

# Occurrence data may provide unreliable thermal preferences and breadth of species

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**Abstract** Accurate information on the thermal preference and specialization of species is needed to understand and predict species geographical range size and vulnerability to climate change. Here we estimate the position and breadth of species within thermal gradients based on the shape of the response curve of species abundance to temperature. The objective of the study is to compare the measurements of this approach based on abundance data with those of the classical approach using species' occurrence data. The relationship between species' relative abundance and minimum winter temperature of 106 bird species wintering in the Iberian Peninsula is modeled at 100 Km<sup>2</sup> resolution with quadratic logistic regressions. From these models we calculated the preferred temperature of species as the temperature at which the abundance is maximized, and the thermal breadth of species as the relative area under the temperature-abundance curve. We also estimated the thermal preferences and breadth of species as the average temperature and temperature range of the UTM cells in which the species are present. The abundance-temperature response curves reveal that birds prefer higher temperatures to overwinter, and are more thermally selective, than is measured by the classical approach. Moreover, response curves detect a higher inter-specific variability in both thermal preferences and thermal breadth of species. As occurrence data gives the same weight to cells with one or many individuals, the average temperature of the cells in which the species is present roughly reflects the average temperature in the region of study and not the environmental preferences of species [*Current Zoology* 61 (6): 972–982, 2016].

**Keywords** Abundance-temperature response curve, Birds, Species occurrence, Thermal breadth, Thermal preferences, Winter

The characterization of the position and breadth of animals within thermal gradients has been proven relevant to predict the geographical range size of species and their vulnerability to climate change (Jiguet et al., 2010; Foden et al., 2013; Slatyer et al., 2013). Thus, an accurate parameterization of the species-specific responses to the environment is needed to base further reliable ecological predictions and conclusions.

Classical approaches based on occurrence data characterize the response of species by considering average position or minimum and maximum recorded values along environmental gradients. For instance, cold tolerance is obtained recording the coldest temperature within the range of occurrence, and the thermal preference of species is usually approached as the average temperature of the cells in which the species is present or as the median temperature between the warmest and the coldest cells in which the species occurs. Similarly, the thermal breadth of species is usually approached as the range of temperatures of the cells in which the species is found (e.g., Davenport and Davenport, 2005;

Jiguet et al., 2006; 2007; Moussus et al., 2011; Gouveia et al., 2014; Hawkins et al., 2014). Occurrence or presence-absence data is much easier to obtain than abundance data in terms of time and money, and this explains why it has been heavily used in determining the position and breadth of organisms within thermal gradients and in forecasting the consequences of climate change. However, the reliability of occurrence data to estimate the suitability of an environment for a certain species is controversial (Pearce and Ferrier, 2001; Cushman and McGarigal, 2004; MacKenzie, 2005; Nielsen et al., 2005; Jiménez-Valverde et al., 2009; Jiménez-Valverde, 2011; Estrada and Arroyo, 2012; Howard et al., 2014; Williams et al., 2014).

Here we measure the thermal preferences and the thermal breadth of species, obtained from quadratic regression models on the response of species relative abundance to temperature (Fig. 1). The environmental preferred temperature ( $T_{\text{PREF}}$ ) is defined as the temperature that maximizes species abundance within the thermal span of the study region. The thermal breadth ( $T_{\text{BREADTH}}$ )

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is defined considering the area under the abundance curve, and represents the plasticity of species to utilize the available thermal space. We contrast these parameters that describe the thermal preferences and breadth of species with those obtained using the classical approach working with occurrence data. The main goal of the study is to analyze the consistency of the estimations of these two methods for 106 bird species wintering in the Iberian Peninsula.

## 1 Materials and Methods

### 1.1 Bird relative abundance and temperature data

Bird relative abundance data were obtained from the Spanish Atlas of Wintering Birds (SEO/BirdLife, 2012). Hundreds of experienced birdwatchers were asked to sample all birds found in 10x10 km UTM cells following a standardized methodology during three consecutive winters (2007–2010, from mid-November to mid-February). At each UTM cell, participants had to survey a minimum of sixty 15-min line transects, covering all the habitats present in proportion to their extent in the 100 km<sup>2</sup> (previously calculated by means of GIS tools). Twenty 15-min transects were made per winter. The relative abundance of species at each 10 × 10 Km UTM cell was calculated as the number of 15-min transects out of 60 in which the species was detected. This relative frequency is highly correlated with standardized bird counts (i.e., birds detected per km in each UTM cell), thus accurately informing about spatial variation in bird abundance (Palomino et al., 2007; SEO/BirdLife, 2012). The original sample size of UTM cells sampled was reduced to 1,689 UTM cells, after discarding those with low sampling effort (less than sixty 15-min line transects per 100 km<sup>2</sup> in the three winters) and low land surface in peninsular Spain (< 50 km<sup>2</sup>; e.g. coastal cells or those sharing the border with France or Portugal). See pages 16–30 in SEO/BirdLife (2012) for more details on methods of the Spanish Winter Bird Atlas.

