

# Integrating detection probabilities in species distribution models of amphibians breeding in Mediterranean temporary ponds

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## ABSTRACT

**Aim** The imperfect detection of species may lead to erroneous conclusions about species–environment relationships. Accuracy in species detection usually requires temporal replication at sampling sites, a time-consuming and costly monitoring scheme. Here, we applied a lower-cost alternative based on a double-sampling approach to incorporate the reliability of species detection into regression-based species distribution modelling.

**Location** Doñana National Park (south-western Spain).

**Methods** Using species-specific monthly detection probabilities, we estimated the detection reliability as the probability of having detected the species given the species-specific survey time. Such reliability estimates were used to account explicitly for data uncertainty by weighting each absence. We illustrated how this novel framework can be used to evaluate four competing hypotheses as to what constitutes primary environmental control of amphibian distribution: breeding habitat, aestivating habitat, spatial distribution of surrounding habitats and/or major ecosystems zonation. The study was conducted on six pond-breeding amphibian species during a 4-year period.

**Results** Non-detections should not be considered equivalent to real absences, as their reliability varied considerably. The occurrence of *Hyla meridionalis* and *Triturus pygmaeus* was related to a particular major ecosystem of the study area, where suitable habitat for these species seemed to be widely available. Characteristics of the breeding habitat (area and hydroperiod) were of high importance for the occurrence of *Pelobates cultripedes* and *Pleurodeles waltl*. Terrestrial characteristics were the most important predictors of the occurrence of *Discoglossus galganoi* and *Lissotriton boscai*, along with spatial distribution of breeding habitats for the last species.

**Main conclusions** We did not find a single best supported hypothesis valid for all species, which stresses the importance of multiscale and multifactor approaches. More importantly, this study shows that estimating the reliability of non-detection records, an exercise that had been previously seen as a naïve goal in species distribution modelling, is feasible and could be promoted in future studies, at least in comparable systems.

## Keywords

Absence reliability, data uncertainty, false absence, species detectability, temporary ponds.

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## INTRODUCTION

Species distribution models (SDMs) attempt to quantify species–environment relationships, a central issue in ecology and conservation (Guisan & Zimmermann, 2000). A critical issue for the utility and validity of any model is the reliability of the data used to build it (Lobo, 2008). For a mobile organism, the recorded presence is usually the only reliable distribution information (Guisan & Thuiller, 2005). While the presence of a species is confirmed by simply detecting it at a site, it is usually not possible to confirm if an animal was truly absent or if the species was present but not detected during the survey (MacKenzie *et al.*, 2006).

Few studies have tried to draw attention to the fundamental issue of detection reliability in SDMs (but see Gu & Swihart, 2004; Lobo, 2008; Lobo *et al.*, 2010). Although data quality is critical for model performance in general (Foody, 2011), the need for an increased awareness in this source of errors lies in the fact that the imperfect detection of species may lead to erroneous conclusions about species–environment relationships (Gu & Swihart, 2004; Mazerolle *et al.*, 2005; MacKenzie, 2006). If lack of absence records is a main source of modelling error (Barry & Elith, 2006), a worse scenario is building a presence–absence model in which absence records do not represent unfavourable sites but are just a result of inaccurate sampling (methodological absences, *sensu* Lobo *et al.*, 2010).

The optimal modelling approach to overcome this source of error is to evaluate species–habitat relationships while explicitly accounting for the probability of detecting the species when present (MacKenzie *et al.*, 2006). When species detection is imperfect, these site–occupancy models are better for predicting species occurrence than more traditional regression analyses (Kéry *et al.*, 2010; Rota *et al.*, 2011). However, this modelling technique is not being widely used by species distribution modellers yet (but see Urban & Swihart, 2009; Adams *et al.*, 2010; or Martin *et al.*, 2010 as some recent examples).

A main statistical limitation of occupancy models is that they require temporal replication at all sampled sites, a condition that may not be always easy to fulfil. An intermediate approach can be to conduct a double-sampling design, consisting in estimating detection probabilities from the data collected at few sites, where repeated surveys were conducted, and then applying this information to the sites surveyed only once (MacKenzie *et al.*, 2006). Following this approach, here we propose that one can integrate information from species detectability at a site, as a surrogate for the reliability of the absence record, into traditional presence–absence models. This surrogacy relies on the premise that the higher the probability of having detected the species when present at a site, the higher the reliability of the absence record. So, with a low-cost approach, it would be easy to select those absence records that really represent sites not occupied by the species and, thus, that are supposed to be unsuitable habitats.

Amphibians are inconspicuous organisms (Mazerolle *et al.*, 2007) for which the probability of detecting a species with a

single visit may be low, species-specific and variable over time (Gómez-Rodríguez *et al.*, 2010d). Moreover, the reliability of absence data is expected to be highly limited in species breeding in temporary ponds as a result of interannual turnover in assemblage composition (Jakob *et al.*, 2003; Gómez-Rodríguez *et al.*, 2010c). Thus, any yearly survey will probably yield many ‘false absences’ since data from several breeding seasons would be needed to characterize the species assemblage associated with a given pond. Previous studies have quantified the relationships between habitat characteristics and amphibian richness, species occurrence or species relative abundance in temporary ponds (e.g. Beja & Alcazar, 2003; Richter-Boix *et al.*, 2007). However, to our knowledge, no study has explicitly accounted for the reliability of absence data.

Most ecological models about amphibian habitat selection focus on four main aspects that have been identified as critical for amphibian ecology:

1. Abiotic characteristics of the breeding habitat, such as pond area or hydroperiod (i.e. annual duration of aquatic phase in temporary waters). Amphibian species are supposed to be sorted along the hydroperiod gradient according to whether they are able to metamorphose in short-duration ponds or tolerant to the presence of major predators in ponds of longer duration (Wellborn *et al.*, 1996). The relationship between species occurrence and pond size is twofold. First, metapopulation theory predicts that the probability of occurrence would increase with pond size because it assumes a functional relationship between the area of a patch and its extinction probability (Hanski, 1998). Second, patch area and habitat heterogeneity are highly interconnected (Rosenzweig, 1995), and the latter provides more niches and diverse ways of exploiting the environmental resources (Tews *et al.*, 2004).
2. Biotic interactions in the breeding habitat, such as competition or predation (e.g. Wells, 2007).
3. Characteristics of the aestivating habitat (i.e. landscape composition) since terrestrial habitats provide refuges for amphibian species during the dry season and also constitute the matrix that interconnects ponds (Gibbons, 2003).
4. Spatial structure of the habitat patches (i.e. distance to nearest site, density of surrounding ponds, etc.), which determines the dispersal or regular movements of individuals among ponds (Smith & Green, 2005).

