




# Are amphibians tracking their climatic niches in response to climate warming? A test with Iberian amphibians

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## Abstract

Current climate warming has already contributed to local extinctions. Amphibians are one of the most sensitive animal groups to climate change, currently undergoing a global decline. Predictive models for Europe and Iberian Peninsula forecast that the future impact of climate change on amphibians will depend on their capacity to alter their distributions by tracking climate warming. In the present study, we explore the responses of Iberian amphibian species to recent climate change, by comparing amphibian distributions between two time periods (1901–1990 vs. 2000–2015). Our findings suggest that, although climatic conditions have changed between the two periods, Iberian amphibians have barely shifted their distribution ranges northwards, with the exception of the southernmost species (*Alytes dickhilleni*). However, most Iberian amphibians appear to have moved their elevational limits upwards in mountains. Approximately half of the species showed different occupied niches between the two time periods, suggesting that many Iberian amphibians have not been able to reach all the new location with optimal climatic conditions for them. Furthermore, disappearing cold climatic conditions (e.g. those found at mountain tops) limit the potential distribution of cold-adapted species, including European widespread species with their southern margin in the Iberian Peninsula, and endemic species. The combination of a limited ability to shift their ranges and profound climatic changes could pose a challenge to the long-term persistence of Iberian amphibian populations.

**Keywords** Amphibians · Distribution ranges · Ecological niche · Iberian Peninsula

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## 1 Introduction

Anthropogenic climate change is considered one of the major threats to biodiversity in the twenty-first century and may underlie several reported extinction events (Thomas et al. 2004; Parmesan 2006; Sinervo et al. 2010; Thuiller et al. 2011). Assessing the vulnerability of species to climate change is critical for effective conservation efforts. Ultimately, vulnerability will depend on the exposure to environmental change and the capacity of species to respond (Williams et al. 2008; Pacifici et al. 2015). Organisms could either shift their distribution ranges to track their climatic envelopes or persist under new environmental conditions through genetic adaptation (e.g. niche evolution), phenotypic plasticity, and behavioural responses. Otherwise, species would go extinct (Chevin et al. 2010; Moritz and Agudo 2013; Sunday et al. 2014). Although adaptive niche shifts in response to climate change have occurred in the past (Martínez-Monzón et al. 2017), rates of projected warming exceed past rates of climatic niche evolution (Hof et al. 2010; Wiens et al. 2010; Quintero and Wiens 2013). Conserved climatic niches, in turn, could impede the long-term persistence of populations in new environments (Wiens et al. 2010). Further, the potential of species to acclimate to global warming seems limited (Gunderson and Stillman 2015; but see Ruiz-Aravena et al. 2014). Therefore, behavioural responses and range shifts may be essential for species to survive climate change (Kearney and Porter 2009; Sunday et al. 2014).

Ectothermic animals, in which biological and ecological processes depend largely on environmental temperature, may be particularly vulnerable to climate change (Aragón et al. 2010a). Amphibians, in particular, are undergoing a strong worldwide decline (Alford and Richards 1999; Houlahan et al. 2000; Stuart et al. 2004), which has been related to climate change in some instances (Collins and Storer 2003; Beebe and Griffiths 2005; Pounds et al. 2006). Regarding European amphibians, correlative species distribution models suggest that the southernmost latitudes, including the Mediterranean basin hotspot, will become unsuitable for many species in the future (Araújo et al. 2006; Carvalho et al. 2010). By using an all-or-nothing approach to consider dispersal, those studies forecast that amphibians in southern Europe (e.g. the Iberian Peninsula) will undergo extensive local extinctions if they are unable to shift distribution ranges. Predicted local extinctions are even more likely given that southern amphibians respond less to climate change by phenological changes than northernmost species (While and Uller 2014). Alternatively, if they are able to track their preferred climates, the impact will be species-specific; some species could even increase their ranges. Although distribution shifts have been described for several species (reviews in Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006), the only study that analysed latitudinal range shifts of an amphibian offered no evidence for a shift (Hickling et al. 2006).