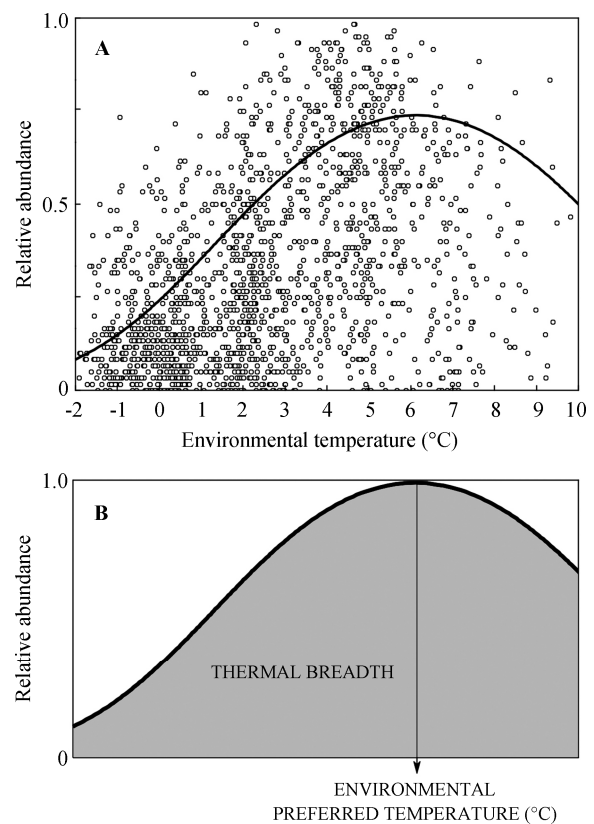
We selected 106 wintering terrestrial and diurnal bird species with good data on winter abundance, excluding species that were detected in less than 40 UTM 10 × 10 km cells, and those that were rare or poorly detectable (i.e., those with less than three 15-min transects per 60 transects censused).

Minimum, maximum and average winter temperature were calculated for each 10 × 10 km UTM cell as the average of the daily temperatures during the period of study (mid-November to mid-February 2007–2010). Data were provided by the Spanish Agencia Estatal de Meteorología (AEMET). These three temperature mea-

surements were highly correlated across UTM cells ( $r > 0.92$  for the three pairwise correlations with  $n = 1,689$ ). Thus, the average minimum temperature was selected as a measurement of the thermal state of the environment, more probably constraining the distribution and abundance of birds (e.g., Root, 1988; Canterbury, 2002). Average minimum winter temperature ranged between -2.1 and 9.8 °C in the 1,689 UTM cells analyzed.

### 1.2 Data analyses

The relationships between the relative abundance of each species ( $A$ ; number of occupied 15-min transects out of 60) and the minimum winter temperature ( $T$ ) were modeled with logistic regression models (binomial



**Fig. 1** (A) Variation of relative winter abundance of *Eri-thacus rubecula* with minimum winter temperature in 1689 UTM 10x10 km<sup>2</sup> cells of Spain (with an observed thermal span from -2 to 10°C), and quadratic fitting equation using logistic regression model. The response variable in these models is the number of sixty 15-min transects where the species was detected. Y-axes are expressed as the proportion of transects in which the species was present. (B) Parameters of interest obtained from regression model in the panel A. Environmental preferred temperature is the temperature at which the species attained the maximum abundance. Thermal breadth is the standardized area under the curve from -2 to 10°C of quadratic logistic regression equations (i.e., from relative abundance 0.0 to maximum modeled abundance assigned to 1).

distribution, link function: logit), using the linear and quadratic terms of winter minimum temperature ( $A = a + bT + cT^2$ ). The logistic regression uses a generalized linear model where the dependent variable is a proportion (occupied transects out of those carried out within each UTM cell), the independent variables are all continuous, and the link is the logistic function. Regression models only accounting for temperature were used to make a more convenient comparison with the classical approaches that parameterize the average position and breadth of species within thermal gradients. Data analyses were carried out with Gretl scripts (release 1.9.5, <http://gretl.sourceforge.net/>). To control for type I error in logistic regression models we applied the sequential Bonferroni adjustment (Rice, 1989) with an experiment-wise error rate of 0.05. The temperature at which the maximum abundance of each species is predicted (environmental preferred temperature,  $T_{\text{PREF}}$ ; Fig. 1) was calculated by solving the equation  $dA/dT = 0$ . The thermal breadth of each species ( $T_{\text{BREADTH}}$ ; Figure 1) was calculated as the area under the regression model within the observed range of variation of the winter minimum temperature, and was obtained by integrating the response curve between  $-2$  and  $10^\circ\text{C}$  (i.e., the observed range of winter minimum temperature in Spain), using the maximal relative abundance of each species standardized to 1 (i.e., in order to make comparable data for species with different maximum relative abundances).

The relationships between temperature and relative abundance may be subjected to bias from spatial autocorrelation, which may impact the estimation of linear and quadratic coefficients of the logistic regression models. Nevertheless, the spatial autocorrelation similarly affects the estimates of  $T_{\text{PREF}}$ ,  $T_{\text{AVERAGE}}$ , and  $T_{\text{MEDIAN}}$ , as both temperature and species abundance/occurrence usually show spatial autocorrelation over large areas. To ascertain the influence of spatial autocorrelation on the estimation of regression coefficients in the equation  $A = a + bT + cT^2$ , we re-analyzed the data using Simultaneous Autoregressive Regression (SAR; Dormann et al., 2007) models with the package SAM v4.0 (Rangel et al., 2010), considering the geographical coordinates of the 1,689 UTM cells. The regression coefficients  $a$ ,  $b$  and  $c$  derived from SAR models were highly correlated with those previously obtained (Pearson correlations,  $r$ , were 0.815 for  $a$ , 0.976 for  $b$  and 0.990 for  $c$ ;  $P \ll 0.001$ ). Moreover, the calculus of  $T_{\text{PREF}}$ , derived from coefficients obtained with SAR models were nearly indistinguishable from those obtained with our previous regression approach ( $r = 0.911$ ,

$P \ll 0.001$ ). Therefore, we have centered the comparative analysis of the response curves of animal abundance to temperature and the “classical” approach based on species occurrences, considering only the results obtained without taking into account the spatial autocorrelation, as we cannot implement a similar autocorrelation procedure with the “classical” approach.

