobis distance was applied. This metric is particularly suited to estimate multidimensional distances when variables show a variable degree of collinearity and their distances need to be calculated within a non-Euclidean space (Farber & Kadmon, 2003). Thus, the more a species pair differs in such desiccation resistance variables, the greater the distance between them. The phylogenetic distance matrix was computed from the cophenetic distances (Sneath & Sokal, 1973) using the most recent *Lumetus* phylogeny published (Pallarés, Arribas, et al., 2017).

We used three different approaches to characterise the realised aridity niche and estimate the environmental pairwise distances among species, applying also the Mahalanobis distance. For this, presence data and the five aridity-related variables mentioned above (Table 1) were considered. Firstly, we estimated the mean values of such variables for each species within their presence areas and performed a principal component analysis (PCA). We then used the species scores on the resulting orthogonal, uncorrelated axes that explained >90% of the variance to obtain an environmental triangular matrix. Secondly, as principal components are not directly interpretable in biological terms, we built another environmental distance matrix based also on the mean environmental conditions in species' presence areas, but considering a set of uncorrelated variables. For this, we assessed multicollinearity between the five aridity-variables using the variance inflation factor (VIF), and retained only those with VIF values below 10 (Zuur et al., 2010). This procedure eliminated the two precipitation-related variables. Finally, as we were interested not only in the mean aridity conditions in which the species are present, but also in their niche breadth and the most extreme conditions they can occupy, we applied an Outlying Mean Index analysis (OMI, Dolédec et al., 2000), as implemented in the R package *ade4* (Dray & Dufour, 2007). The OMI is a multivariate analysis in which a PCA on the environmental data is first performed, and the standardised environmental data in combination with the species presences are used to perform the niche analysis. Then, several niche parameters are obtained: (1) the position of the species in the environmental space; (2) the niche breadth or tolerance; and (3) a marginality index, which represents the distance between the mean conditions of the habitat used by the species and the reference or general habitat conditions of the considered area (i.e., those conditions tolerated by a hypothetical, ubiquitous species uniformly distributed in the environmental space). We obtained a distance matrix

for each of these parameters. These analyses were performed in R v. 4.0.4 (R Core Team, 2019).

2.5 | Estimating the relevance of aridity predictors

We determined the explanatory capacity of the selected environmental variables and the probable geographical distribution of the considered species using the Niche of Occurrence (NOO) included within the ModestR software v. 6.2 (García-Roselló et al., 2014; www.ipez.es/modestr/). NOO uses the information about the observed occurrences of a species to estimate its probable distribution, seeking to overcome three main inconveniences of other SDM procedures: (1) the use of absence data, which are less reliable than presence data; (2) the use of complex modelling techniques; and (3) the often arbitrary selection of a geographical extent (García-Roselló et al., 2019; Lobo, 2016). Thus, we delimited the accessible area of each species as the one composed by the river basins with presence observations that, in turn, enables the connection of all the available occurrences (i.e., all the selected basins must be connected). The catchment information provided by the HydroSHEDS project (www.hydrosheds.org/; Linke et al., 2019) was used for this purpose. As river basins are delimited following a hierarchical coding system, NOO selects the minimum level of river basins with species occurrences that generates a contiguous and connected area. Delimiting this geographical extent using natural landform units allows to minimise the effects of contingent events and dispersal factors in delimiting the distribution of species (Acevedo et al., 2012), selecting those areas that are more likely to be accessible to the species.

From the 23 environmental variables (Table 1), those with a VIF >10 were excluded, and the remaining ones scrutinised to: (1) estimate their percentage contribution in species distributions; and (2) identify those with the highest capacity to discriminate between the environmental conditions in the presence cells (2.5' resolution) against those prevailing in the geographical extent selected for each species. The geographical extent was delimited independently for each species (see above) in order to facilitate a better estimate of the relevance of those environmental factors that discriminate between presence and absence localities (see Acevedo et al., 2012). The contribution of each environmental variable was estimated by using an Instability Index included within the ModestR software, which divides each continuous predictor into bins and compares the relative frequency of the cells with presence data against those of the selected geographical extent for each bin (Guisande et al., 2017). For each species, the explanatory variables showing greatest percentage of contribution to the Instability Index (80% of total variability) were assumed to be those with the highest capacity to discriminate the occurrence cells in the accessible region. The values of the so selected environmental predictors were used to generate binary distribution maps representing the geographical projection of the realised niche of the species (see details in García-Roselló et al., 2019).

3 | RESULTS

3.1 | Fundamental and realised aridity niche

Enochrus halophilus and *E. salomonis* were the most sensitive to desiccation amongst the eight species, showing the lowest survivorship (60% and 80%, respectively) and highest water loss rate values in the controlled desiccation exposure, although the latter had a relatively high body water content. All of the remaining species showed high survival rates (>80%) after recovery from desiccation, and *E. fuscipennis* was the most desiccation resistant as this species also showed the lowest water loss rates values (Figure 2, Table S1).

The complete geographical extent of the study group encompassed most of the Palearctic region, covering an extensive aridity gradient (e.g., values from 0 to 100 of the aridity index). The studied species have been recorded in a wide range of aridity across such gradient, and most of them have occurrences in areas with high values of the aridity index (i.e., drier areas; Figure 3) and low values of minimum annual precipitation (Figure S1). *E. ochropterus* was the species comparatively most restricted to wetter areas according to the aridity indexes (Figure 3).

As the Mantel tests applied using the different environmental matrices yielded consistent results, only the comparisons with the environmental matrix obtained from the PCA are shown, for simplicity. The comparisons with the other environmental matrices are shown in Table S2.

The first axis from the PCA explained 99.2% of the variance of the mean aridity conditions in species presence areas and was positively correlated with the climatic moisture index, precipitation of the driest month and precipitation of the driest quarter and negatively correlated with the aridity index and the potential evapotranspiration of the driest quarter (Figure 4). This axis discriminated the species niches in an aridity gradient from drier (negative values) to wetter conditions (positive values). The OMI ordination was qualitatively similar but the first axis was correlated with the aridity variables in the opposite way (from wetter [negative values] to drier conditions [positive values]; Figure S2a). The OMI showed a high niche overlap among the species (Figure S2b). *E. jesuarribasi* and *E. politus* were located towards the driest conditions and showed the highest marginality and the lowest tolerance values (i.e., narrower niche breadth; Figures 4 and S2). Among the species whose niches were located towards wetter conditions, *E. ochropterus* was the one showing a higher marginality. *E. bicolor* and *E. fuscipennis* were the most tolerant (i.e., wider niche breadth) species (Figure 2b,c).

Our results suggest a lack of congruence between the physiological distances (that is, desiccation resistance or the fundamental aridity niche) and environmental distances (realised aridity niche; see Mantel tests results in Table 2 and Figure 5). This result was consistent for all the different metrics of environmental distance used to characterise the realised aridity niches of the species (Table S2). No phylogenetic signal in desiccation resistance nor any of the environmental distance metrics was detected, although the association between phylogenetic distances and those computed from the breadth of the aridity niche of the OMI analysis showed a low *p*-value (Table S2).