Here, we develop a novel approach to show how detection probabilities can be incorporated in SDMs. Using data from a double-sampling design, we demonstrate a method to account for the reliability of non-detection records, which can be used as weight in SDMs. We illustrate this approach with amphibians breeding in a system of temporary ponds in Doñana National Park (DNP), in south-western Spain. For each pond where a species was not detected, we used the single-visit probability of detection computed from a different survey (Gómez-Rodríguez *et al.*, 2010d) to estimate the reliability of each non-detection record, taking into account the history of pond surveys (number and date of sampling visits). We test four competing hypotheses of which environmental factors are

correlated with amphibian distribution in DNP: (1) characteristics of their breeding habitat, (2) characteristics of their aestivating habitat, (3) spatial distribution of breeding habitat patches, and (4) general local characteristics of the major ecosystems in DNP.

## METHODS

### Study area

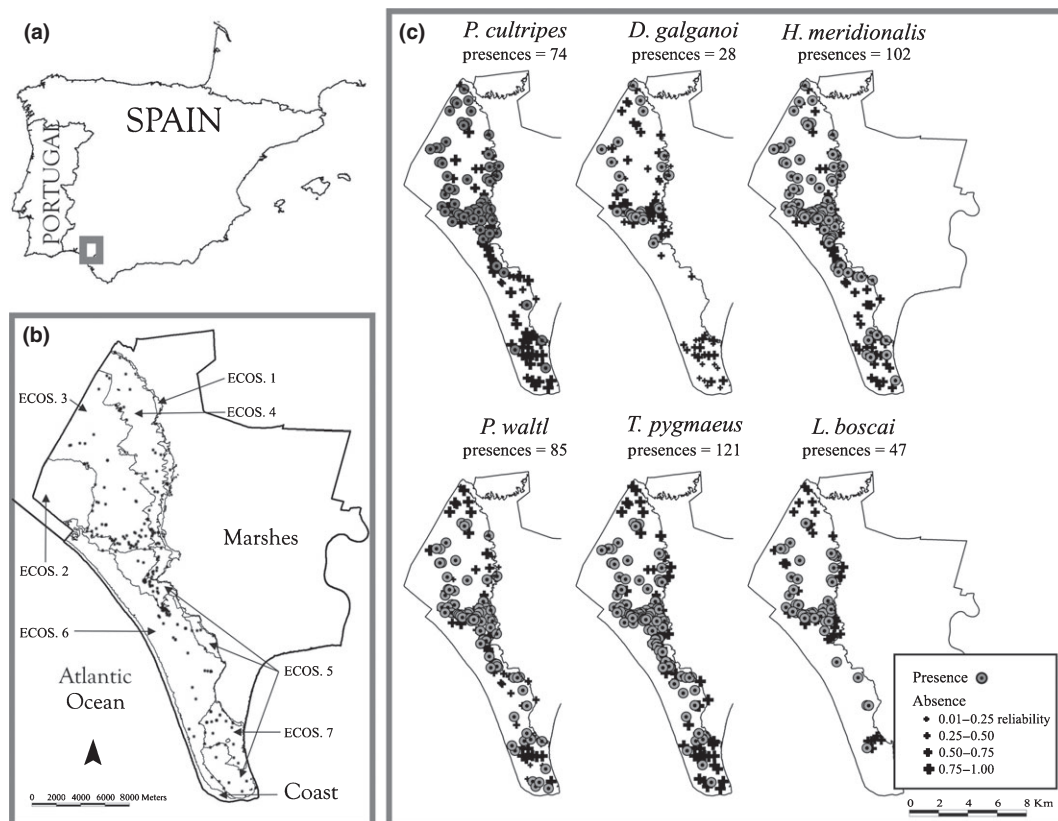
The study was conducted in the aeolian sands ecoregion of DNP in south-western Spain (Fig. 1, see Siljeström *et al.*, 1994). DNP is considered to be one of the largest and most important wetlands in southern Europe. Within this region, Montes *et al.* (1998) differentiated eight ecoresections based on differences in their geomorphologic, stratigraphic and hydrodynamic characteristics (Fig. 1). Many temporary ponds of natural origin are located amid relatively small topographic depressions and flood during the rainy season. The area also includes two natural large permanent ponds and small artificial permanent water bodies (maintained for watering cattle and

locally named *zacallones*). Pond size is largely variable, from rain puddles (several square metres) to large temporary ponds (> 1 ha). Hydroperiod varies among ponds and years, from one to 10 months (Gómez-Rodríguez *et al.*, 2009; Díaz-Paniagua *et al.*, 2010). Many pond basins are completely or partially enclosed by a fringe of dense vegetation mainly composed of *Erica scoparia* L., *E. ciliaris* L., *Calluna vulgaris* (L.) Hull and *Ulex minor* Roth. A detailed description of DNP temporary ponds can be found in the studies by Gómez-Rodríguez *et al.* (2009) and Díaz-Paniagua *et al.* (2010).

### Field sampling

#### Amphibian sampling

We sampled 221 amphibian breeding sites (169 natural ponds and 52 *zacallones*) located in seven different ecoresections (Fig. 1). Amphibian data were collected during the breeding season in a 4-year survey (from 2003 to 2006) (Table 1). Some ponds did not flood in 2005 and could therefore not be sampled. We could not monitor all ponds every year. A total of



**Figure 1** (a) Location of Doñana National Park, (DNP), in south-western Spain. (b) Location of the study ponds. The map also shows the different ecoresections within the aeolian sands in DNP. Note that ecoresection number eight (terrestrial human-transformed areas) consists on isolated and small locations, not visible in this graphical representation. (c) Presence–absence data of each species in the study area. Absences are weighted according to their reliability, as obtained from the probability of detection after all the sampling visits conducted in that pond. Absence records with null reliability are not shown.