We followed previous studies to calculate “classical” parameters related to the thermal preferences and breadth of species (Davenport and Davenport, 2005; Jiguet et al., 2006; Jiguet et al., 2007; Moussus et al., 2011). We considered the occurrence of each species in each UTM cell to estimate the average ( $T_{\text{AVERAGE}}$ ), the median ( $T_{\text{MEDIAN}}$ ) and the range ( $T_{\text{RANGE}}$ ; maximum minus minimum temperature) of winter minimum temperatures where the species occur (Appendix).

## 2 Results

There were significant relationships between relative abundance and temperature for 88 out of the 106 species after sequential Bonferroni correction to control for type I error (91 were significant at  $P < 0.001$ ; see the Appendix). The high level of significance attained by the models is expected considering that winter temperatures in our study region were well below the thermoneutral zone of these organisms (around  $18\text{--}21^\circ\text{C}$  for many bird species; Calder and King, 1974; Kendeigh et al., 1977). Nevertheless, the percentage of deviance in winter relative abundance accounted for by winter minimum temperature in the logistic regression models was very low (average = 7.0%,  $SD = 9.4\%$ ), with only 13 species with figures higher than 20% (Appendix).

Data from the species abundance-temperature response curves showed some consistencies and important differences with the results of the classical approach based on species occurrences (Table 1; and see Figure 2 for examples with four bird species). The thermal preferences of species were significantly related in both approaches ( $T_{\text{PREF}} - T_{\text{AVERAGE}}$ :  $r = 0.77$ ,  $n = 106$ ,  $P \ll 0.001$ ; Figure 3a;  $T_{\text{PREF}} - T_{\text{MEDIAN}}$ :  $r = 0.687$ ,  $n = 106$ ,  $P \ll 0.001$ ). Nevertheless, response curves reveal that, on average, species preferred higher temperatures than average temperatures estimated from occurrence data ( $T_{\text{PREF}}$  vs.  $T_{\text{AVERAGE}}$ , paired t-test:  $t = -2.35$ ,  $df = 105$ ,  $P = 0.021$ ;  $T_{\text{PREF}}$  vs.  $T_{\text{MEDIAN}}$ , paired t-test:  $t = -2.75$ ,  $df = 105$ ,  $P = 0.007$ ; see Table 1). Nevertheless, several species reached maximum relative abundances at winter minimum temperatures ( $T_{\text{PREF}}$ ) lower than  $0^\circ\text{C}$  (e.g., *Corvus corax*, *Dryocopus martius*, *Pyrrhocorax graculus*, *Regulus regulus*, *Turdus torquatus*, *Prunella collaris*), in-

dicating that they were more abundant in the coldest areas of Spain. Thus,  $T_{\text{PREF}}$  was 2–4°C lower than  $T_{\text{AVERAGE}}$  or  $T_{\text{MEDIAN}}$  for these species. There was more variation in  $T_{\text{PREF}}$  than in  $T_{\text{AVERAGE}}$  or  $T_{\text{MEDIAN}}$  (see *SD* in Table 1; *F* test of variances  $P \ll 0.001$  in both tests).

Conversely, the pattern with the thermal breadth of species derived from the two approaches was radically different, as both measures were inversely related ( $T_{\text{BREADTH}} - T_{\text{RANGE}}$ :  $r = -0.38$ ,  $n = 106$ ,  $P \ll 0.01$ ; Fig. 3B). For example, *Cisticola juncidis*, *Sylvia melanocephala* or *Carduelis chloris* reached their highest abundances in the warmest areas of Spain ( $T_{\text{PREF}} = 10^\circ\text{C}$ ), showing very narrow thermal breadths in the abundance-temperature response curve approach ( $T_{\text{BREADTH}}$ ), while they occupied a broad range of UTM cells according to winter minimum temperature (from -2 to  $10^\circ\text{C}$ ), but were very scarce in many of them. The converse was observed with species such as *Pterocles alchata*, *Dryocopus martius* or *Certhia familiaris* that inhabited cold areas of Spain with a relatively narrow thermal range (low figures of  $T_{\text{RANGE}}$ ), but whose relative abundances were not tightly related to winter minimum temperature, thus having broad thermal breadths measured by  $T_{\text{BREADTH}}$ . Moreover, thermal breadths (obtained using the response curve approach) were narrower than thermal ranges (obtained using occurrence data; paired t-tests,  $t = -6.25$ ,  $df = 105$ ,  $P \ll 0.001$ , see  $T_{\text{BREADTH}}$  and

$T_{\text{RANGE}}$  in Table 1).

Parameters derived from the response-curve approach showed three- to four-fold higher interspecific variation in thermal preferences ( $T_{\text{PREF}}$  CV = 142%,  $T_{\text{AVERAGE}}$  CV = 35%,  $T_{\text{MEDIAN}}$  CV = 43%), and two-fold interspecific variability in thermal breadth ( $T_{\text{BREADTH}}$  CV = 26%,  $T_{\text{RANGE}}$  CV = 13%; Table 1) than parameters obtained from the classical occurrence approach. These results demonstrate that the parameterization of the abundance-temperature relationship by means of nonlinear regression approaches might be a better discriminant of inter-specific differences in thermal preferences and breadth than occurrence data.