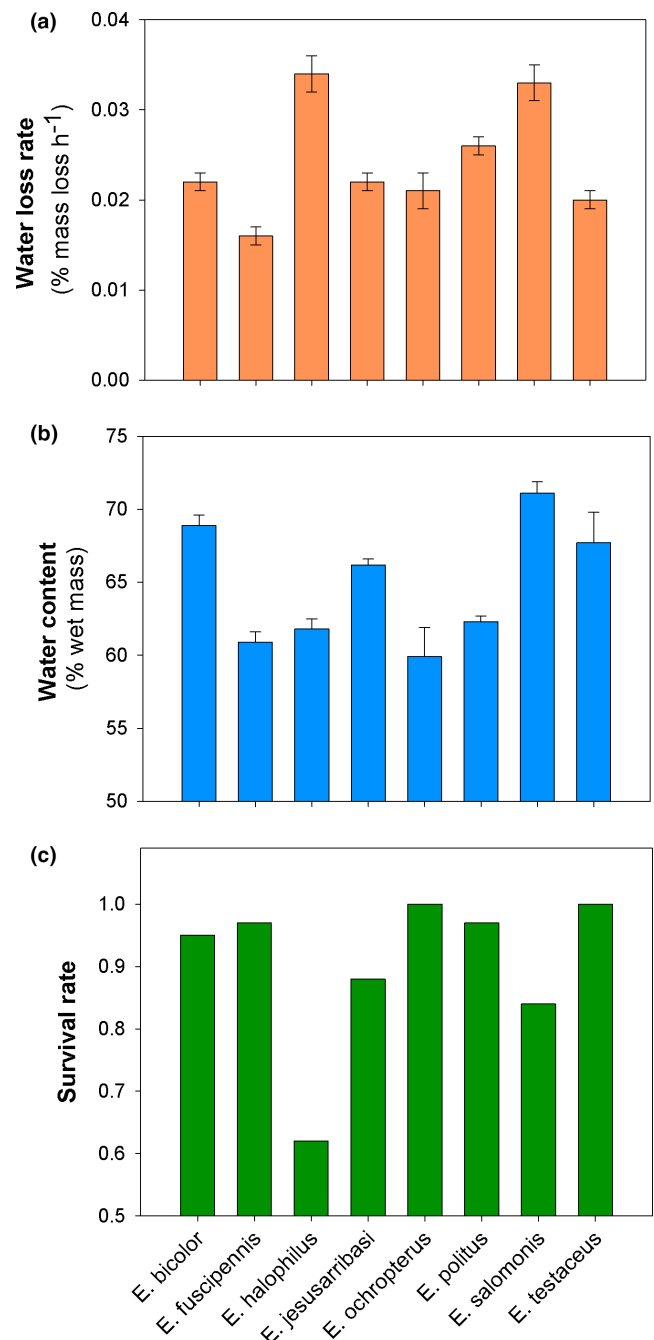


FIGURE 2 Physiological variables measured in desiccation resistance experiments with *Enochrus* species: (a) water loss rate (mean \pm SD); (b) total body water content (mean \pm SD); and (c) and percentage of surviving individuals after recovery from desiccation exposure (data from Pallarés, Arribas, et al., 2017). See also Table S1

3.2 | Relevance of aridity variables as drivers of species distributions

Ten out of 23 variables had VIF values <10 and were retained for estimating their percentage contribution in species distributions (Table 3). For most species, the variable with the highest percentage of contribution to the Instability Index was a precipitation-related

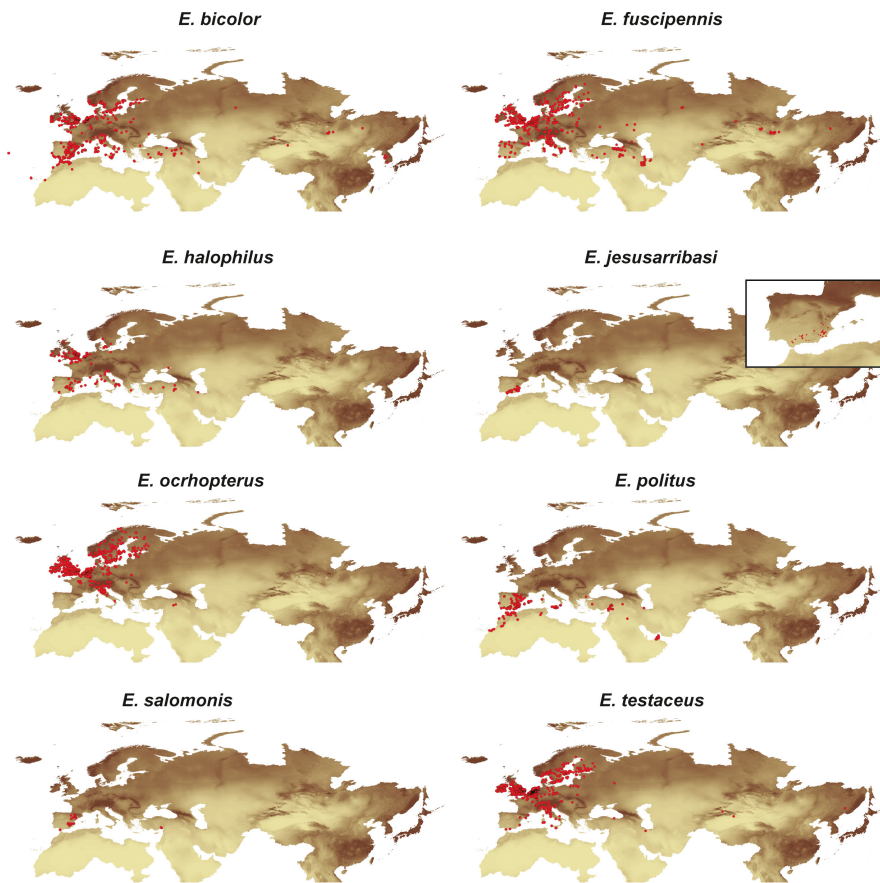


FIGURE 3 Occurrence records of *Enochrus* species (red points) and aridity index over the extent of occurrence of the whole study group. Lighter brown colour represents areas with higher aridity

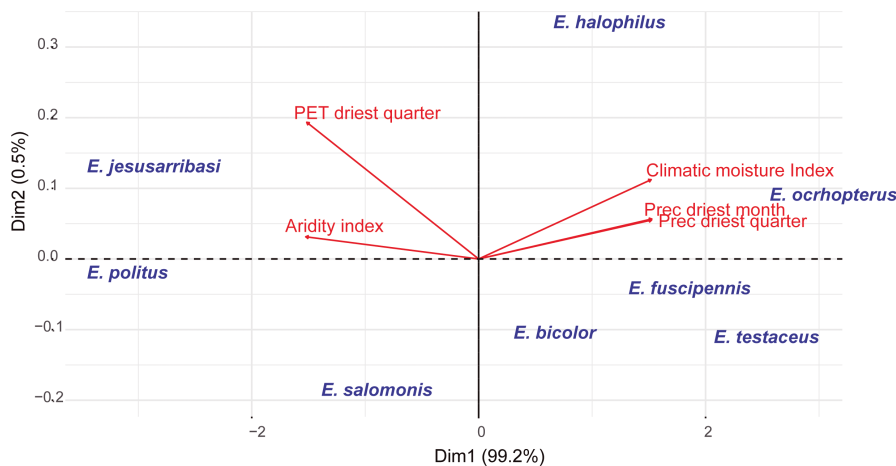


FIGURE 4 Principal component analysis (variables factor map and species positions along the first two axes)

one (precipitation of the warmest or coldest quarter), with percentage contributions ranging between 19.0% and 25.2% among the species (Table 3). The mean percentage contribution of aridity-related variables was lower than that of non-related variables except for *E. jesuarribasi*, *E. politus*, and *E. salomonis*. Presence areas of these three species were characterised by drier conditions (i.e., higher and lower values of the aridity and climatic moisture indexes, respectively), compared with the remaining species (Table 3). The predicted distributions estimated by NOO are shown in Figure S3.