Ecoresection code: 1: Ecotone marshes-stabilized sands; 2: Dry stabilized sands at higher elevation; 3: Wet stabilized sands at higher elevation; 4: Stabilized sands at low elevation; 5: Semi-stabilized dunes; 6: Mobile dunes; 7: Former beaches.

**Table 1** Number of ponds surveyed during each breeding season (sampling period indicated in brackets) and mean number of sampling visits (total number of ponds surveyed over the entire study period = 221).

	2003 (February–May)	2004 (January–June)	2006 (March–May)
Total number of ponds surveyed	94	95	129
Number of visits per pond (mean $\pm$ SD)	1.5 $\pm$ 1.1	1.7 $\pm$ 1.4	1.1 $\pm$ 0.4
Number of ponds surveyed			
Only that year	29	61	50
All years	16	16	16
In 2003 and 2004	2	2	
In 2004 and 2006		16	16
In 2003 and 2006	47		47

The number of ponds is detailed as number of ponds visited only in that season, in all seasons or in two of the three seasons.

140 ponds were visited in only one of the 3 years whereas 16 ponds were visited every year (Table 1). In 2006, a year with scarce autumn rainfall, we visited all ponds monitored in the previous years and surveyed the flooded ones ( $n = 129$ ). Most ponds were visited once per year except 19 ponds, which were sampled monthly during the whole amphibian breeding seasons to compute the species monthly detection probabilities (see Gómez-Rodríguez *et al.*, 2010d). The number of visits to a given pond ranged from 1 to 12 (mean =  $2.01 \pm 2.42$  SD).

We used dipnetting techniques (Heyer *et al.*, 1994) to sample the amphibian larvae. We identified *in situ* the individuals captured in each sampling unit (three consecutive sweeps on a stretch of *c.* 1.5 m length) and then released them back. Sampling effort was proportional to pond size, except when not logistically achievable because of the large size of the water body, in which case we tried to sample all different pond microhabitats. Larval sampling was complemented with visual surveys in and around the pond to detect eggs, larvae and metamorphic individuals. Since this study analyses the habitat requirements for amphibian breeding, we only included data from breeding attempts, not just the occurrence of a species. So we excluded the contingent detection of adults or calling activity because the sampling protocol was not optimized for detection of this life stage (Heyer *et al.*, 1994).

#### Predictors and underlying hypotheses

We selected habitat variables to test the competing hypotheses regarding amphibian habitat selection, based on available ecological information. The habitat variables can be grouped into the following sets (see Table 2):

**Breeding habitat.** We recorded two major structuring drivers of amphibian communities: pond hydroperiod (Wellborn

*et al.*, 1996) and pond size (Werner *et al.*, 2007). Hydroperiod was categorized in four wide groups because a ranked ordination of ponds hydroperiod is similar both in wet and dry years (Gómez-Rodríguez *et al.*, 2009). Since most ponds were visited only once, hydroperiod categories were based on characteristics related to flooding duration such as the presence of particular plant species (i.e. four main groups of aquatic plants can be differentiated according to their water dependence: floodplain species, wetland species, anchored species and free-floating species, see Díaz-Paniagua *et al.*, 2010), as well as basin topography (i.e. pond depth, basin slope, etc.) and past recordings of hydroperiod in those ponds (C. Díaz-Paniagua, unpublished data). Pond size was extracted from a 5-m resolution pond map layer obtained at a large flooding event (Gómez-Rodríguez *et al.*, 2010b).

**Aestivating habitat.** We have differentiated three terrestrial habitat types according to a gradient of moist–arid environment (forest habitat > scrub habitat > dune habitat). Aridity may be a barrier to interpond movements for amphibians and also a source for hydric stress during aestivation, when individual survival may be severely compromised because of dehydration (Pinder *et al.*, 1992). We used the ecosystem cartography of DNP (Montes *et al.*, 1998) to assess the percentage of each terrestrial habitat category in a 200-m buffer area from the edge of each pond.

**Spatial distribution of breeding habitats.** These are variables related to pond accessibility from nearby water bodies. As a measure of pond accessibility, we classified in three categories the proportion of pond shore surrounded by adjacent hygrophyte vegetation (Table 2) using aerial photography (Junta de Andalucía, 2003). As a measure of pond connectivity, we measured the edge-to-edge distance to the nearest pond and to the marshes, using the 5-m resolution pond map layer with ARCVIEW GIS 3.2. We also counted the number of nearby water bodies (excluding the marshes) surrounding each study pond in a 200-m buffer area from the edge of the pond. This distance has been reported for routinary movements between ponds in other amphibian species (Marsh *et al.*, 1999). To account for interannual variability in pond connectivity attributable to meteorological conditions, we categorized surrounding ponds according to their size, which is generally related to the hydroperiod/permanence of temporary ponds in the study area (see Fortuna *et al.*, 2006). So we discriminated ponds flooding in very wet years (all ponds, including those of small size) from those ponds that flood even during dry years (ponds larger than 4000 m<sup>2</sup>).

**Ecosection type.** We recorded the ecosection in which the pond was located, as extracted from the ecosystem cartography in Montes *et al.* (1998). This is an indirect predictor, with no direct biological relevance for a species, but it informs us whether habitat selection is affected by spatial autocorrelation or conditioned by local attributes related to ecosystem type (i.e. dry zones, ecotones, etc.) that may have not been considered in the remaining sets of variables.

In total, 11 variables were used in 12 competing models (see Table 2).

**Table 2** Set of candidate models evaluated within each hypothesis. The variable and its form (continuous/categorical/ordered categorical) are specified.