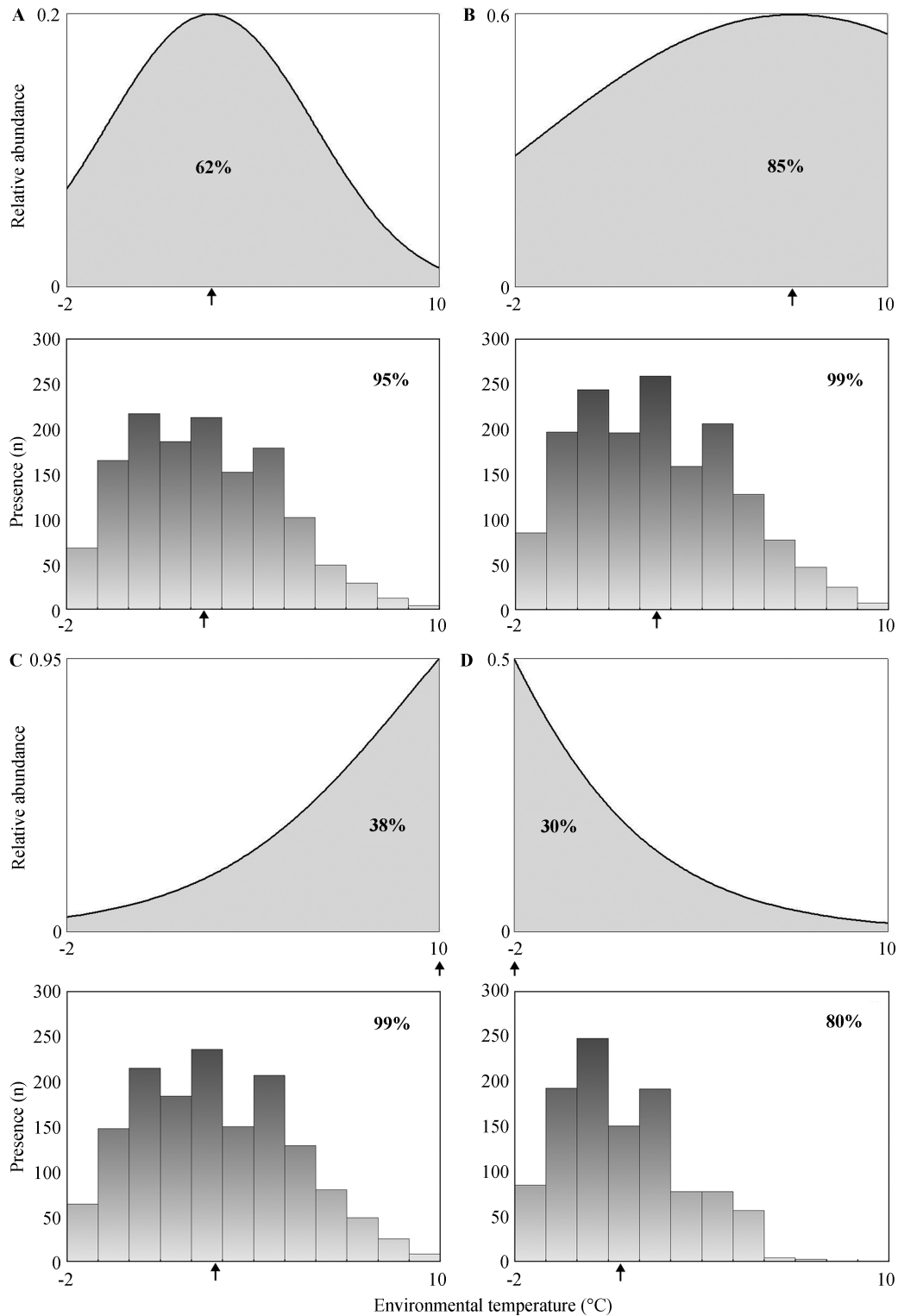
### 3 Discussion

The analytical approach of this study highlights the importance of considering quantitative data on animal abundance to model the response of organisms to temperature. Results of thermal preferences and breadth derived from response curves of animal abundance were different from those obtained using the “classical” approach based on occurrence data. The discrepancies between the two methods for estimating the position and breadth of birds in thermal gradients probably lie in the fact that data on occurrence of species over large spatial sample units is low informative and has an asymmetric and uncertain value. The absence of a species in

**Table 1** Parameters defining the thermal preferences and breadth of species as obtained with the response-curve and classical-occurrence approaches