4 | DISCUSSION

Whilst a great focus has been put on temperature as a major biogeographic driver, less is known about the impact of aridity on animal species persistence and distribution (Ochoa-Ochoa et al., 2019). Our results suggest a lack of association between estimates of the realised and fundamental aridity niche. This, together with the relative minor influence of aridity-related variables in explaining the distribution of the considered species, indicates that physiological

TABLE 2 Results of Mantel permutation tests (number of permutations = 9,999) used to analyse associations among physiological (*physiol*), environmental (*env*) and phylogenetic (*phylo*) distance matrices

| Matrices | <i>r</i> | <i>p</i> -Value |
|------------------------------------|----------|-----------------|
| <i>physiol</i> versus <i>phylo</i> | -0.004 | 0.463 |
| <i>physiol</i> versus <i>env</i> | -0.066 | 0.597 |
| <i>env</i> versus <i>phylo</i> | 0.032 | 0.402 |

desiccation resistance was not an important constraint for the colonisation of arid environments by this clade of water beetles.

4.1 | Lack of association between fundamental and realised aridity niches

Most of the species, including those that showed the lowest desiccation resistance in physiological experiments (*E. halophilus* and *E. salomonis*), are present in relatively arid areas. *E. ochropterus* was the species with the least arid realised niche and it showed a relatively high realised niche marginality (towards less arid conditions). However, such restriction to relatively wetter areas seems to be unrelated with a physiological limitation, as this species had a resistance to desiccation comparable to that of its congeners present in drier areas. Accordingly, we found no correlations between the physiological distance matrix and any of the metrics used to characterise the realised aridity niche. A previous study found a significant correlation between salinity tolerance estimated from distribution data and aridity climatic variables in *Enochrus* species, including those studied here (Arribas et al., 2014). In light of our results on desiccation resistance, which are based on similar physiological mechanisms to salinity tolerance (Bradley, 2009), the relationship found by Arribas et al. (2014) may not hold if the fundamental instead of

the realised salinity niche were considered. Our results also indicate a lack of phylogenetic signal in estimates of both the realised and fundamental aridity niche, although such result should be confirmed by a study with the complete clade using phylogenetic comparative methods. The association between niche breadth (estimated with the OMI analysis) and the phylogenetic matrix (*p*-value = 0.012 in Mantel test) should be taken with caution because Mantel tests may exhibit high type I error (Guillot & Rousset, 2013; Harmon & Glor, 2010) and so it is recommended that conservative significance levels (e.g. 0.01) are used.

Our results suggest that, despite the differences in desiccation resistance among the studied *Lumetus* species, all of them appear to have a high basal physiological capacity to cope with aridity. Many aquatic lineages have had to survive more arid conditions than currently occur at some point during their evolutionary history (Dorn et al., 2014; Pinceel et al., 2013), which could have promoted the evolution of improved desiccation resistance. In line with this, our results are congruent with the exaptation hypothesis proposed by Arribas et al. (2014) and Pallarés, Arribas, et al. (2017) for *Lumetus*, according to which a high ancestral desiccation resistance, which has apparently remained conserved in this clade, facilitated the development of salinity tolerance. Indeed, our findings indicate that such a high desiccation resistance could have provided a physiological advantage for the colonisation of inland waters in arid and semi-arid areas. It is possible that this clade of beetles conserves a high desiccation resistance from relatively recent terrestrial ancestors, as secondary colonisations of the terrestrial medium (and back to water) seem to have been frequent within the family Hydrophilidae (Bernhard et al., 2006; Bloom et al., 2014; Short & Fikáček, 2013). This raises the questions as to whether such hypothesised pre-adaptation to dry habitats is a peculiarity of this beetle lineage, and the extent to which the ability of aquatic species to adapt to ongoing aridification could be conditioned by their evolutionary history. It is possible that other aquatic macroinvertebrates that lack such

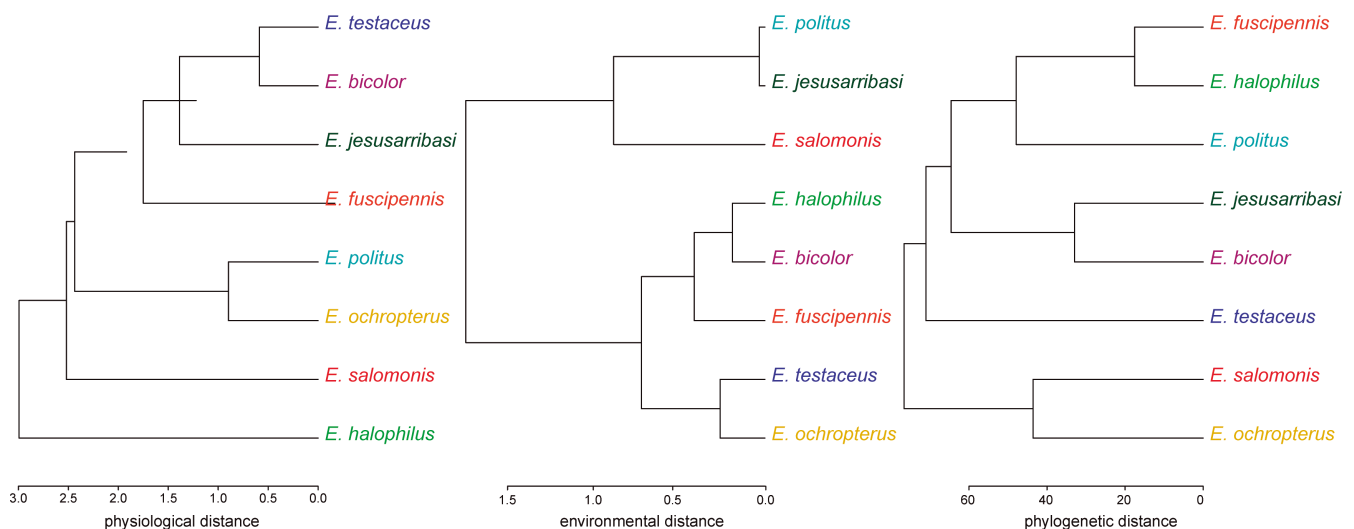


FIGURE 5 Dendrograms representing species dissimilarities in physiological desiccation resistance (fundamental aridity niche), the different estimates of the realised aridity niche and phylogenetic relatedness