Hypothesis	Model	Habitat variables	Observations
Ecosection Breeding habitat	1. Ecosection	Ecosection	Factor
	2. Pond size	Pond size + (Pond size) <sup>2</sup>	Continuous
	3. Hydroperiod	Hydroperiod	Ordered factor: ephemeral pond (flooded 1–2 months in a wet year), intermediate temporary pond (3–6 months in a wet year), long-duration temporary pond (7–11 months in a wet year) <i>zacallon</i>
Aestivating habitat	4. Global breeding habitat	Hydroperiod + Pond size	(see previous observations)
	5. Suitable	Forest + Scrub	Continuous
	6. Unsuitable	Dunes	Continuous
	7. Global aestivating habitat	Forest + Scrub + Dunes	(see previous observations)
Spatial distribution of breeding habitats	8. Accesibility	Surrounding vegetation (Surr. veg.)	Ordered factor: no hygrophyte vegetation, intermediate hygrophyte vegetation (surrounding 25–75% of the pond shore), hygrophyte vegetation surrounding more than 75% of the pond
	9. Closest source	Distance to marshes + Distance to nearest pond	Continuous
	10. Sources (wet year)	Number of ponds	Continuous
	11. Sources (dry year)	Number of large ponds	Continuous
	12. Global breeding habitats distribution	Surr. veg. + Distance to marshes + Distance to nearest pond + Number of ponds + Number of large ponds	(see previous observations)

## Statistical analyses

### *Estimation of absence data reliability*

A non-detection record (equivalent to a recorded absence) represents a lack of evidence that the species bred in that given pond during the entire study period. Recorded presences were assumed to be completely reliable ( $P^* = 1$ ). Detection reliability was computed from species-specific single-visit detection probability values, calculated and reported in a previous study for each month of survey (Gómez-Rodríguez *et al.*, 2010d). The single-visit detection probability ( $P_i$ ) of a species is the probability that it will be detected at a pond in one sampling visit, given that the species breeds in the pond. To compute such probability values, Gómez-Rodríguez *et al.* (2010d) sampled every month 19 temporary ponds (also included in this study) and two permanent ponds in DNP during the amphibian breeding season in three different years: February – May 2003, January – May 2004 and March – May 2006. They estimated the single-visit probability of detection ( $P_i$ ) for each species and sampling month using single-species occupancy models (MacKenzie *et al.* 2002, MacKenzie *et al.*, 2006) with the program PRESENCE (MacKenzie *et al.* 2002).

In this study, we estimate the reliability of each non-detection record as the probability of having detected the species given the timing of survey for that particular case (i.e. taking into account the dates in which the pond was surveyed). So we computed the probability of detecting a species after  $k$  visits, i.e. reliability, ( $P^*$ ) by applying the formula provided by MacKenzie *et al.* (2006), where  $P_i$  is the single-visit probability of detection, which depends on the species and month of survey:

$$P^* = 1 - \prod_{i=1}^k (1 - P_i)$$

### *Species distributions models*

We developed a set of twelve *a priori* candidate models (Table 2) for each species, based on scientific, available field and expert knowledge, to assess which variables best explained the species' probability of breeding attempt in a given pond during the study period. Models were classified under the aforementioned four main hypotheses, depending on the type of habitat characteristics included (Table 2). Within each



**Table 3** Models with highest Akaike's weight (Akaike  $\omega$ ) and their corresponding AUC ( $\pm$  standard error) are shown for each species\*. Results are shown for the two approaches for SDMs building. The number of valid cases used to compute the AUC is specified in the SDMs accounting for the absence data reliability.

	SDMs accounting for absence data reliability			Traditional SDMs		
	Model	Akaike $\omega$	AUC $\pm$ SE (valid cases)	Model	Akaike $\omega$	AUC $\pm$ SE
<i>Pelobates cultripedis</i>	4. Global breeding habitat	0.989	0.824 $\pm$ 0.048 (117)	1. Ecosection	0.810	0.775 $\pm$ 0.027
				4. Global breeding habitat	0.185	0.803 $\pm$ 0.039
<i>Discoglossus galganoi</i>	7. Global aestivating habitat	0.326	0.863 $\pm$ 0.189 (37)	1. Ecosection	0.919	0.754 $\pm$ 0.026
	5. Suitable	0.249	0.823 $\pm$ 0.127 (37)			
	6. Unsuitable	0.16	0.661 $\pm$ 0.068 (37)			
	11. Sources (dry year)	0.066	0.681 $\pm$ 0.098 (37)			
	10. Sources (wet year)	0.046	0.516 $\pm$ 0.090 (37)			
	2. Pond size	0.039	0.490 $\pm$ 0.110 (37)			
<i>Hyla meridionalis</i>	1. Ecosection	1	0.814 $\pm$ 0.035 (165)	1. Ecosection	1.000	0.806 $\pm$ 0.029
<i>Pleurodeles waltl</i>	2. Pond size	0.29	0.627 $\pm$ 0.074 (110)	4. Global breeding habitat	0.809	0.720 $\pm$ 0.039
				3. Hydroperiod	0.122	0.688 $\pm$ 0.034
	3. Hydroperiod	0.233	0.585 $\pm$ 0.069 (110)			
	4. Global breeding habitat	0.198	0.609 $\pm$ 0.067 (110)			
	10. Sources (wet year)	0.103	0.592 $\pm$ 0.067 (110)			
	11. Sources (dry year)	0.093	0.556 $\pm$ 0.049 (110)			
<i>Triturus pygmaeus</i>	1. Ecosection	0.762	0.695 $\pm$ 0.032 (202)	1. Ecosection	0.785	0.726 $\pm$ 0.030
	12. Global breeding habitats distribution	0.096	0.748 $\pm$ 0.033 (202)	12. Global breeding habitats distribution	0.098	0.736 $\pm$ 0.033
<i>Lissotriton boscai</i>	7. Global aestivating habitat	0.483	0.727 $\pm$ 0.056 (97)	8. Accessibility	0.383	0.735 $\pm$ 0.039
	12. Global breeding habitats distribution	0.376	0.798 $\pm$ 0.043 (97)	5. Suitable	0.314	0.759 $\pm$ 0.036
				7. Global aestivating habitat	0.196	0.766 $\pm$ 0.035

SDM, species distribution models.

\*Only the minimum number of models necessary to achieve a global Akaike's weight above 0.85 is shown.

hypothesis, we developed single-predictor models to test the relevance of specific habitat characteristics, and a global one, including all predictors, to compare the alternative main hypotheses. A previous exploration with generalized additive models (GAMs) (Hastie & Tibshirani, 1990) evidenced that only the species–pond size relationship might be curvilinear and therefore a quadratic term was only considered for this variable. We did not construct a complete model (i.e. including all variables together) since it would have included far more variables than reasonable given the sample size. We did not consider all possible combinations of variables, as this approach typically inflates the number of models beyond the number that can be reliably analysed (Burnham & Anderson, 2002).