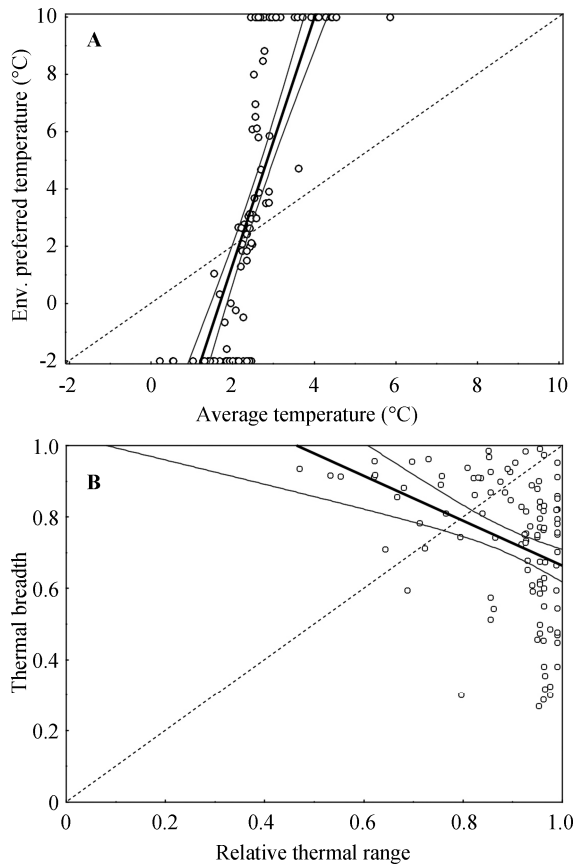
Thermal parameters	mean	<i>SD</i>	CV%	min / max
<b>THERMAL PREFERENCES</b>				
<b>Abundance-temperature response curve</b>				
Environmental preferred temperature ( $^\circ\text{C}$ ), $T_{\text{PREF}}$	3.46	4.92	142	-2 / 10
<b>Classical occurrence approach</b>				
Average temperature of occurrence ( $^\circ\text{C}$ ), $T_{\text{AVERAGE}}$	2.48	0.88	35	0.20 / 5.85
Median temperature of occurrence ( $^\circ\text{C}$ ), $T_{\text{MEDIAN}}$	2.31	1.00	43	-0.50 / 6.89
<b>THERMAL BREADTH</b>				
<b>Abundance-temperature response curve</b>				
Thermal breadth, $T_{\text{BREADTH}}$	0.73	0.19	26	0.27 / 0.99
<b>Classical occurrence approach</b>				
Relative thermal range, $T_{\text{RANGE}}$	0.89	0.12	13	0.47 / 0.99

Figures are parameter averages obtained from 106 bird species wintering in peninsular Spain, sampled at 1689 UTM  $10 \times 10 \text{ km}^2$  cells. The parameters of the response curve approach derive from quadratic logistic regression models on the effect of temperature on species abundance:  $T_{\text{PREF}}$ , winter minimum temperature that maximizes the modeled relative abundance of the species;  $T_{\text{BREADTH}}$ , area under the curve defined by the quadratic logistic regression equation (after the maximum abundance is standardized to 1). In the classical occurrence approach only the UTM cells where the species are present are considered to obtain the following parameters:  $T_{\text{AVERAGE}}$ , average temperature of the cells in which the species is present;  $T_{\text{MEDIAN}}$ , median temperature between the coldest and the warmest cells in which the species is present;  $T_{\text{RANGE}}$ , range of temperatures of the cells in which the species is present, relativized by a maximum temperature span of  $12^\circ\text{C}$  in Spain, to make possible its comparison with  $T_{\text{BREADTH}}$ .



**Fig. 2** Abundance-temperature response curve of four bird species in continental Spain obtained as shown in Figure 1, and results derived from the classical occurrence approach (considering temperature of the cells in which the species were present)

Species are selected to illustrate a broad range of abundance-temperature patterns: *Columba palumbus* (A), *Turdus merula* (B), *Motacilla alba* (C) and *Corvus corone* (D). The solid lines represent the fitting equation of quadratic logistic regression models. Below each panel, Presence shows the histograms of temperatures of the UTM cells in which the species were present. Small arrows show the thermal preferences (maximum abundance modeled by quadratic logistic regressions and average of occupied UTM cells); percentage figures in bold type show the thermal breadth of species obtained in each approach (see text and Figure 1 for more details).



**Fig. 3 Relationships between thermal characteristics of species as derived from the response curve (Y-axes) and the classical occurrence approaches (X-axes)**

A. Thermal preferences of species. B. Thermal breadth of species. Solid line represents the fitted linear relationship (with 95% confidence intervals); dashed line represents the identity of results in both approaches. For more details see Table 1 and Figure 2.

the area covered by a UTM cell of  $50 \times 50$  or  $10 \times 10$  km<sup>2</sup>, if true (Comte and Grenouillet, 2013), has a unique possible value of zero individuals; but the presence of a species may have a very large span of figures ranging from one to thousands of individuals. On the contrary, abundance data gives a broad spectrum of suitability to the UTM cells where the species are present. This concern has been previously acknowledged in the analysis of spatial variation of binomial response variables, with an overall higher variability and bias of results for binary data (McCullough and Nelder, 1989; Guisan and Zimmermann, 2000; Venables and Ripley, 2002; Cushman and McGarigal, 2004; Dormann et al., 2007). Our results suggest that species might be considered to be less specialized and to select colder areas to overwinter than they actually do, if we use the classical approach using species' occurrence data instead of the response curves of species' abundances to temperature. Moreover, there was far more variation in  $T_{\text{PREF}}$  than in  $T_{\text{AVERAGE}}$

or  $T_{\text{MEDIAN}}$ , supporting that the classical occurrence approach fails to provide a good proxy for abundance-temperature response curves, and underestimates the interspecific variation of birds to thermal gradients. The environmental tolerance or breadth of organisms is a cornerstone in ecology, enabling us to understand the rarity of species, their vulnerability to extinction and to predict how they may respond to potential future climate change (Foden et al., 2013; Slatyer et al., 2013). Therefore, an accurate estimation method must be used when describing the environmental responses of species for conservation management policies or further research on the effects of climate warming.