TABLE 3 Percentage contribution of the considered variables in explaining the distribution of *Enochrus* species by using the Instability Index of Guisande et al., (2017)

| Variables | <i>E. bicolor</i> | <i>E. jesuarribasi</i> | <i>E. halophilus</i> | <i>E. ochropterus</i> | <i>E. politus</i> | <i>E. testaceus</i> | <i>E. salomonis</i> | <i>E. fuscipennis</i> |
|-------------------------------------|----------------------|------------------------|----------------------|-----------------------|----------------------|---------------------|----------------------|-----------------------|
| Aridity-related | | | | | | | | |
| Aridity index | 5 (0 to 95.9) | 7.2 (62.9 to 85.2) | 3.1 (18.9 to 86.1) | 3.4 (0 to 81.9) | 16.5 (44.4 to 95.5) | 3.6 (0 to 93.5) | 12.3 (30.1 to 82.5) | 1.6 (0 to 90.7) |
| Climatic moisture index | 5.6 (-1.0 to 0.9) | 16.9 (-0.8 to -0.34) | 1.4 (-0.7 to 0.5) | 0.8 (-0.5 to 0.8) | 18.1 (-0.95 to 0.05) | 3.3 (-0.9 to 0.7) | 14.7 (-0.71 to 0.27) | 3.7 (-0.9 to 0.8) |
| PET of driest quarter | 13.1 (1.4 to 210.1) | 17.3 (146.0 to 189.7) | 23.3 (17.6 to 196.8) | 20.1 (8.1 to 184.9) | 6.7 (26.4 to 243.6) | 17.2 (5.3 to 172.5) | 4.7 (28.2 to 178.4) | 19.2 (0 to 205.5) |
| Mean contribution | 7.9 | 13.8 | 9.3 | 8.1 | 13.8 | 8 | 10.6 | 8.1 |
| Non-aridity-related | | | | | | | | |
| Mean diurnal range | 10.6 (3.9 to 14.9) | 0 (10.2 to 14.2) | 7.2 (3.9 to 14.9) | 10.1 (3.9 to 12.8) | 2.2 (6.0 to 15.3) | 11.0 (4.2 to 12.6) | 9.5 (8.5 to 14.9) | 11.4 (4.0 to 15.5) |
| Isothermality | 12.3 (19.0 to 55.5) | 15.4 (39.0 to 44.0) | 11.5 (20.7 to 43.8) | 10.6 (19.0 to 42.0) | 9.5 (27.0 to 58.0) | 14.2 (18.6 to 43.7) | 13.8 (36.2 to 44.3) | 17.7 (20.6 to 46.0) |
| Mean temperature of wettest quarter | 9.4 (1.5 to 24.1) | 3.8 (7.6 to 19.7) | 9 (1.3 -19.9) | 15.2 (-1.9 to 19.4) | 0.0 (-2.7 to 24.0) | 11.1 (1.9 to 24.1) | 3.1 (5.0 to 17.6) | 5.9 (-0.3 to 21.0) |
| Precipitation of warmest quarter | 8.4 (2 to 729) | 3.1 (23 to 72) | 12.8 (10 to 394) | 3.7 (16 to 542) | 22.2 (0 to 138) | 8.3 (13 to 503) | 19.0 (20 to 182) | 5.3 (5 to 520) |
| Precipitation of coldest quarter | 25 (3 to 1074) | 23.3 (74 to 305) | 21.2 (78 to 604) | 21.6 (56 to 769) | 18.9 (30 to 420) | 22.6 (3 to 621) | 13.9 (68 to 374) | 25.2 (4 to 941) |
| Precipitation seasonality | 10.5 (10.3 to 122.9) | 11.6 (31.9 to 72.1) | 10.4 (9.9 to 75.7) | 14.6 (8.4 to 72.4) | 3.9 (22.7 to 114.6) | 8.7 (8.3 to 87.6) | 8.9 (20 to 72.3) | 10 (8.4 to 114.8) |
| Elevation | 0 (7.2 to 15.3) | 1.4 (8.0 to 12.4) | 0 (9.0 to 14.4) | 0 (6.8 to 14.5) | 2 (7.4 to 14.1) | 0 (7.0 to 15.2) | 0 (7.7 to 12.7) | 0 (7.1 to 14.5) |
| Mean contribution | 10.9 | 8.4 | 10.3 | 10.8 | 8.4 | 10.8 | 9.8 | 10.8 |

The range of values of each variable in the presence observations is shown in parentheses. Only those environmental predictors selected (VIF < 10) are included. Mean contribution of aridity-related and non-related variables is also shown.

an ancestral desiccation resistance have poor capacity to adapt to increasingly drying conditions, as a recent study has demonstrated for several aquatic invertebrate species in south-western Australia (Carey et al., 2021).

Indeed, extending comparisons of the fundamental and realised aridity niche to other water beetle lineages, and also to other aquatic invertebrate groups with different strategies to cope with desiccation, would provide interesting insights to understand distributions of aquatic species along aridity gradients (Datry, 2012). Some aquatic taxa are able to survive desiccation through dormancy for long periods (e.g. some cladocerans or copepods—Lubzens et al., 2010). Others can survive desiccation at any life stage such as some copepods (e.g. Naess & Nilssen, 1991) or combine desiccation resistance traits (desiccation-resistant eggs or juveniles) and resilience traits (recolonising adults), such as some Odonata (Silsby, 2001) and Trichoptera (Hoffmann & Resh, 2003; Whiles et al., 1999). Taxa with these strategies could potentially show wide aridity realised niches (as most of the species studied here), when compared with other taxa highly sensitive to desiccation (e.g., some species of mayflies, decapod shrimps, isopods, amphipods, or crayfishes that rely on perennial water refuges to survive drying; Boulton et al., 2014).

We acknowledge that our data may be limited by the use of single population estimates of desiccation resistance to reflect species estimates, ignoring the probable presence of microevolutionary intraspecific variability and phenotypic plasticity (e.g., Rajpurohit et al., 2013; Whitman & Ananthakrishnan, 2009). Populations in more arid areas might have developed enhanced desiccation resistance by local adaptation, but in any case, this would not change our conclusions about the high basal desiccation resistance of the study species. Plasticity in desiccation resistance has been observed at least in one of the species studied here, *E. jesurribasi* (Botella-Cruz et al., 2021; Pallarés et al., 2017). In any case, although intraspecific comparisons could provide important insights about adaptation to desiccation stress, we could assume that variation in desiccation resistance between species is larger than that within species. This assumption is supported by a recent study that explores inter and intraspecific variation of cuticular hydrocarbons (which determine the waterproofing capacity of the cuticle) in *Enochrus* species (Botella-Cruz et al., 2019). Furthermore, it has been suggested that physiological plasticity (Terblanche & Hoffmann, 2020), and plastic desiccation responses in particular (Kellermann et al., 2020), might have a limited impact on species distributions, perhaps due to its associated fitness costs (Eriksson & Rafajlović, 2022).

4.2 | Minor role of aridity predictors in species distributions

Aridity was not an important predictor able to explain the geographical distribution of the studied species in our analyses. The predicted distribution of all of the species, except from *E. ochropterus*, encompassed arid areas, and the comparative influence of aridity-related variables was in general relatively minor. Together with the lack of

association between estimates of the fundamental and realised aridity niche, these results are overall consistent with the hypothesis that desiccation resistance was not an important physiological constraint for the occupation of arid areas in the species studied (Figure 1c).