Climate has already changed and challenged the biodiversity of species-rich regions, such as the Iberian Peninsula (Benito-Garzón et al. 2009). Temperatures in the Iberian Peninsula, for instance, have increased 0.3 °C on average during the last two decades of the twentieth century (Hulme and Sheard 1999; Jones et al. 1999). Understanding how Iberian amphibians have responded to the climate change of past decades could help to predict the most likely responses to future climate change. Thanks to the participation of many devoted field volunteers, we have assembled a database for amphibian occurrences in Spain and Portugal from the end of the twentieth century to the early twenty-first century (Montori et al. 2014), through which it is now possible to explore recent range shifts. Additionally, a recently developed, remotely sensed, environmental layer dataset (MERRAclim; Vega et al. 2017) enables us to explore how climate has changed in recent decades (i.e. the 1980s, 1990s, and 2000s).

In the present study, we integrated amphibians' occurrences through time and the MERRAclim dataset to explore the responses of Iberian amphibian species to recent climate change. Using the data on the distribution of Iberian amphibians within two time periods (1901–1990 and 2000–2015), we explored whether species have shifted their distribution ranges as climate has changed. We predict that, if amphibians have a considerable capacity to change their distributions, both the northern and southern distribution limits would shift northwards. To the contrary, if dispersal barriers in the north (the Cantabrian Sea and the Pyrenees Mountains) limit the potential dispersal of Iberian amphibians, we expect northern limits to remain unchanged, while the overall ranges would shrink as a consequence of northward shifts of southern limits. Additionally, species could also go upwards in elevation (Pounds et al. 1999; Konvicka et al. 2003; Wilson et al. 2005). Thus, we also explored changes in the elevational limits. In addition, we used the MERRAclim dataset to assess whether Iberian amphibians have successfully tracked climatic conditions. Alternatively, species could be inhabiting regions with novel climatic conditions. To compare the occupied climatic niches of species during the two time periods considered, we used the statistical framework developed by Broennimann et al. (2012). This framework has been widely applied to assess niche conservatism or divergence (Serra-Varela et al. 2015; Ahmadzadeh et al. 2016). However, due to the short time span of our dataset, we deem it unlikely to be able to identify climatic niche evolution. Thus, here we used the framework proposed by Broennimann et al. (2012) to explore only potential changes in the climatic conditions undergone by species (i.e. differences in the occupied climatic niche, sensu Sillero 2011). Additionally, we used this framework to unveil disappearing climates and the potential consequences for Iberian amphibians.

## 2 Methods

### 2.1 Species-occurrence data

Our dataset included 386,372 records of amphibians from the Iberian Peninsula (344,465 records from Spain and 41,907 from Portugal), gathered, until December of 2015, by the Spanish Herpetological Society (data available at <http://siare.herpetologica.es>) and the Portuguese Institute for Nature Conservation and Forests (<http://www2.icnf.pt>). This dataset included records collected through a specific Citizen Science platform (Montori et al. 2014). As an initial step, we cleaned the dataset from erroneous and duplicated records. Each record included the geographic coordinates and the date of observation. Based on the observation date, we split the occurrence data into two different time periods: 1901–1990 and 2000–2015. We considered only native species that, during the 1901–1990 period, were found in at least 40 of the 6204 10 × 10 km cells (Universal Transverse Mercator Units, UTMs, ETRS89 UTM 30 N) covering the Iberian Peninsula. This reduced the sample to 22 species (Table S1). It is noteworthy, however, that records were collected by chance and that the rate of new records has increased in recent years as a consequence of increased sampling effort (Montori et al. 2014). Therefore, it was necessary to control for temporal variation in sampling effort, as well as to carefully interpret the effect of new records on estimates of occupied climatic niches (see below).

### 2.2 Range shifts

For each species, we estimated the latitudinal distribution in the Iberian Peninsula during 1901–1990 and during 2000–2015, as the mean latitude of the centroids of the 20

northernmost and 20 southernmost cells occupied in each time period (as in e.g. Thomas and Lennon 1999; Brommer 2004; Hickling et al. 2006). To estimate shifts in range margins, we computed the change in the mean latitude of the centroids of the northernmost and southernmost cells of each species' distribution between the two periods (Table S1). We used a single-sample  $t$  test to determine whether such variation was significantly greater than 0 km, with species as the statistical unit. Most of amphibian species in the Iberian Peninsula, however, have a marked northern distribution (Fig. S1). Therefore, the possibility to shift northwards could be limited by the Cantabrian Sea and Pyrenees Mountains. Consequently, we also examined the effect of the initial (i.e. during the 1901–1990 period) latitude of the northern margin of the range on the estimated latitudinal change. To that end, we regressed the latitudinal change in northern range margins against the initial latitude. If northern species are limited to shift their northern range margin, we would expect a significant impact of initial latitudinal distribution on the magnitude of change. Furthermore, to analyse in more detail the effect of initial latitudinal range, we analysed separately 'northern' and 'southern' species, classified according to the median (4809 UTM coordinate, in km) of the northern latitudinal margin.