The low percentage of variation in winter relative abundance explained by winter minimum temperature (range : 0.0%–42.3%) indicates that even in the restrictive winter season of temperate latitudes, with very long nights, low food availability and very low temperatures (Fretwell, 1972; Newton, 1998), other environmental predictors should be considered to explain spatial variation of abundance in this endotherm taxon (Seoane et al., 2008; Aragón et al., 2010; Carvalho et al., 2013; but see Triviño et al., 2011 for the breeding season in the Iberian Peninsula). For example, Carrascal and Palomino (2012) found that temperature *per se* has a small influence on winter bird species richness in Spain after controlling for other environmental predictors related to habitat structure and orography. Ferger et al. (2014) found for bird species richness in Mount Kilimanjaro that models that included only climatic variables explained considerably less variance, and had a significantly worse fit to the data, than the respective models including habitat structure and food availability. Thus, climate variables acted indirectly through vegetation heterogeneity, fruit abundance and invertebrate biomass. These results are in agreement with previous findings that suggest that birds can probably withstand severe cold if enough food is available during winter (Newton, 1980; Jenni, 1987; Carrascal et al., 2012; Villén-Pérez and Carrascal, 2014).

In conclusion, estimates of thermal position and breadth of species within thermal gradients derived from the response curves of animal abundance to temperature should enhance comparative biogeographical and macroecological studies, as they are expected to detect a broader interspecific variation and to have a more functional meaning than classical approaches based only on occurrence data. When data on abundance of organisms is available, we recommend the use of the shape of the response curve of species abundance

to temperature, instead of characterizing the response of species to thermal gradients by considering the average position or minimum and maximum recorded values.

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**Appendix** Data for 106 terrestrial bird species wintering in the Iberian Peninsula, corresponding to winter censuses on 1,689 UTM 10 × 10 km<sup>2</sup> cells (years 2007–2010)

Specie	Abundance-Temperature response curve				Classical occurrence approach		
	<i>P</i>	<i>R</i> <sup>2</sup>	<i>T</i> <sub>PREF</sub>	<i>T</i> <sub>BREADTH</sub>	<i>T</i> <sub>AVERAGE</sub>	<i>T</i> <sub>MEDIAN</sub>	<i>T</i> <sub>RANGE</sub>
<i>Accipiter gentilis</i>	< 0.001 *	1.0	-2.0	0.93	1.9	1.8	10.7
<i>Accipiter nisus</i>	0.116	0.3	2.1	0.95	2.5	2.2	11.9
<i>Aegithalos caudatus</i>	< 0.001 *	3.0	1.5	0.77	2.3	2.2	11.6
<i>Aegypius monachus</i>	< 0.001 *	2.8	3.5	0.89	2.8	3.0	9.1
<i>Alauda arvensis</i>	< 0.001 *	2.0	-2.0	0.68	2.3	2.0	11.2
<i>Alcedo atthis</i>	< 0.001 *	5.9	10.0	0.83	4.1	4.4	11.0
<i>Alectoris rufa</i>	< 0.001 *	1.7	8.0	0.86	2.5	2.2	11.9
<i>Anthus pratensis</i>	< 0.001 *	16.2	8.5	0.67	2.7	2.4	11.9
<i>Anthus spinoletta</i>	0.801	0.0	2.0	0.99	2.4	2.3	11.5
<i>Aquila chrysaetos</i>	< 0.001 *	2.0	-1.6	0.91	1.9	1.9	10.0
<i>Burhinus oedicnemus</i>	< 0.001 *	7.5	10.0	0.72	4.4	4.5	11.0
<i>Buteo buteo</i>	< 0.001 *	3.3	2.1	0.77	2.5	2.1	11.5
<i>Carduelis cannabina</i>	0.252	0.2	-2.0	0.88	2.5	2.1	11.4
<i>Carduelis carduelis</i>	< 0.001 *	9.9	10.0	0.45	2.6	2.3	11.9
<i>Carduelis chloris</i>	< 0.001 *	15.1	10.0	0.30	2.7	2.3	11.7
<i>Carduelis spinus</i>	0.003	0.7	10.0	0.84	2.8	2.7	11.5
<i>Certhia brachydactyla</i>	0.031	0.4	-2.0	0.82	2.4	2.2	11.9
<i>Certhia familiaris</i>	< 0.001 *	1.5	-2.0	0.93	0.5	0.7	5.6
<i>Cettia cetti</i>	< 0.001 *	4.1	10.0	0.59	3.0	2.6	11.9
<i>Cinclus cinclus</i>	< 0.001 *	3.0	-2.0	0.86	1.4	1.3	8.0
<i>Circus aeruginosus</i>	0.002	0.7	10.0	0.85	3.0	2.2	10.7
<i>Circus cyaneus</i>	< 0.001 *	4.3	-2.0	0.75	1.8	1.4	11.1
<i>Cisticola juncidis</i>	< 0.001 *	22.7	10.0	0.27	3.9	4.5	11.4
<i>Coccothraustes coccothraustes</i>	< 0.001 *	1.7	-2.0	0.83	1.9	2.0	11.5
<i>Columba livia</i>	0.825	0.0	3.1	0.97	2.4	2.0	11.6
<i>Columba oenas</i>	< 0.001 *	2.3	-2.0	0.88	1.4	1.1	8.2
<i>Columba palumbus</i>	< 0.001 *	8.6	2.6	0.62	2.4	2.2	11.5
<i>Corvus corone</i>	< 0.001 *	24.5	-2.0	0.30	1.5	1.1	9.6
<i>Corvus corax</i>	< 0.001 *	4.3	-2.0	0.59	2.3	2.1	11.5
<i>Corvus monedula</i>	0.642	0.1	6.1	0.98	2.5	2.1	11.1
<i>Cyanopica cyanus</i>	< 0.001 *	2.2	3.9	0.81	2.6	2.9	9.2
<i>Dendrocopos major</i>	< 0.001 *	9.6	-2.0	0.47	1.9	1.8	11.5
<i>Dendrocopos minor</i>	< 0.001 *	1.3	3.5	0.96	2.9	3.1	8.4
<i>Dryocopus martius</i>	< 0.001 *	2.6	-2.0	0.92	0.5	0.8	6.4
<i>Elanus caeruleus</i>	< 0.001 *	1.5	10.0	0.95	3.5	3.7	10.9
<i>Emberiza calandra</i>	< 0.001	0.8	2.4	0.82	2.3	2.0	11.1
<i>Emberiza cia</i>	< 0.001 *	7.8	-2.0	0.47	2.1	1.9	11.9
<i>Emberiza cirius</i>	< 0.001 *	3.2	-2.0	0.65	2.1	2.0	11.2
<i>Emberiza citrinella</i>	< 0.001 *	5.9	-2.0	0.71	1.3	1.0	8.7
<i>Emberiza schoeniclus</i>	0.858	0.0	10.0	0.97	2.4	2.0	10.2
<i>Erithacus rubecula</i>	< 0.001 *	20.0	6.1	0.70	2.6	2.3	11.9
<i>Falco columbarius</i>	< 0.001 *	2.2	-0.7	0.91	1.8	1.5	9.1
<i>Falco peregrinus</i>	0.719	0.0	-2.0	0.99	2.4	2.1	10.2
<i>Falco tinnunculus</i>	< 0.001 *	3.1	10.0	0.46	2.6	2.2	11.4