Despite the general poor capacity of aridity predictors to explain species distributions, it is worth noting that the species for which such explanatory capacity was higher in our models are those more restricted to drier (rather than wetter) conditions (*E. jesurribasi*, *E. politus*, and *E. salomonis*). These species had the narrowest aridity niches, and *E. jesurribasi* and *E. politus* also showed a relatively high niche marginality, indicating a preference for drier conditions. Many species from other animal groups present in extreme arid environments are broadly distributed along aridity gradients (e.g., Wiens et al., 2013). The occupation of the most extreme part (i.e., more stressful conditions) of the aridity gradient in these desiccation resistant *Enochrus* species is therefore intriguing, as no apparent physiological constraint would limit the occupation of wetter conditions, and suggest that other non-physiological factors are important in shaping their distributions, in line with the second hypothesis proposed here (Figure 1b). Specialisation of the realised niche occurs also in most aquatic insects along salinity gradients, as saline-tolerant species are rare in freshwaters despite being physiologically capable to survive in such conditions (Arribas et al., 2019). It is possible that specialisation in abiotically stressful environments such as saline or arid aquatic habitats provides refuge from competition and predation, which are more intense in less stressful habitats (Berdugo et al., 2019; Herbst, 2001). Therefore, a comprehensive understanding of the distribution patterns observed here would need to consider the interactions between biotic interactions and stress tolerance in driving habitat occupation across stress gradients, as well as the role of historical factors (Davis & Scholtz, 2001) and dispersal limitation, and other processes that occur at smaller spatial scales, requiring the use of proximal environmental predictors (Anderson et al., 2021; Schultz et al., 2022).

It is important to note that in our distributional dataset, most records were concentrated in Europe and only a few records of some species were found in eastern Asia and southern Arabian Peninsula. Despite this possible sampling bias, we used the best available information to characterise species climatic niches, considering as far as possible the heterogeneity of environmental conditions in which they are present. In any case, it is likely that the addition of new records in such under-sampled areas would reinforce, rather than change our conclusions, as these areas have similar or higher aridity than the most sampled ones.

4.3 | Implications in a context of aridification

In many arid regions of the world, which already contain temporary water bodies, aridification is expected to change water regimes from perennial to temporary and from temporary to ephemeral (or terrestrial) (Kundzewicz et al., 2008; Strachan et al., 2015), with profound impacts on aquatic biota (e.g., Atkinson et al., 2021; Carey

et al., 2021). In the face of such changes, species may shift their geographical distribution or persist (Davis et al., 2013; Grimm et al., 1997; Rahel, 2002). The water beetle species studied here could be relatively resilient in this context, thanks to their high physiological desiccation resistance, and could even benefit from a possible decrease in competition in arid environments as less tolerant species are removed.

If we aim to predict aquatic species responses to aridification and establish appropriate management actions, comparative studies relating species' physiological, behavioural, and morphological traits to cope with desiccation with distributions are needed. Although a growing number of experimental studies are providing data in such direction for a number of aquatic taxa (e.g., Gough et al., 2012; Guareschi & Wood, 2020; Jermacz & Kobak, 2015), there is still an important research gap on this issue. Mesocom or field studies would be also helpful in assessing how desiccation responses measured in the laboratory translate into real-world contexts. Furthermore, our study shows that physiological constraints by themselves are not sufficient to explain species distributions along aridity gradients. Therefore, the integration of interactions between physiology and environment at local, organismal scales could greatly contribute to better understand the ecology and distribution of aquatic species, as well as their responses to aridification.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

Conceptualisation: S.P., D.S.-F. Developing methods: S.P., D.S.-F. Conducting the research: S.P., A.M., A.P. Data analysis: S.P., J.M.L. Preparation of figures and tables: S.P. Data interpretation: S.P., J.M.L., A.M., D.S.-F. Writing: S.P., A.M., J.M.L., A.P., D.S.-F.

DATA AVAILABILITY STATEMENT

Physiological data supporting this paper are available as [Supplementary Material](#), and occurrence data have been deposited in the public repository FigShare (<https://doi.org/10.6084/m9.figshare.15149070>).

ORCID

Susana Pallarés [ID https://orcid.org/0000-0001-8677-7475](https://orcid.org/0000-0001-8677-7475)

Andrés Millán [ID https://orcid.org/0000-0003-0036-363X](https://orcid.org/0000-0003-0036-363X)

Jorge M. Lobo [ID https://orcid.org/0000-0002-3152-4769](https://orcid.org/0000-0002-3152-4769)

David Sánchez-Fernández [ID https://orcid.org/0000-0003-1766-0761](https://orcid.org/0000-0003-1766-0761)

REFERENCES

- Abellán, P., Arribas, P., & Svenning, J. C. (2012). Geological habitat template overrides late Quaternary climate change as a determinant of range dynamics and phylogeography in some habitat-specialist water beetles. *Journal of Biogeography*, 39, 970–983. <https://doi.org/10.1111/j.1365-2699.2011.02654.x>
- Acevedo, P., Jiménez-Valverde, A., Lobo, J. M., & Real, R. (2012). Delimiting the geographical background in species distribution modelling. *Journal of Biogeography*, 39, 1383–1390. <https://doi.org/10.1111/j.1365-2699.2012.02713.x>
- Anderson, R. O., White, C. R., Chapple, D. G., & Kearney, M. R. (2021). A hierarchical approach to understanding physiological associations with climate. *Global Ecology and Biogeography*, 31, 332–346. <https://doi.org/10.1111/geb.13431>
- Araújo, M. B., & Pearson, R. G. (2005). Equilibrium of species' distributions with climate. *Ecography*, 28, 693–695. <https://doi.org/10.1111/j.2005.0906-7590.04253.x>
- Arribas, P., Andújar, C., Abellán, P., Velasco, J., Millán, A., & Ribera, I. (2014). Tempo and mode of the multiple origins of salinity tolerance in a water beetle lineage. *Molecular Ecology*, 23, 360–373. <https://doi.org/10.1111/mec.12605>
- Arribas, P., Gutiérrez-Cánovas, C., Botella-Cruz, M., Cañedo-Argüelles, M., Carbonell, J. A., Millán, A., ... Sánchez-Fernández, D. (2019). Insect communities in saline waters consist of realized but not fundamental niche specialists. *Philosophical Transactions of the Royal Society B*, 374, 20180008.
- Arribas, P., Velasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., ... Bilton, D. T. (2012). Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39(5), 984–994. <https://doi.org/10.1111/j.1365-2699.2011.02641.x>
- Atkinson, S. T., Cale, D., Pinder, A., Chambers, J. M., Halse, S. A., & Robson, B. J. (2021). Substantial long-term loss of alpha and gamma diversity of lake invertebrates in a landscape exposed to a drying climate. *Global Change Biology*, 27, 6263–6279. <https://doi.org/10.1111/gcb.15890>
- Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., ... Maestre, F. T. (2020). Global ecosystem thresholds driven by aridity. *Science*, 367, 787–790. <https://doi.org/10.1126/science.aay5958>
- Berdugo, M., Maestre, F. T., Kéfi, S., Gross, N., Le Bagousse-Pinguet, Y., & Soliveres, S. (2019). Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. *Journal of Ecology*, 107, 190–202. <https://doi.org/10.1111/1365-2745.13006>
- Bernhard, D., Schmidt, C., Korte, A., Fritzsche, G., & Beutel, R. G. (2006). From terrestrial to aquatic habitats and back again - molecular insights into the evolution and phylogeny of Hydrophiloidea (Coleoptera), using multigene analyses. *Zoologica Scripta*, 35, 597–606.
- Bilton, D. T., Freeland, J. R., & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Annual Review of Ecology, Evolution and Systematics*, 32, 159–181. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114016>
- Bloom, D. D., Fikáček, M., & Short, A. E. Z. (2014). Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. *PLoS One*, 9, e98430. <https://doi.org/10.1371/journal.pone.0098430>
- Bogan, M. T., Chester, E. T., Detry, T., Murphy, A. L., Robson, B. J., Ruhli, A., ... Whitney, J. E. (2017). Resistance, resilience, and community