A significant northward shift of the northern margin of a distribution could be indicative of a response to climate change. However, in the case of species in expansion, range size also would increase in both the northern and the southern limits. Therefore, the comparison between the shift in northern margin and what has occurred in the southern margin is fundamental to ascertain whether the change in distribution is a possible response to climate change. Moreover, an increase in sampling effort in recent years would increase the number of records and hence the known margin of distribution at both northern and southern limits. The number of records increases with sampling effort, and thus the difference in the number of records between time periods is a good indicator of the difference in the sampling effort between periods (see Thomas and Lennon 1999; Brommer 2004; Zuckerberg et al. 2009). Indeed, the number of records augmented significantly between 1901–1990 and 2000–2015 periods (mean  $\pm$  standard deviation,  $3172 \pm 4067$  records,  $t_{21} = 3.66$ ,  $p = 0.002$ ). Consequently, to statistically control the sampling effort, we regressed the change in latitudinal distribution in kilometres against the difference in the number of new records (Thomas and Lennon 1999; Brommer 2004; Zuckerberg et al. 2009). The intercept of the regression line with the  $y$ -axis indicates the effective shift in the range, controlled for changes in the sampling effort.

For each species, we also assessed the shift in the elevation range between the 1901–1990 and 2000–2015 periods. We identified the limits of the elevation range of each species during each study period as the mean altitude of the 20 most elevated and 20 least elevated cells of the corresponding distribution area. For this, we used the 7.5 arc-second elevation layer from the Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010) dataset developed by the US Geological Survey and the National Geospatial-Intelligence Agency (Danielson and Gesch 2011). For each species, we then calculated the change in the elevation-range limits between 1901–1990 and 2000–2015 and used a single-sample  $t$  test to determine whether such variation was significantly greater than 0 m, with species as the statistical unit.

### 2.3 Changes in occupied climatic niches

We used the statistical framework of Broennimann et al. (2012) to quantify and compare the occupied climatic niches of amphibian species between 1901–1990 and 2000–2015. To characterise occupied climatic niches, we used occurrence data for each species and time

period, and the bioclimatic layers corresponding to the 1980s (for the first period) and the 2000s (for the second period) from the MERRAclim dataset (Vega et al. 2017). We focused on six bioclimatic variables: annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual mean precipitation (Bio12), precipitation of the wettest month (Bio13), and precipitation of the driest month (Bio14). These climatic variables represent temperature and precipitation average and extremes, which could constrain species distributions. With the values of those climatic variables for the whole Iberian Peninsula including the two time periods, we created two Principal Component Analysis (PCA) axes (Table S2, Fig. S2) following the PCA-Env approach (Broennimann et al. 2012). Then, we calculated the density of occurrences of each species and time periods in PCA-space, using kernel density functions (resolution chosen for the gridded environmental space;  $R = 100$ ). Subsequently, we computed the niche overlap between time periods for each species based on Schoener's  $D$  statistic (Schoener 1968).

We used the equivalency test to assess whether occupied climatic niches were equivalent between time periods. In each run of the niche equivalency test, we pooled all occurrences for each species and time period (i.e. 1901–1990 and 2000–2015) and then randomly split them into two datasets while keeping constant the number of occurrences per time period. With those randomised datasets, we recalculated niche overlap (Schoener's  $D$ ). To assess the significance of the niche equivalency tests, the resulting empirical distributions of expected niche overlaps were compared with observed values. If observed overlap values fall within the empirical distribution of expected niche overlap values, niche equivalency is rejected. We only considered equivalent niches that showed higher than expected niche overlap values (alternative hypothesis: “greater” overlap).