## Continued Appendix

Specie	Abundance-Temperature response curve				Classical occurrence approach		
	P	R <sup>2</sup>	T <sub>PREF</sub>	T <sub>BREADTH</sub>	T <sub>AVERAGE</sub>	T <sub>MEDIAN</sub>	T <sub>RANGE</sub>
<i>Fringilla coelebs</i>	< 0.001 *	2.7	3.1	0.79	2.5	2.2	11.9
<i>Fringilla montifringilla</i>	< 0.001 *	3.0	-2.0	0.81	1.7	1.5	10.1
<i>Galerida cristata</i>	0.003	0.7	10.0	0.76	2.6	2.1	11.5
<i>Galerida theklae</i>	< 0.001 *	2.5	8.8	0.82	2.8	2.5	11.5
<i>Garrulus glandarius</i>	< 0.001 *	2.9	1.3	0.75	2.2	2.1	11.9
<i>Grus grus</i>	< 0.001 *	1.7	3.9	0.90	2.9	2.7	10.5
<i>Gyps fulvus</i>	< 0.001 *	5.2	-2.0	0.61	1.9	1.9	11.5
<i>Hieraaetus fasciatus</i>	< 0.001 *	3.0	10.0	0.91	4.3	4.2	9.9
<i>Lanius meridionalis</i>	< 0.001 *	2.0	6.5	0.89	2.6	2.2	11.3
<i>Loxia curvirostra</i>	< 0.001 *	4.8	-2.0	0.63	2.0	1.8	11.6
<i>Lullula arborea</i>	< 0.001 *	2.5	2.8	0.75	2.3	2.1	11.1
<i>Luscinia svecica</i>	< 0.001 *	6.9	10.0	0.78	5.9	6.9	8.6
<i>Melanocorypha calandra</i>	< 0.001 *	2.3	-2.0	0.73	1.9	1.7	11.1
<i>Milvus milvus</i>	< 0.001 *	6.4	-2.0	0.57	1.9	1.4	10.3
<i>Monticola solitarius</i>	< 0.001 *	8.8	10.0	0.73	4.4	4.5	11.1
<i>Motacilla alba</i>	< 0.001 *	36.1	10.0	0.38	2.8	2.4	11.9
<i>Motacilla cinerea</i>	< 0.001 *	2.7	5.9	0.91	2.9	2.8	11.9
<i>Oenanthe leucura</i>	< 0.001 *	5.8	10.0	0.74	4.4	4.3	10.4
<i>Otis tarda</i>	< 0.001 *	1.7	0.3	0.91	1.7	1.3	7.4
<i>Parus ater</i>	< 0.001 *	2.7	-2.0	0.55	2.1	2.0	11.6
<i>Parus caeruleus</i>	< 0.001 *	5.4	1.9	0.68	2.2	2.1	11.5
<i>Parus cristatus</i>	< 0.001 *	2.3	-2.0	0.60	2.4	2.2	11.6
<i>Parus major</i>	< 0.001 *	3.4	3.7	0.78	2.5	2.2	11.9
<i>Parus palustris</i>	< 0.001 *	1.3	1.1	0.92	1.5	1.8	7.5
<i>Passer domesticus</i>	< 0.001 *	22.4	10.0	0.48	2.7	2.3	11.9
<i>Passer hispaniolensis</i>	< 0.001 *	4.3	4.7	0.86	3.6	3.8	9.9
<i>Passer montanus</i>	< 0.001 *	2.7	-2.0	0.74	1.9	1.6	9.5
<i>Petronia petronia</i>	< 0.001 *	8.8	-2.0	0.54	1.5	1.0	10.3
<i>Phoenicurus ochruros</i>	< 0.001 *	30.4	10.0	0.54	2.9	2.6	11.9
<i>Phylloscopus collybita</i>	< 0.001 *	42.3	10.0	0.32	3.1	2.8	11.6
<i>Pica pica</i>	< 0.001 *	9.0	2.6	0.59	2.3	2.1	11.3
<i>Picus viridis</i>	< 0.001 *	2.6	-0.5	0.80	2.3	2.1	11.5
<i>Prunella collaris</i>	0.012	0.5	-2.0	0.96	1.9	2.0	8.8
<i>Prunella modularis</i>	< 0.001 *	3.0	3.2	0.75	2.4	2.3	11.4
<i>Pterocles alchata</i>	< 0.001 *	1.8	3.0	0.91	2.5	2.2	6.6
<i>Pterocles orientalis</i>	< 0.001	0.8	2.7	0.94	2.1	2.1	10.7
<i>Ptyonoprogne rupestris</i>	< 0.001 *	24.0	10.0	0.32	4.5	4.6	11.7
<i>Pyrrhonorax pyrrhonorax</i>	< 0.001 *	2.0	0.0	0.87	2.0	2.1	10.6
<i>Pyrrhonorax graculus</i>	0.003	0.7	-2.0	0.96	1.6	2.0	7.5
<i>Pyrrhula pyrrhula</i>	< 0.001 *	1.7	-0.2	0.87	2.1	2.1	10.3
<i>Regulus ignicapilla</i>	< 0.001 *	2.3	2.1	0.77	2.2	2.1	11.6
<i>Regulus regulus</i>	< 0.001 *	12.2	-2.0	0.51	1.4	1.1	10.3
<i>Remiz pendulinus</i>	< 0.001 *	1.5	10.0	0.91	4.1	3.6	10.0
<i>Saxicola torquatus</i>	< 0.001 *	34.3	10.0	0.38	3.0	2.6	11.6