- recovery in intermittent rivers and ephemeral streams. Chapter 4.8. In: A. Boulton, T. Datry, & N. Bonada (Eds). *Intermittent rivers and ephemeral streams*. (pp. 349–376). Academic Press.
- Bond, N. R., Lake, P. S., & Arthington, A. H. (2008). The impacts of drought on freshwater ecosystems: An Australian perspective. *Hydrobiologia*, 600, 3–16. <https://doi.org/10.1007/s10750-008-9326-z>
- Botella-Cruz, M., Pallarés, S., Millán, A., & Velasco, J. (2019). Role of cuticle hydrocarbons composition in the salinity tolerance of aquatic beetles. *Journal of Insect Physiology*, 117, 103899. <https://doi.org/10.1016/j.jinsphys.2019.103899>
- Botella-Cruz, M., Velasco, J., Millán, A., Hetz, S., & Pallarés, S. (2021). Cuticle hydrocarbons show plastic variation under desiccation in saline aquatic beetles. *Insects*, 12, 285. <https://doi.org/10.3390/insects12040285>
- Botella-Cruz, M., Villastrigo, A., Pallarés, S., López-Gallego, E., Millán, A., & Velasco, J. (2017). Cuticle hydrocarbons in saline aquatic beetles. *PeerJ*, 5, e3562. <https://doi.org/10.7717/peerj.3562>
- Boulton, A. J., Brock, M. A., Robson, B. J., Ryder, D. S., Chambers, J. M., & Davis, J. A. (2014). *Australian Freshwater Ecology: Processes and Management*, 2nd ed. Wiley-Blackwell.
- Bozinovic, F., Calosi, P., & Spicer, J. I. (2011). Physiological correlates of geographic range in animals. *Annual Review of Ecology, Evolution and Systematics*, 42, 155–179. <https://doi.org/10.1146/annurev-ecolsys-102710-145055>
- Bradley, T. (2009). *Animal Osmoregulation*. Oxford University Press.
- Calosi, P., Bilton, D. T., Spicer, J. I., & Atfield, A. (2008). Thermal tolerance and geographical range size in the *Agabus brunneus* group of European diving beetles (Coleoptera: Dytiscidae). *Journal of Biogeography*, 35, 295–305.
- Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., & Lytle, D. A. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, 42, 778–790. <https://doi.org/10.1111/jbi.12457>
- Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., ... Bonada, N. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *Journal of Biogeography*, 47, 1861–1874.
- Carey, N., Chester, E. T., & Robson, B. J. (2021). Life-history traits are poor predictors of species responses to flow regime change in headwater streams. *Global Change Biology*, 27, 3547–3564. <https://doi.org/10.1111/gcb.15673>
- Castellano, S., & Balleto, E. (2002). Is the partial Mantel test inadequate? *Evolution*, 56, 1871–1873. <https://doi.org/10.1111/j.0014-3820.2002.tb00203.x>
- Catullo, R. A., & Keogh, J. S. (2014). Aridification drove repeated episodes of diversification between Australian biomes: Evidence from a multi-locus phylogeny of Australian toadlets (Uperoleia: Myobatrachidae). *Molecular Phylogenetics and Evolution*, 79, 106–117. <https://doi.org/10.1016/j.ympev.2014.06.012>
- Céréghino, R., Françoise, L., Bonhomme, C., Carrias, J. F., Compin, A., Corbara, B., ... Leroy, C. (2020). Desiccation resistance traits predict freshwater invertebrate survival and community response to drought scenarios in a Neotropical ecosystem. *Ecological Indicators*, 119, 106839. <https://doi.org/10.1016/j.ecolind.2020.106839>
- Chester, E. T., Miller, A. D., Valenzuela, I., Wickson, S. J., & Robson, B. J. (2015). Drought survival strategies, dispersal potential and persistence of invertebrate species in an intermittent stream landscape. *Freshwater Biology*, 60, 2066–2083. <https://doi.org/10.1111/fwb.12630>
- Chester, E. T., & Robson, B. J. (2011). Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. *Freshwater Biology*, 56, 2094–2104. <https://doi.org/10.1111/j.1365-2427.2011.02644.x>
- Chown, S. L., & Nicolson, S. (2004). *Insect Physiological Ecology: Mechanisms and patterns*. Oxford University Press.
- Chown, S. L., Sørensen, J., & Terblanche, J. (2011). Water loss in insects: An environmental change perspective. *Journal of Insect Physiology*, 57, 1070–1084. <https://doi.org/10.1016/j.jinsphys.2011.05.004>
- Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19651–19658. <https://doi.org/10.1073/pnas.0901650106>
- Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel, S. W., & Fargione, J. E. (2013). Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, 3, 63–67. <https://doi.org/10.1038/nclimate1634>
- Datry, T. (2012). Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: Effects of duration of dry events. *Freshwater Biology*, 57, 563–574. <https://doi.org/10.1111/j.1365-2427.2011.02725.x>
- Datry, T., Pella, H., Leigh, C., Bonada, N., & Hugueny, B. (2016). A landscape approach to advance intermittent river ecology. *Freshwater Biology*, 61, 1200–1213. <https://doi.org/10.1111/fwb.12645>
- Davis, A. L. V., & Scholtz, C. H. (2001). Historical vs. ecological factors influencing global patterns of scarabaeine dung beetle diversity. *Diversity and Distributions*, 7, 161–174. <https://doi.org/10.1111/j.1472-4642.2001.00102.x>
- Davis, J., Pavlova, A., Thompson, R., & Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: Key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Global Change Biology*, 19, 1970–1984. <https://doi.org/10.1111/gcb.12203>
- Davis, J., Sim, L., Thompson, R. M., Pinder, A., Box, J. B., Murphy, N. P., ... Sunnucks, P. (2018). Patterns and drivers of aquatic invertebrate diversity across an arid biome. *Ecography*, 41, 375–387. <https://doi.org/10.1111/ecog.02334>
- Dias, A. T., Krab, E. J., Mariën, J., Zimmer, M., Cornelissen, J. H., Ellers, J., ... Berg, M. P. (2013). Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia*, 172, 667–677. <https://doi.org/10.1007/s00442-012-2541-3>
- Dolédéc, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, 81, 2914–2927.
- Dorn, A., Musilová, Z., Platzer, M., Reichwald, K., & Cellerino, A. (2014). The strange case of East African annual fishes: Aridification correlates with diversification for a savannah aquatic group? *BMC Evolutionary Biology*, 14, 1–13. <https://doi.org/10.1186/s12862-014-0210-3>
- Dray, S., & Dufour, A. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Edney, E. B. (1977). *Water balance in land arthropods*. Springer.
- Eriksson, M., & Rafajlović, M. (2022). The role of phenotypic plasticity in the establishment of range margins. *Philosophical Transactions of the Royal Society B*, 377(1846), 20210012. <https://doi.org/10.1098/rstb.2021.0012>
- Farber, O., & Kadmon, R. (2003). Assessment of alternative approaches for bioclimatic modelling with special emphasis on the Mahalanobis distance. *Ecological Modelling*, 160, 115–130.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- García-Roselló, E., Guisande, C., González-Vilas, L., González-Dacosta, J., Heine, J., Pérez-Costas, E., & Lobo, J. M. (2019). A simple method to estimate the probable distribution of species. *Ecography*, 42, 1613–1622. <https://doi.org/10.1111/ecog.04563>
- García-Roselló, E., Guisande, C., Heine, J., Pelayo-Villamil, P., & Manjarrés-Hernández, A. (2014). Using ModestR to download, import and clean species distribution records. *Methods in Ecology and Evolution*, 5, 708–713.