To test whether niches were more similar than expected by chance between time periods, we used niche similarity tests. To that end, we computed niche overlap values between the environmental conditions at occurrences in 1901–1990 and randomly generated occurrences within the available environmental space in 2000–2015 (with 2000s MERRAclim layers). In this way, we explored whether the observed niches in the 1901–1990 time period are more similar to those occupied in the 2000–2015 than would be expected by chance. This test shows whether niches are similar due to the selection of locations with similar conditions (to some extent active habitat selection) or the consequence of mere availability of the environmental space (Warren et al. 2008; Broennimann et al. 2012). We performed the analyses as implemented in the *ecospat* R-package (Broennimann et al. 2015), and we evaluated the significance of both tests using 100 permutations (Warren et al. 2008; Broennimann et al. 2012). Since results from niche equivalency and similarity tests could vary depending on the definition of the geographical background (i.e. the environmental space that we consider available to the species; Mateo et al. 2014), we conducted all comparisons including the entire study area (the Iberian Peninsula) and only the area within buffers of a radius of 200 km created around the occurrence points of each species and time period.

To examine whether Iberian amphibians have tracked occupied climatic niches between 1901–1990 and 2000–2015, we compared how available environmental space and occupied niches changed between periods. Specifically, we visually explored whether species occupied all the previously occupied PCA-space, based on the available PCA-space using both the entire Iberian Peninsula and buffers around points as the background. Additionally, we identified disappearing combinations of the environmental space (PCA-space) between time periods (see Fig. 2). New records in previously unknown areas could also lead to an apparent change in occupied climatic niches. For instance, most records in the south-western Iberian

Peninsula corresponded to the period 2000–2015. Because, as far as we know, methods to account for increased sampling effort in niche equivalency and similarity tests are not currently available, we visually inspected the influence of new records on estimates of occupied climatic niches and we carefully interpreted results.

### 3 Results

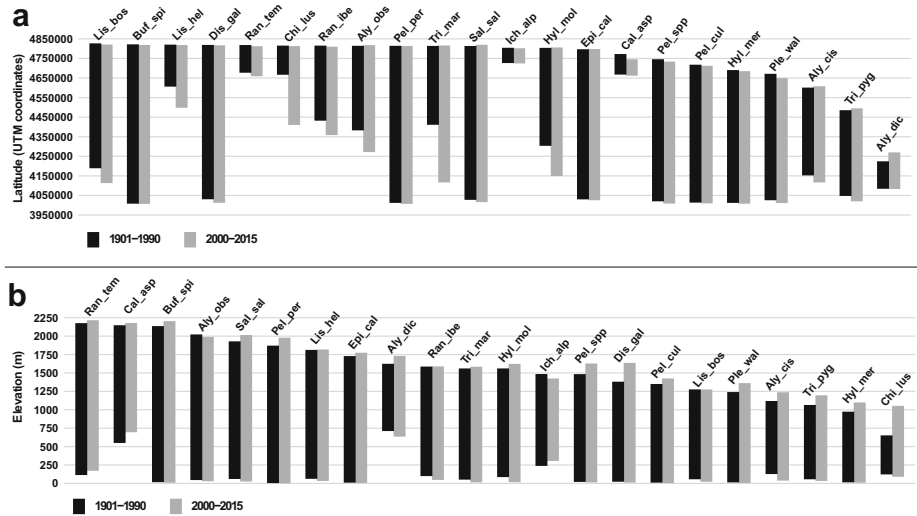
#### 3.1 Have Iberian amphibians shifted their geographical ranges?

Overall, between 1901–1990 and 2000–2015, the northern margins of the distribution ranges of Iberian amphibians did not shift significantly ( $t_{21} = 0.40$ ,  $p = 0.69$ ; Fig. 1a, S1). The difference in sampling effort between periods was unrelated to observed changes along northern margins ( $r = -0.01$ ,  $p = 0.96$ ). When we controlled for the initial latitude of the northern margin, we found a marked negative correlation between the initial latitude and the latitudinal change of the northern margins ( $r = -0.61$ ,  $p < 0.001$ ; Fig. S3A). The southernmost species (*Alytes dickhilleni*) showed a pronounced change northwards in its northern margin (about 45 km). *Triturus pygmaeus* and *Alytes cisternasii*, the species with the second and third southernmost northern margin, also showed a change northwards of almost 1 km between the two periods (Fig. 1a). The correlation between initial latitude and the latitudinal change was strongly affected by one data point (*A. dickhilleni*) and proved non-significant when we removed this species ( $r = -0.12$ ,  $p = 0.59$ ). However, when ‘northern’ and ‘southern’ species were analysed separately, the effect of initial north latitudinal range was even more evident (southern species:  $r = -0.79$ ,  $p = 0.004$ , Fig. S3B; northern species:  $r = -0.63$ ,  $p = 0.036$ , Fig. S3C).