## Continued Appendix

Specie	Abundance-Temperature response curve				Classical occurrence approach		
	<i>P</i>	<i>R</i> <sup>2</sup>	<i>T</i> <sub>PREF</sub>	<i>T</i> <sub>BREADTH</sub>	<i>T</i> <sub>AVERAGE</sub>	<i>T</i> <sub>MEDIAN</sub>	<i>T</i> <sub>RANGE</sub>
<i>Serinus citrinella</i>	< 0.001 *	9.5	-2.0	0.71	0.2	-0.5	7.7
<i>Serinus serinus</i>	< 0.001 *	32.5	10.0	0.35	3.1	2.8	11.6
<i>Sitta europaea</i>	< 0.001 *	1.2	-2.0	0.75	2.0	2.0	11.4
<i>Streptopelia decaocto</i>	< 0.001 *	15.7	10.0	0.49	3.2	3.1	11.7
<i>Sturnus unicolor</i>	< 0.001 *	4.2	5.8	0.82	2.6	2.3	11.9
<i>Sturnus vulgaris</i>	< 0.001 *	5.4	10.0	0.77	3.1	2.7	11.2
<i>Sylvia atricapilla</i>	< 0.001 *	31.8	10.0	0.45	3.6	3.6	11.5
<i>Sylvia melanocephala</i>	< 0.001 *	38.3	10.0	0.29	3.7	3.6	11.5
<i>Sylvia undata</i>	< 0.001 *	2.4	10.0	0.76	2.6	2.3	11.9
<i>Tetrax tetrax</i>	< 0.001 *	1.6	3.0	0.94	2.6	2.0	9.7
<i>Troglodytes troglodytes</i>	0.007	0.6	2.7	0.83	2.2	2.1	11.6
<i>Turdus iliacus</i>	0.013	0.5	1.9	0.90	2.3	2.2	11.4
<i>Turdus merula</i>	< 0.001 *	4.0	7.0	0.85	2.6	2.3	11.9
<i>Turdus philomelos</i>	< 0.001 *	12.7	4.7	0.67	2.7	2.4	11.6
<i>Turdus pilaris</i>	< 0.001 *	12.5	-2.0	0.59	1.0	0.6	8.3
<i>Turdus torquatus</i>	< 0.001	0.8	-2.0	0.93	1.3	1.0	10.3
<i>Turdus viscivorus</i>	< 0.001 *	8.5	-2.0	0.50	2.1	2.1	11.5
<i>Upupa epops</i>	< 0.001 *	22.8	10.0	0.61	4.1	4.3	11.3

Parameters in the abundance-temperature response curve are obtained from quadratic logistic regression models of winter species relative abundance on minimum winter temperature. *T*<sub>PREF</sub>: environmental preferred temperature (i.e., minimum winter temperature at which the maximum abundance of the species is predicted); *T*<sub>BREADTH</sub>: thermal breadth (i.e., area under the curve of the logistic regression model from -2 to 10°C; relativized to 1 for maximum abundance predicted by the logistic equation). Parameters in the classical occurrence approach are calculated from minimum winter temperatures in the UTM cells with occurrence of the species. *T*<sub>AVERAGE</sub>: average temperature of the cells where the species were present; *T*<sub>MEDIAN</sub>: median temperature between the warmest and the coolest cells in which the species were present; *T*<sub>RANGE</sub>: difference between the maximum and minimum winter temperatures of the UTM cells in which the species were present. *R*<sup>2</sup>, *P*: percentage of deviance explained and significance of the logistic regression model of the abundance-temperature response curve approach (\*: significance at *P* ≤ 0.05 after sequential Bonferroni correction).