- Gough, H. M., Gascho Landis, A. M., & Stoeckel, J. A. (2012). Behaviour and physiology are linked in the responses of freshwater muskels to drought. *Freshwater Biology*, 57, 2356–2366. <https://doi.org/10.1111/fwb.12015>
- Grimm, N. B., Chacón, A., Dahm, C. N., Hostetler, S. W., Lind, O. T., Starkweather, P. L., & Wurtsbaugh, W. W. (1997). Sensitivity of aquatic ecosystems to climatic and anthropogenic changes: The Basin and Range, American Southwest and Mexico. *Hydrological Processes*, 11, 1023–1041. [https://doi.org/10.1002/\(SICI\)1099-1085\(19970630\)11:8<1023:AID-HYP516>3.0.CO;2-A](https://doi.org/10.1002/(SICI)1099-1085(19970630)11:8<1023:AID-HYP516>3.0.CO;2-A)
- Guareschi, S., & Wood, P. J. (2020). Exploring the desiccation tolerance of the invasive bivalve *Corbicula fluminea* (Müller 1774) at different temperatures. *Biological Invasions*, 22, 2813–2824. <https://doi.org/10.1007/s10530-020-02291-9>
- Guillot, G., & Rousset, F. (2013). Dismantling the Mantel tests. *Methods in Ecology and Evolution*, 4, 336–344. <https://doi.org/10.1111/2041-210x.12018>
- Guisande, C., García-Roselló, E., Heine, J., González-Dacosta, J., González-Vilas, L., García-Pérez, B. J., & Lobo, J. M. (2017). SPEDInstabR: An algorithm based on a fluctuation index for selecting predictors in species distribution modelling. *Ecological Informatics*, 37, 18–23.
- Harmon, L. J., & Glor, R. E. (2010). Poor statistical performance of the Mantel test in phylogenetic comparative analyses. *Evolution*, 64, 2173–2178. <https://doi.org/10.1111/j.1558-5646.2010.00973.x>
- Helaouët, P., & Beaugrand, G. (2009). Physiology, ecological niches and species distribution. *Ecosystems*, 12, 1235–1245. <https://doi.org/10.1007/s10021-009-9261-5>
- Herbst, D. B. (2001). Gradients of salinity stress, environmental stability and water chemistry as a templet for defining habitat types and physiological strategies in inland salt waters. *Hydrobiologia*, 466, 209–219.
- Hidalgo-Galiana, A., Sánchez-Fernández, D., Bilton, D. T., Cieslak, A., & Ribera, I. (2014). Thermal niche evolution and geographical range expansion in a species complex of western Mediterranean diving beetles. *BMC Evolutionary Biology*, 14, 1–17. <https://doi.org/10.1186/s12862-014-0187-y>
- Hoffmann, A., & Resh, V. H. (2003). Oviposition in three species of limnephiloid caddisflies (Trichoptera): Hierarchical influences on site selection. *Freshwater Biology*, 48, 1064–1077. <https://doi.org/10.1046/j.1365-2427.2003.01074.x>
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- Jäch, M. A., & Balke, M. (2008). Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia*, 595, 419–442. <https://doi.org/10.1007/s10750-007-9117-y>
- Jermacz, Ł., & Kobak, J. (2015). Life on the edge: Survival and behavioural responses of freshwater gill-breathing snails to declining water level and substratum drying. *Freshwater Biology*, 60, 2379–2391. <https://doi.org/10.1111/fwb.12664>
- Jiménez, L., & Soberón, J. (2022). Estimating the fundamental niche: Accounting for the uneven availability of existing climates in the calibration area. *Ecological Modelling*, 464, 109823. <https://doi.org/10.1016/j.ecolmodel.2021.109823>
- Kearney, M. R. (2006). Habitat, environment and niche: What are we modelling? *Oikos*, 115, 186–191. <https://doi.org/10.1111/j.2006.0030-1299.14908.x>
- Kearney, M. R., Munns, S. L., Moore, D., Malishev, M., & Bull, C. M. (2018). Field tests of a general ectotherm niche model show how water can limit lizard activity and distribution. *Ecological Monographs*, 88, 672–693. <https://doi.org/10.1002/ecm.1326>
- Kellermann, V., Loeschcke, V., Hoffmann, A. A., Kristensen, T. N., Fløjgaard, C., David, J. R., & Overgaard, J. (2012). Phylogenetic constraints in key functional traits behind species' climate niches: Patterns of desiccation and cold resistance across 95 *Drosophila* species. *Evolution*, 66, 3377–3389.
- Kellermann, V., McEvey, S. F., Sgrò, C. M., & Hoffmann, A. A. (2020). Phenotypic plasticity for desiccation resistance, climate change, and future species distributions: Will plasticity have much impact? *The American Naturalist*, 196, 306–315. <https://doi.org/10.1086/710006>
- Kundzewicz, Z. W., Mata, L. J., Arnell, N. W., Döll, P., Jimenez, B., Miller, K., ... Shiklomanov, I. (2008). The implications of projected climate change for freshwater resources and their management. *Hydrological Sciences Journal*, 53, 3–10. <https://doi.org/10.1623/hysj.53.1.3>
- Linke, S., Lehner, B., Ouellet Dallaire, C., Ariwi, J., Grill, G., Anand, M., ... Thieme, M. (2019). Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. *Scientific Data*, 6, 283. <https://doi.org/10.1038/s41597-019-0300-6>
- Lobo, J. M. (2016). The use of occurrence data to predict the effects of climate change on insects. *Current Opinion in Insect Science*, 17, 62–68. <https://doi.org/10.1016/j.cois.2016.07.003>
- Lubzens, E., Cerda, J., & Clark, M. (2010). *Dormancy and resistance in harsh environments*, Vol. 21. Springer Science & Business Media.
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27, 209–222.
- Morán-Ordóñez, A., Pavlova, A., Pinder, A. M., Sim, L., Sunnucks, P., Thompson, R. M., & Davis, J. (2015). Aquatic communities in arid landscapes: Local conditions, dispersal traits and landscape configuration determine local biodiversity. *Diversity and Distributions*, 21, 1230–1241. <https://doi.org/10.1111/ddi.12342>
- Murphy, A. L., Pavlova, A., Thompson, R., Davis, J., & Sunnucks, P. (2015). Swimming through sand: Connectivity of aquatic fauna in deserts. *Ecology and Evolution*, 5, 5252–5264. <https://doi.org/10.1002/ece3.1741>
- Naess, T., & Nilssen, J. P. (1991). Diapausing fertilized adults. a new pattern of copepod life cycle. *Oecologia*, 86, 368–371. <https://doi.org/10.1007/BF00317602>
- Ochoa-Ochoa, L. M., Mejía-Domínguez, N. R., Velasco, J. A., Marske, K. A., & Rahbek, C. (2019). Amphibian functional diversity is related to high annual precipitation and low precipitation seasonality in the New World. *Global Ecology and Biogeography*, 28(9), 1219–1229.
- Pallarés, S., Arribas, P., Bilton, D. T., Millán, A., & Velasco, J. (2015). The comparative osmoregulatory ability of two water beetle genera whose species span the fresh-hypersaline gradient in inland waters (Coleoptera: Dytiscidae, Hydrophilidae). *PLoS One*, 10, e0124299. <https://doi.org/10.1371/journal.pone.0124299>
- Pallarés, S., Arribas, P., Bilton, D. T., Millán, A., Velasco, J., & Ribera, I. (2017). The chicken or the egg? Adaptation to desiccation and salinity tolerance in a lineage of water beetles. *Molecular Ecology*, 26, 5614–5628. <https://doi.org/10.1111/mec.14334>
- Pallarés, S., Botella-Cruz, M., Arribas, P., Millán, A., & Velasco, J. (2017). Aquatic insects in a multistress environment: Cross-tolerance to salinity and desiccation. *Journal of Experimental Biology*, 220, 1277–1286. <https://doi.org/10.1242/jeb.152108>
- Pallarés, S., Velasco, J., Millán, A., Bilton, D. T., & Arribas, P. (2016). Aquatic insects dealing with dehydration: Do desiccation resistance traits differ in species with contrasting habitat preferences? *PeerJ*, 4, e2382. <https://doi.org/10.7717/peerj.2382>
- Pérez-Quintero, J. C. (2012). Environmental determinants of freshwater mollusc biodiversity and identification of priority areas for conservation in Mediterranean water courses. *Biodiversity and Conservation*, 21, 3001–3016. <https://doi.org/10.1007/s10531-012-0351-x>
- Pinceel, T., Brendonck, L., Larmuseau, M. H., Vanhove, M. P., Timms, B. V., & Vanschoenwinkel, B. (2013). Environmental change as a driver of diversification in temporary aquatic habitats: Does the genetic structure of extant fairy shrimp populations reflect historic aridification? *Freshwater Biology*, 58, 1556–1572. <https://doi.org/10.1111/fwb.12137>