Southern range margins of Iberian amphibians significantly shifted southwards by  $56.27 \pm 83.15$  km on average ( $t_{21} = 3.17$ ,  $p = 0.005$ , Fig. 1a). The sampling effort did not account for changes on the southern margins ( $r = 0.25$ ,  $p = 0.26$ ). The initial latitudinal position of southern margins significantly influenced shifts: species with the northernmost southern range showed the largest shifts southwards ( $r = -0.44$ ,  $p = 0.04$ ). Shift along southern margins were unrelated to the shifts on northern margins ( $r = -0.04$ ,  $p = 0.88$ ).

The complete distribution range of Iberian amphibians increased its latitudinal extension from 1901–1990 to 2001–2015 (in average  $55.11 \pm 84.70$  km;  $t_{21} = 3.05$ ,  $p = 0.006$ , Fig. 1a). The magnitude of this change was unrelated to the sampling effort ( $r = -0.25$ ,  $p = 0.27$ ) or the initial latitude of northern margins ( $r = 0.16$ ,  $p = 0.46$ ). However, it was marginally related to the initial latitude of southern margins ( $r = 0.40$ ,  $p = 0.065$ ); species with southern margins in the northern Iberian Peninsula increased their ranges slightly more than did species distributed more towards the south. In fact, changes in southern margins were strongly correlated with range increases ( $r = 0.99$ ,  $p < 0.001$ ; Fig. S4). On the contrary, changes along the northern margins were unrelated to range variations ( $r = 0.19$ ,  $p = 0.39$ ).

Regarding altitude, in the period considered, the highest margin of Iberian amphibians ascended an average of  $84.27 \pm 99.31$  m ( $t_{21} = 3.98$ ,  $p = 0.0007$ ; Fig. 1b). Meanwhile, change in the lowest margin did not differ significantly from 0 ( $-12.13 \pm 50.37$  m;  $t_{21} = 1.13$ ,  $p = 0.27$ ). The change in mean altitude did not differ from 0, either ( $-34.16 \pm 50.37$  m;  $t_{21} = 1.56$ ,  $p = 0.13$ ). The difference in sampling effort between periods was unrelated to observed changes in the highest margins ( $r = -0.02$ ,  $p = 0.93$ ). There was a significant negative concave-up relationship (Fig. S5) between mean elevation of species in 1901–1990 period



**Fig. 1** **a** Latitudinal species’ ranges in 1901–1990 (black) and 2000–2015 (grey). **b** Altitudinal species’ ranges in 1901–1990 (black) and 2000–2015 (grey). For abbreviations of the species names see Table S1

and the change in the highest margin (linear effect:  $F_{1, 19} = 15.49, p < 0.001$ ; quadratic effect:  $F_{1, 19} = 11.52, p = 0.003$ ). That is, species distributed at the lowest elevations registered a higher expansion upwards. All species, except *Alytes obstetricans*, *Ichthyosaura alpestris*, and *Lissotriton boscai*, showed a change upwards.

### 3.2 Have occupied climatic niches changed?

Based on the niche equivalency test, most Iberian amphibians did not occupy equivalent occupied niches between the periods 1901–1990 and 2000–2015 (Table 1). In fact, in 8 out of 22 species, the occupied niches were no more similar than expected by chance between time periods, with the whole Iberian Peninsula as the background. Moreover, when we reduced available climates to buffers of 200 km around points, the proportion of species with different occupied niches increased to half of the comparisons (11 out of 22; Table 1).

For the entire Iberian Peninsula, the general climate warmed slightly, and the coldest and driest climates disappeared between 1901–1990 and 2000–2015. More precisely, temperature has increased considerably between time periods, notably in the Pyrenees and other mountainous regions. Precipitation has decreased in the southern Iberian Peninsula, the Mediterranean region, and the Pyrenees, and alternatively, it has increased in the north-western Iberian Peninsula. Remarkably, summer droughts appear to have increased across all the Iberian Peninsula (Fig. S6). Coincidentally, many species showed changes in occupied niches that were similar, both in direction and magnitude, to shifts in the general climate (Fig. 2). As a result, from 1901–1990 to 2000–2015, a fraction of the occupied environmental space became unoccupied despite remaining available for some species (Fig. 2a, b, e, f; Supplementary Material). Currently, cold and dry conditions are found mainly in mountainous areas. Thus, species formerly inhabiting these areas, whether widespread (e.g. *Salamandra salamandra*; Fig. 2b, f) or endemic (e.g. *Calotriton asper*; Fig. 2d, h), did not have analogous climates available for