Candidate models were built using generalized linear models (GLMs) (McCullagh & Nelder, 1989) with binomial errors and a logit link (function 'glm' in 'Stats' package of R software, R Development Core Team, 2010). The response variable was the presence–absence (breeding evidence vs. no breeding evidence) of the species in a given pond during the entire study period. We explicitly accounted for the reliability of the data by weighting each case by its reliability ( $P^*$ ).

To identify the best model within the set of candidate models, we followed a model selection approach based on Akaike's information criterion (AIC) and multimodel inference of parameters (Burnham & Anderson, 2002; see Vicente *et al.*, 2010 for an example in distribution modelling) so that estimates of model parameters were based on the entire set of models rather than on the one selected as best. We ranked models according to their AIC values to obtain Akaike's model weights ( $\omega$ ), ranging between 0 (low model importance) and 1 (high model importance) and quantifying the uncertainty that each model is the target best model (see Burnham & Anderson, 2002). Afterwards, we computed the relative importance of each parameter by summing the Akaike's weights across all the models in the set where the variable occurred (Burnham & Anderson, 2002). For each parameter, we also computed its model-averaged estimate and its unconditional standard error, which incorporated model selection uncertainty into estimates of precision (Burnham & Anderson, 2002). Model-averaged estimates are less biased compared to the estimator from just the selected best model and are especially useful if no model is clearly best (Burnham & Anderson, 2002).

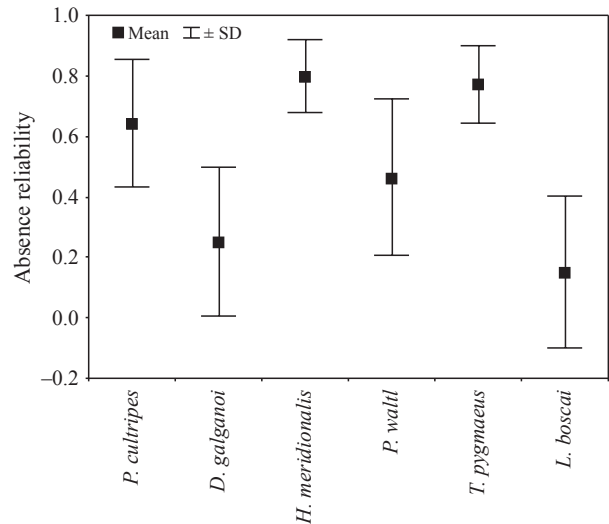
Models were evaluated based on the Area Under Curve, AUC (function ‘somers2’, library ‘Hmisc’), the percentage of explained deviance ( $D^2$ ) and the adjusted  $D^2$ , which takes into account the number of parameters in the model (Guisan & Zimmermann, 2000). We computed the AUC only from cases with high reliability. We set  $P^* \geq 0.80$  to identify cases with high reliability except in the case of *Lissotriton boscai* (Lataste, 1879), for which we set  $P^* \geq 0.50$  since only two ponds showed  $P^* \geq 0.80$  (note that  $P^*$  was always higher than 0.5 in all positive cases). We assessed the standard error of each evaluation statistic using a parametric bootstrap (1000 samples) in which the species prevalence in each sample was kept constant and equal to the one in the real data set. Bootstrap is recommended to assess the stability of a model when the data set is too small to be split into separate data sets for model building and evaluation (Guisan & Zimmermann, 2000), as in this study.

For the purpose of comparison, we also built traditional SDMs following the same procedure. In these models, the reliability of absence data was not accounted for, and thus, the cases were not weighted. Similarly, AUC was computed from all the cases.

## RESULTS

We detected eight species in the study area: *Bufo calamita* Laurenti, 1768; *Pelobates cultripes* (Cuvier, 1829); *Discoglossus galganoi* Capula, Nascetti, Lanza, Bullini & Crespo, 1985; *Pelophylax perezi* (Seoane, 1885); *Hyla meridionalis* Boettger, 1874; *Pleurodeles waltl* Michahelles, 1830; *Triturus pygmaeus* (Wolterstorff, 1905) and *L. boscai*. However, we could not estimate the probability of detection nor build models for *B. calamita* and *P. perezi*, since a single-visit probability of detection was lacking for most sampling visits (see Gómez-Rodríguez *et al.*, 2010d), and thereby, these species were excluded from the study. *Triturus pygmaeus* and *H. meridionalis* were the species that bred in a larger proportion of ponds (55% and 46%, respectively), whereas *D. galganoi* was only detected in 13% of the ponds (Fig. 1). In any given pond, the reliability of non-detection records differed widely among species (Kruskal–Wallis test:  $H = 462.19$ , d.f. = 5;  $P < 0.001$ ; Fig. 2). *Triturus pygmaeus* and *H. meridionalis* showed the highest mean probability of detection in ponds where we did not detect the species, thereby evidencing high levels of reliability in their absence data (Fig. 2). On the contrary, *D. galganoi* and *L. boscai* were the species with less reliable absence data, their reliability being null in 73 ponds and in 124 ponds, respectively.

We observed differences in model ranking and model weights among species, evidencing that there was not a ‘best supported hypothesis’ valid for all of them (Fig. 3, see Table S1 in the Supporting Information for details). Only *P. cultripes* and *H. meridionalis* showed a model clearly ranked as best (Akaike  $\omega > 0.98$ ), whereas the rest of the species showed similar support for competing models, although those models were within the same main hypothesis except in the case of