- R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rahel, F. J. (2002). Using current biogeographic limits to predict fish distributions following climate change. In N. A. Mcginn (Ed.), *Fisheries in a Changing Climate* (pp. 99–109). American Fisheries Society.
- Rajpurohit, S., Nedved, O., & Gibbs, A. G. (2013). Meta-analysis of geographical clines in desiccation tolerance of Indian drosophilids. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 164, 391–398. <https://doi.org/10.1016/j.cbpa.2012.11.013>
- Razeng, E., Morán-Ordóñez, A., Brim Box, J., Thompson, R., Davis, J., & Sunnucks, P. (2016). A potential role for overland dispersal in shaping aquatic invertebrate communities in arid regions. *Freshwater Biology*, 61, 745–757. <https://doi.org/10.1111/fwb.12744>
- Razeng, E., Smith, A. E., Harrison, K. A., Pavlova, A., Nguyen, T., Pinder, A., ... Sunnucks, P. (2017). Evolutionary divergence in freshwater insects with contrasting dispersal capacity across a sea of desert. *Freshwater Biology*, 62, 1443–1459. <https://doi.org/10.1111/fwb.12959>
- Sánchez-Fernández, D., Aragón, P., Bilton, D. T., & Lobo, J. M. (2012). Assessing the congruence of thermal niche estimations derived from distribution and physiological data. A test using diving beetles. *PLoS One*, 7, e48163. <https://doi.org/10.1371/journal.pone.0048163>
- Sánchez-Fernández, D., Lobo, J. M., & Hernández-Manrique, O. L. (2011). Species distribution models that do not incorporate global data misrepresent potential distributions: A case study using Iberian diving beetles. *Diversity and Distributions*, 17, 163–171. <https://doi.org/10.1111/j.1472-4642.2010.00716.x>
- Sánchez-Fernández, D., Lobo, J. M., Millán, A., & Ribera, I. (2012). Habitat type mediates equilibrium with climatic conditions in the distribution of Iberian diving beetles. *Global Ecology and Biogeography*, 21, 988–997. <https://doi.org/10.1111/j.1466-8238.2011.00743.x>
- Schultz, E. L., Hülsmann, L., Pillet, M. D., Hartig, F., Breshears, D. D., Record, S., ... Evans, M. E. (2022). Climate-driven, but dynamic and complex? A reconciliation of competing hypotheses for species' distributions. *Ecology Letters*, 25, 38–51. <https://doi.org/10.1111/ele.13902>
- Short, A. E. Z., & Fikáček, M. (2013). Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). *Systematic Entomology*, 38, 723–752. <https://doi.org/10.1111/syen.12024>
- Silby, J. D. (2001). *Dragonflies of the world*. CSIRO Publishing.
- Sneath, P. H. A., & Sokal, R. R. (1973). *Numerical taxonomy: The principles and practice of numerical classification*. Freeman.
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Soberón, J., & Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS One*, 12, e0175138. <https://doi.org/10.1371/journal.pone.0175138>
- Strachan, S. R., Chester, E. T., & Robson, B. J. (2015). Freshwater invertebrate life history strategies for surviving desiccation. *Springer Science Reviews*, 3, 57–75. <https://doi.org/10.1007/s40362-015-0031-9>
- Terblanche, J. S., & Hoffmann, A. A. (2020). Validating measurements of acclimation for climate change adaptation. *Current Opinion in Insect Science*, 41, 7–16. <https://doi.org/10.1016/j.cois.2020.04.005>
- Title, P. O., & Bemmels, J. B. (2018). ENVIREM: An expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, 41, 291–307. <https://doi.org/10.1111/ecog.02880>
- Vander Vorste, R., Stubbington, R., Acuña, V., Bogan, M. T., Bonada, N., Cid, N., ... Ruhí, A. (2021). Climatic aridity increases temporal nestedness of invertebrate communities in naturally drying rivers. *Ecography*, 44, 1–10.
- Velasco, J., & Millán, A. (1998). Insect dispersal in a drying desert stream: Effects of temperature and water loss. *The Southwestern Naturalist*, 43, 80–87.
- Watling, J. I., & Braga, L. (2015). Desiccation resistance explains amphibian distributions in a fragmented tropical forest landscape. *Landscape Ecology*, 30, 1449–1459. <https://doi.org/10.1007/s10980-015-0198-0>
- Whiles, M. R., Goldowitz, B. S., & Charlton, R. E. (1999). Life history and production of a semi-terrestrial limnephilid caddisfly in an intermittent Platte River wetland. *Journal of the North American Benthological Society*, 18, 533–544. <https://doi.org/10.2307/1468385>
- Whitman, D. W., & Ananthakshnan, T. N. (2009). *Phenotypic plasticity of insects. Mechanisms and Consequences*. Science Publishers.
- Wiens, J. J., Kozak, K. H., & Silva, N. (2013). Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). *Evolution*, 67, 1715–1728. <https://doi.org/10.1111/evo.12053>
- Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2093–2106.
- Yee, D. A., & Kehl, S. (2015). Chapter 39 – Order Coleoptera. In J. H. Thorp, & D. C. Rogers (Eds.), *Thorp and covich's freshwater invertebrates: Ecology and general biology* (4th ed., pp. 1003–1042). Elsevier.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

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