**Table 1** Niche similarity and equivalency tests for occupied niches between time periods for each species, following Broennimann et al. (2012). We used either the whole Iberian Peninsula as background or buffers of 200 km around occurrences as the background. **D**: Schoener's **D** niche overlap statistic; under **Equivalency**: **p** value of equivalency test (significant tests mean that overlap values are greater than expected); under **Similarity**: **p** value of similarity test

	Iberian Peninsula			Buffers around points		
	<i>D</i>	Equivalency <i>p</i> -values	Similarity <i>p</i> -values	<i>D</i>	Equivalency <i>p</i> -values	Similarity <i>p</i> -values
<i>Alytes cisternasii</i>	0.329	1.000	<b>0.020</b>	0.397	1.000	0.099
<i>Alytes dickhilleni</i>	0.395	0.901	0.228	0.000	1.000	1.000
<i>Alytes obstetricans</i>	0.621	1.000	<b>0.020</b>	0.582	0.238	0.069
<i>Bufo calamita</i>	0.617	<b>0.010</b>	<b>0.030</b>	0.606	<b>0.010</b>	<b>0.030</b>
<i>Bufo spinosus</i>	0.588	1.000	0.089	0.611	<b>0.010</b>	0.069
<i>Calotriton asper</i>	0.546	1.000	<b>0.010</b>	0.518	0.099	<b>0.010</b>
<i>Chioglossa lusitanica</i>	0.444	1.000	0.139	0.475	1.000	0.089
<i>Discoglossus galganoi</i>	0.521	1.000	<b>0.020</b>	0.538	0.733	<b>0.030</b>
<i>Hyla meridionalis</i>	0.576	0.980	<b>0.020</b>	0.572	<b>0.010</b>	<b>0.040</b>
<i>Hyla molleri</i>	0.381	1.000	0.208	0.353	1.000	0.267
<i>Ichthyosaura alpestris</i>	0.693	0.782	<b>0.010</b>	0.615	<b>0.030</b>	<b>0.040</b>
<i>Lissotriton boscai</i>	0.388	1.000	0.406	0.395	1.000	0.327
<i>Lissotriton helveticus</i>	0.697	0.683	<b>0.010</b>	0.702	<b>0.030</b>	<b>0.020</b>
<i>Pelobates cultripes</i>	0.584	0.693	<b>0.020</b>	0.535	<b>0.010</b>	<b>0.020</b>
<i>Pelophylax perezi</i>	0.639	0.782	<b>0.040</b>	0.639	0.347	0.099
<i>Pelodytes spp.</i>	0.550	1.000	<b>0.020</b>	0.579	0.059	0.119
<i>Pleurodeles waltl</i>	0.615	0.079	<b>0.010</b>	0.625	0.881	<b>0.040</b>
<i>Rana iberica</i>	0.567	1.000	0.059	0.585	1.000	<b>0.030</b>
<i>Rana temporaria</i>	0.609	1.000	<b>0.010</b>	0.575	1.000	<b>0.010</b>
<i>Salamandra salamandra</i>	0.556	1.000	0.069	0.552	1.000	0.099
<i>Triturus marmoratus</i>	0.468	1.000	0.129	0.450	1.000	0.248
<i>Triturus pygmaeus</i>	0.658	<b>0.010</b>	<b>0.010</b>	0.536	<b>0.010</b>	<b>0.020</b>