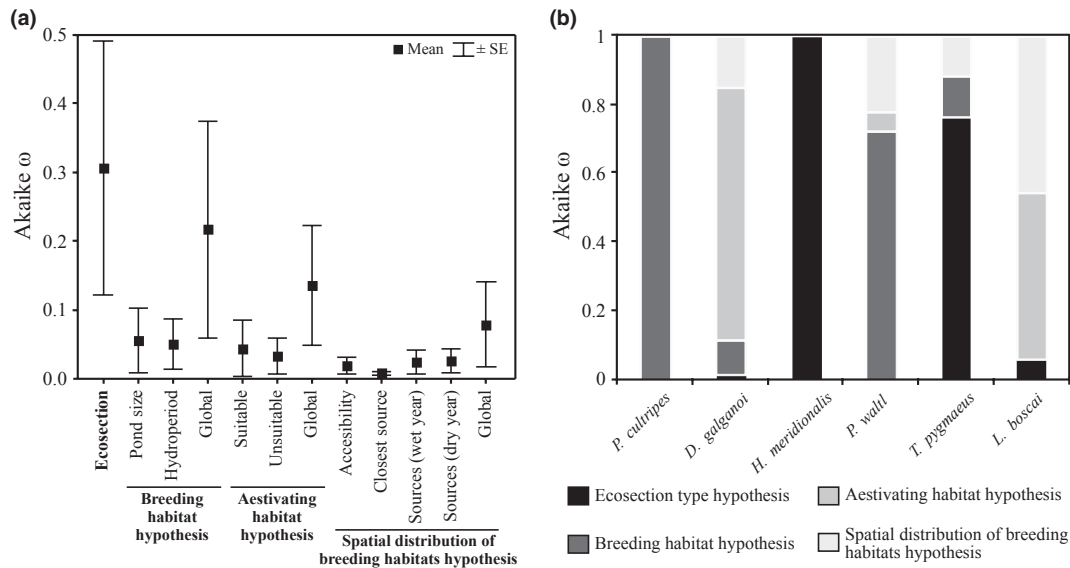


**Figure 2** Mean value and standard deviation of absence data reliability in the ponds where the non-detection of the species was recorded. Absence reliability represents the probability of having detected the species, given presence, after the sampling visits conducted during the entire study period.

*L. boscai* (Fig. 3). The hypotheses that obtained a higher mean support were the ‘ecosection’, the ‘global breeding habitat’ and the ‘global aestivating habitat’, whereas the ones with lower mean support were the ones related to the ‘spatial distribution of breeding habitats’, except the one including all the variables (Fig. 3).

Models ranked as best showed a useful to good value of AUC ( $> 0.80$ ) in the case of anurans and lower values for urodele species (Table 3). Similarly, SDMs accounting for data reliability showed higher AUC values than traditional SDMs in the case of anurans. In the case of urodeles, AUC values were similar between both types of models except in the case of *P. waltl*, for which traditional regression models seemed to work better. We also observed differences in model ranking and model weights between the two regression methods, the most remarkable difference being the larger support obtained for the ecosection hypothesis with traditional SDMs (Table 3).

In models accounting for the reliability of non-detection records, the ecosection hypothesis obtained a great support from species breeding in a large proportion of ponds (*H. meridionalis* and *T. pygmaeus*) (Fig. 3 and Table 4) as they mainly occurred in a single ecosection (Ecosection 3: ‘Wet stabilized sands at higher elevation’) (Fig. 4). Models within the ‘breeding habitat hypothesis’ explained best the distribution of species with long larval development (*P. waltl* and *P. cultripes*) (Fig. 3). Their probability of occurrence increased with pond size (see Supporting Information: Tables S2 and S3 for details) and hydroperiod in temporary ponds (Fig. 4). Models related to the ‘aestivating habitat hypothesis’ best explained the distribution of *D. galganoi*, while this hypothesis as well as the ‘spatial distribution of breeding habitat patches’



**Figure 3** (a) Mean value and standard error of the Akaike's weight of each model across all species. (b) For each species, the Akaike's weight of each main hypothesis is shown.

**Table 4** Relative importance of parameters obtained for species distribution models accounting for the reliability of non-detection records.

	<i>Pelobates cultripes</i>	<i>Discoglossus galganoi</i>	<i>Hyla meridionalis</i>	<i>Pleurodeles waltl</i>	<i>Triturus pygmaeus</i>	<i>Lissotriton boscai</i>
Ecosection	0.0	1.4	<b>100</b>	0.2	<b>76.2</b>	5.8
Pond size	<b>99.5</b>	6.4	0.0	<b>48.8</b>	9.1	0.0
Hydroperiod	<b>99.4</b>	5.9	0.0	<b>43.1</b>	12.1	0.0
Forest	0.0	<b>57.5</b>	0.0	1.9	0.0	<b>48.3</b>
Scrub	0.0	<b>57.5</b>	0.0	1.9	0.0	<b>48.3</b>
Dunes	0.0	<b>48.6</b>	0.0	4.0	0.0	<b>48.3</b>
Surrounding vegetation	0.0	2.4	0.0	0.7	10.8	<b>45.5</b>
Distance to marshes	0.0	1.8	0.0	1.9	10.5	<b>38.0</b>
Distance to nearest pond	0.0	1.8	0.0	1.9	10.5	<b>38.0</b>
Number of ponds	0.0	4.8	0.0	10.4	9.6	<b>37.6</b>
Number of large ponds	0.0	6.7	0.0	9.4	9.6	<b>37.6</b>

Parameters with highest relative abundance are shown in bold.