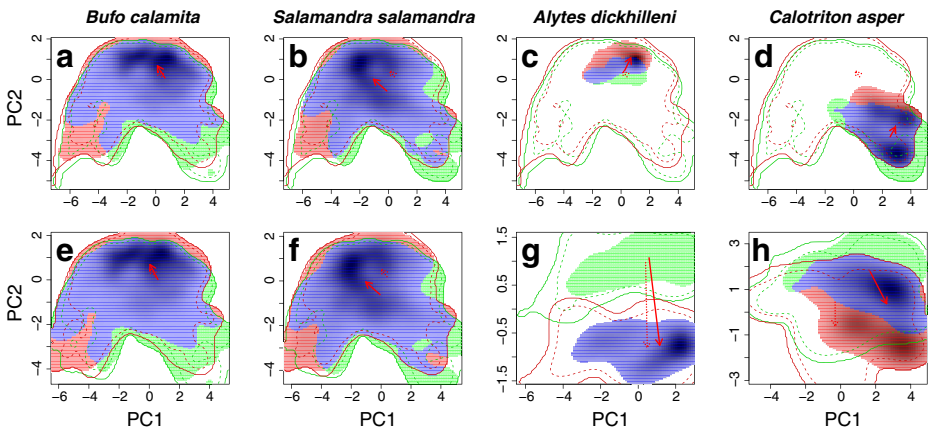
the 2000–2015 period (see Fig. S6). When we restricted available climates to buffers around points, we found that the combination of environmental conditions (i.e. the PCA-space) changed drastically between time periods, for some narrow-ranging species such as *Alytes dickhilleni* (Fig. 2g).

An increase in species' records in specific regions during 2000–2015 could also partly explain changes in occupied niches. For instance, presence records of *Alytes cisternasii*, *Chioglossa lusitanica*, *Discoglossus galganoi*, *Lissotriton boscai*, and both *Bufo* and *Hyla* species increased considerably in the south-western Iberian Peninsula from 1901–1990 to 2000–2015. This may account for some of the novel environmental conditions occupied by these species in the PCA-space, as suggested by the PCA-Env loadings corresponding to the southern and south-western Iberian Peninsula (Table S2; Fig. 2, Fig. S1).

## 4 Discussion

The ability to shift distribution ranges following climate envelopes and the potential of behavioural responses to buffer climate change will be decisive for species persistence (Kearney et al.





**Fig. 2** Available environmental space (i.e. PCA-space) for selected species using (first row) the whole Iberian Peninsula as the background or (second row) buffers of 200 km around occurrence points as the background. Green lines: available PCA-space in the 1901–1990 (based on 1980’s MERRAclim layers). Red lines: available PCA-space in the 2000–2015 (based on 2000’s MERRAclim layers). Green shading: occupied environmental niche in the 1901–1990 period. Red shading: occupied environmental niche in the 2000–2015 period. Blue shading: overlap of occupied environmental niches between time periods. Red arrows: changes in mean environmental conditions (dotted) and occupied niches (solid)

2009; Pecl et al. 2017). Amphibians in southern Europe (e.g. in the Iberian Peninsula) have already been identified as particularly vulnerable to climate change (Araújo et al. 2006; Carvalho et al. 2010). In this study, we show that climatic conditions have changed in the Iberian Peninsula during the considered time period. Amphibian species have expanded their latitudinal ranges between time periods, but in a counterintuitive manner: mainly via southward shifts of southern range margins. The northern limit, in general, remained unaltered, with the exception of the southernmost species (*Alytes dickhilleni*). The capacity of Iberian amphibians for latitudinal distribution changes appeared to be constrained in the north by geographical barriers such as the Cantabrian Sea and the Pyrenees Mountains. Notably, most Iberian amphibian species appear to have moved their altitudinal limits upwards (Fig. 1b). Shifting in elevation rather than over longer latitudinal gradients could represent a faster and easier way to track their preferred climatic conditions. Nonetheless, approximately half of the species occupied different niches between the two time periods. Therefore, many Iberian amphibians were not able to reach all the previously occupied climatic conditions, despite these being available.

Undeniably, range shifts are among the most common responses to climate change (reviews in Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). However, the ability to shift distributions varies among taxa (Parmesan 2006; Brown et al. 2016). Some organisms have been able to disperse long distances in relatively short time spans, presumably tracking their preferred climates (e.g. birds; Tingley et al. 2009). Similarly, Iberian reptiles have realigned their distributions, presumably as a response to recent climate change (Moreno-Rueda et al. 2012). However, our findings suggest that Iberian amphibians experience limited capacity to respond to climate change by shifting their distributions, albeit responses have been heterogeneous across species, with several species varying their altitudinal distribution. Remarkably, our findings match those reported by Hickling et al. (2006), who also found negligible changes in the distribution of an amphibian species in Great Britain, with a trend towards southward shifts. Moreover, in addition to the geographical barriers to dispersal (i.e. the Cantabrian Sea and the Pyrenees Mountains), most amphibians may have an intrinsically

limited capacity to adjust their ranges in response to climate change (Wells 2007). Ecological traits such as the strong site fidelity to breeding sites may underpin the ‘slow’ response of amphibians to the rapid environmental change (Zeisset and Beebee 2008).

Climate change involves new trends in both temperature and precipitation, which in turn may influence different aspects of amphibians’ biology, depending on the sensitivity of different life history traits. In amphibians, although it seems species-specific, several studies have found that while temperature affects mainly phenology, changes in precipitation may alter population dynamics and, hence, population persistence (While and Uller 2014; Ficetola and Maiorano 2016; also see Aragón et al. 2010b). Over the entire Iberian Peninsula, temperatures increased slightly from the late twentieth century to the early twenty-first century. Yet, the amount of precipitation did not change consistently (Fig. 2; see also Rodríguez-Puebla and Nieto 2010). How temperature and precipitation have changed in recent decades could partly explain the lack of range shifts in amphibians. If differences in temperature have outpaced differences in precipitation, amphibians could have responded by changing their phenology, rather than shifting their distribution ranges (Beebee 1995; Walther et al. 2002; While and Uller 2014).

Nonetheless, we show that environmental conditions (i.e. combinations of temperature and precipitation in the PCA-space) have changed profoundly, especially at a regional scale. As a result of the absence of range shifts in a changing climate, many species have changed their occupied climatic niches between the late twentieth and early twenty-first century. Partly, this could be explained by increased sampling in specific regions that would result in an apparent niche shift. However, we found the same pattern for species that were already well sampled in the period 1901–1990. For instance, *A. dickhilleni*, whose distribution was already well sampled, may be inhabiting entirely non-analogous climates at the scale of its distribution (i.e. buffers around points; Fig. 2g). Additionally, many species have been unable to disperse to all the suitable environmental conditions available to them. Moreover, our findings suggest that extremely cold and dry climates (associated with mountainous areas in the Iberian Peninsula) are disappearing. In fact, mountains are expected to show high rates of disappearing climates (Williams et al. 2007; McCain and Colwell 2011). This limits the potential distribution of cold-adapted species, represented in the Iberian Peninsula by widespread European amphibian species with their southern margin in the peninsula (e.g. *Rana temporaria*; see Supplementary Material), and endemic species such as *Calotriton asper* (Fig. 2d, h). Our findings indicate that some climatic conditions found in mountainous and adjacent areas have disappeared, limiting the potential distribution of cold-adapted species, including endemic species such as *C. asper* (also see de Pous et al. 2016). Hence, if amphibians are responding to climate change mainly by moving upslope in mountains, they may be reaching a dead end. In fact, our findings show that amphibians already inhabiting relatively high elevation regions have shown very limited or null capacity to respond to climate change by ascending in elevation (Fig. S5).

Altogether, our results suggest that Iberian amphibians have not reshaped their ranges in response to recent climate change, but have moved upwards in elevation (i.e. mountains). Environmental conditions, however, have already changed markedly, and as a consequence, the climatic niches occupied by many species have also transformed. At this point, however, we should add a cautionary note. The serendipitous nature of the occurrence dataset we used could have masked the signal of range shifts and the conservation of occupied climatic niches. Herpetologists could have inadvertently sampled new populations out of the already known distribution ranges, increasing our knowledge of their geographical distribution and the

climatic conditions they occupy (Montori et al. 2014). In the present study, we show that, despite being slightly biased, regional databases may provide essential information to assess the capacity of biodiversity to respond to recent climate change. Further, the climate data suggest that the Iberian Peninsula is undergoing rapid environmental change. Especially alarming is how environmental conditions have changed at the regional scale (e.g. for the southernmost *A. dickhilleni*), as well as the disappearance of cold climates, which support many amphibians in the Iberian Peninsula. Moreover, although precipitation has hardly differed in recent decades, climate change forecasts predict a marked decline in precipitation (Rodríguez-Puebla and Nieto 2010). As regards the capacity to respond by shifting ranges, all Iberian amphibians appear to be similarly vulnerable. Exposure to climate change, however, may be higher for southern and cold-adapted amphibians, which may require special conservation efforts. Here, we argue that programmes developed to monitor amphibian populations, with systematic sampling designs and coupled with remotely sensed environmental data, could help anticipate future species' responses. This information could then be incorporated into species-niche models to improve our predictions and find the populations most prone to local extinction.

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