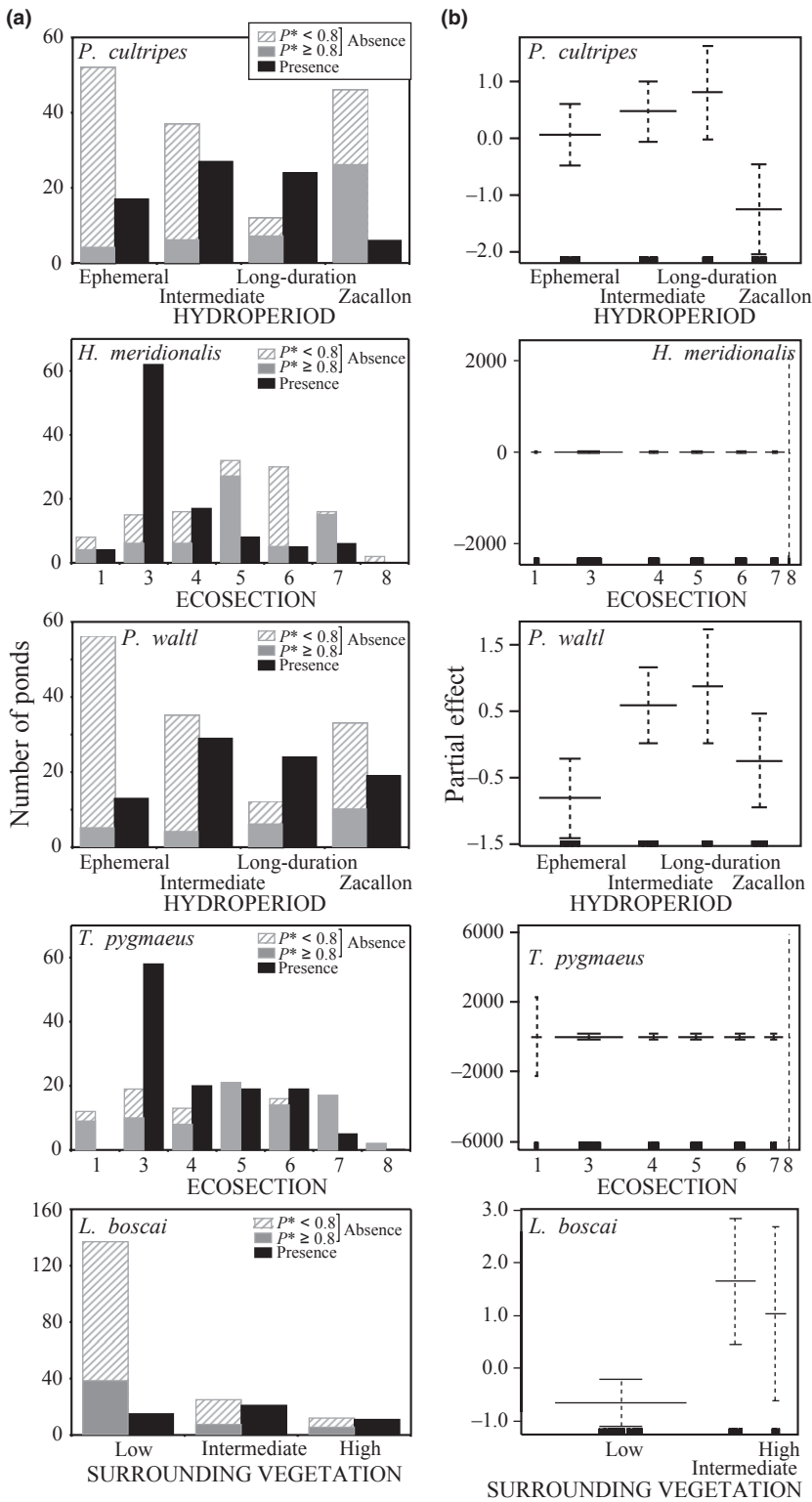
one explained the distribution of *L. boscai* (Fig. 3 and Supporting Information for details). The presence of both species was positively related to dunes and negatively with forest, but showed contrasting responses to the presence of scrub habitat in the surroundings (see Supporting Information: Tables S2 and S3). Remarkably, the presence of *L. boscai* was positively associated with the number of ponds persisting in dry years (i.e. number of large ponds) but not with the number of ponds persisting in wet years (i.e. number of ponds).

## DISCUSSION

This study illustrates how to account for the reliability of absence data in SDMs, taking the case of amphibian species in Mediterranean temporary ponds as an example. Our results evidenced a wide variability in the reliability of non-detection

records for different amphibian species when the number of surveys or its timing (choice of sampling months) is not the same for all inventoried sites (i.e. ponds in this study). As a consequence, one should not assume that all non-detections are valid absences and, instead, question their individual reliability. Although uncertainty in the reliability of absences was previously recognized as a potential source of problems in SDMs (Lobo, 2008), our results accurately show that non-detection records should be considered with particular care when a species' detectability is low and/or can change over time, as it is the case of *L. boscai* and *D. galganoi* (following Gómez-Rodríguez *et al.*, 2010d), both endemic species of the Iberian Peninsula. In addition, this study also indicates that accounting for absence data reliability is of special relevance in the case of rare species. Thus, the less common species (i.e. *L. boscai* or *D. galganoi*, following Díaz-Paniagua *et al.*, 2006) had less reliable absences than more common species, as those





**Figure 4** (a) Number of observed presences and absences in each category of habitat factors with high relative importance. Data are shown both for all absences and for absences with high reliability ( $P^* \geq 0.8$ ). (b) Partial effects ( $\pm$  standard error) of categorical factors with high relative importance. \*For each species, partial effects are obtained from a global model including all factors with high relative importance ( $> 0.376$ ) using command plot.gam (library 'gam', R project).

with large occupancy (i.e. *T. pygmaeus* and *H. meridionalis*, following Díaz-Paniagua *et al.*, 2006) or persisting longer in the ponds because of their long larval period (i.e. *Pelobates cultripes*). It should be noted that, following Gómez-Rodríguez *et al.* (2010d), there are two major causes of the unreliability of non-detection records: (1) 'methodological constraints', attrib-

uted to a low efficiency of the sampling survey, and (2) 'phenological constraints', attributed to inadequate survey timing (i.e. the pond was surveyed before the species had reached the pond for breeding). Identifying the cause of data unreliability would be useful to minimize errors in future surveys. However, we would like to stress that, once data are

collected, the cause of data unreliability is irrelevant as the consequence is always the same: absences should be taken with caution.

Unreliable absences, like those found in this study, may cause severe errors in SDMs, as one faces the risk of considering sites unsuitable that are in fact occupied by the species (i.e. detection failure). To avoid the error caused by such methodological absences (*sensu* Lobo *et al.*, 2010), we propose a novel approach to explicitly account for absence reliability in SDMs, using objective and quantifiable criteria. This improved framework allows incorporating information on species detectability at each particular survey site into traditional modelling techniques (GLMs). The rationale behind it is that the relevance of information contained in a non-detection record is conditional on the probability of having detected the species at that site if it was really present. If the probability is high, we can be certain that the species was not there; otherwise, we would have detected it. In that case, the absence is reliable. We propose this approach as one step further from the suggestions in Lobo *et al.* (2010), who recommend the use of expert opinion or conceptual designs to avoid the indiscriminate inclusion of zeros from badly surveyed localities in model building.

One of the main advantages of our approach is that it does not dismiss all non-detection records but, instead, weights its relevance according to estimated reliability. In this regard, our approach constitutes an alternative to using presence-only models (see Elith *et al.*, 2006) when the data are susceptible to false absences (see Gibson *et al.*, 2007; Rota *et al.*, 2011 as some recent examples). In fact, as it partially uses information on non-detection records to provide more confidence on the most reliable ones, our methods minimize the problem of placing random pseudo-absences in favourable sites (Engler *et al.*, 2004; Lobo, 2008). Rota *et al.* (2011) reported that the performance of logistic regressions diminished for less detectable species because non-detections were ambiguous, an issue that highlights the need for accounting for absence data reliability in SDMs for these species. It must be stressed that this approach is not intended to replace an adequate survey nor occupancy models (see MacKenzie *et al.*, 2006) that simultaneously estimate species occupancy and detectability from intensive sampling. On the contrary, it is a low-cost alternative for improving the reliability of data from monitoring schemes in which multiple surveys of all sites were not feasible.

Here, we also evidence that SDMs accounting for data reliability outperformed traditional regression models for anurans, especially for highly inconspicuous species, such as *D. galganoi*, although it was not clearly advantageous in the case of urodeles. Overall, SDMs did not provide good results for urodeles in this study, suggesting that alternative hypotheses to the ones considered could be necessary to explain their distribution in the study area. In this sense, past events and/or historic processes may be important for these species given their strong site fidelity and limited dispersal ability (Smith & Green, 2005). We would like to highlight that, for amphibians

in DNP, traditional SDMs seemingly failed to identify relevant hypotheses as the one that received the largest support for most species was the 'ecosection' hypothesis. If this were indeed the case, it would imply a lack of active habitat selection by the species. On the contrary, using the enhanced modelling framework, we found evidence of active habitat selection although we did not find environmental correlates that were valid for all the amphibian species considered. This confirms previous studies that reported species-specific responses to habitat factors (i.e. Beja & Alcazar, 2003; Van Buskirk, 2005). It also stresses the importance of multifactor approaches for modelling amphibian distributions, since the characteristics of both the pond and the landscape (terrestrial and surrounding aquatic habitat) proved important for the different species. The ecosection hypothesis obtained high support from *H. meridionalis* and *T. pygmaeus*, as these species occurred in almost every pond in the 'wet stabilized sands at higher elevation'. The breeding habitat hypothesis obtained high support for *P. waltl* and *P. cultripes*. Our results were in accordance with previous studies reporting that these species require ponds with long hydroperiod for breeding success (Díaz-Paniagua *et al.*, 2005), usually of large size, but avoid the artificial permanent water bodies, especially *P. cultripes*. Terrestrial characteristics were the most important predictors of *D. galganoi* and *L. boscai* occurrence. However, as the shape of the responses was contrary to expected in some cases, the relevance of this hypothesis may not be solely related to terrestrial habitat usage by adults (i.e. movements between ponds or terrestrial residence). Instead, it could also be indirectly associated with the hydrological dynamics of DNP (i.e. large density and variability of temporary ponds in the area nearby the dunes, see Gómez-Rodríguez *et al.*, 2010a). The occurrence of *L. boscai*, a species reported to breed in ponds of intermediate hydroperiod in the area (Díaz-Paniagua *et al.*, 2005), would be also related to the formation of ponds of intermediate/long hydroperiod in the surroundings but not to the formation of ephemeral ones that only flood in wet years.

It should be noted that, for most species, the best models had low explanatory power although still providing reasonable discrimination ability, appropriate for many uses (following Pearce & Ferrier, 2000). Low explanatory power is expected in binomial models where probability values ranging from 0 to 1 (predictive values) are compared to a binary variable (presence-absence). An alternative explanation could be the potential lack of compliance of the study system with the equilibrium assumption of SDMs: suitable habitats should be occupied and unsuitable habitats should be empty. In fact, in our study area, absence of a species from suitable habitats may also be due to environmental stochasticity, a characteristic of Mediterranean ecosystems, or because the large availability of breeding sites in wet years (Gómez-Rodríguez *et al.*, 2008, 2010b) might result in a system where more habitat patches are available than necessary given the number of individuals (i.e. empty ponds as a result of an absence of colonization rather than non-suitability, see Pulliam, 2000). This scenario would result in many contingent absences (*sensu* Lobo *et al.*, 2010)

being included in the model as unsuitable sites when they are not really so. On the other hand, unsuitable habitats may also be occupied when a species does not always choose the best available site (Pulliam, 1996). As typical r-strategists, amphibian species in the study area may be reproducing in as many different ponds as possible to increase their reproductive success. Notwithstanding, we should not disregard that model performance might have been increased by including additional predictors, such as biotic interactions attributed to the presence of competitors or predators (e.g. Wells, 2007) or by modelling larval density rather than simple species occurrence (see Van Buskirk, 2005).

To conclude, we proposed and successfully illustrated a novel implementation for incorporating the reliability of non-detection records in SDMs of amphibian species using Mediterranean temporary ponds as a model system. We showed that estimating the reliability of absences, an exercise that had been previously seen as a naïve goal in SDMs (Lobo *et al.*, 2010), may be feasible and affordable. A critical point is that, because it is based on a double-sampling scheme, financial costs are reduced by intensively sampling only a limited set of sites. It should be noted, however, that accounting for absence reliability minimizes just one of the potential sources of uncertainty that may affect the performance of SDMs in these stochastically and dynamically changing environments. SDMs are static in nature (Guisan & Zimmermann, 2000), and hence prediction errors are inevitable if there is temporal variability in the habitat relationships (Fielding, 2002), as happens in our system of temporary ponds (Gómez-Rodríguez *et al.*, 2009). As a consequence, future studies should also try incorporating the uncertainty caused by temporal variability in both habitats and populations into SDMs.

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## REFERENCES

- Adams, M.J., Chelgren, N.D., Reinitz, D., Cole, R.A., Rachowicz, L.J., Galvan, S., McCreary, B., Pearl, C.A., Bailey, L.L., Bettaso, J., Bull, E.L. & Leu, M. (2010) Using occupancy models to understand the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecological Applications*, **20**, 289–302.
- Barry, S. & Elith, J. (2006) Error and uncertainty in habitat models. *Journal of Applied Ecology*, **43**, 413–423.
- Beja, P. & Alcazar, R. (2003) Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. *Biological Conservation*, **114**, 317–326.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference. A practical information-theoretic approach*. Springer, New York.
- Díaz-Paniagua, C., Gómez-Rodríguez, C., Porthault, A. & de Vries, W. (2005) *Los anfibios de Doñana*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente, Madrid.
- Díaz-Paniagua, C., Gómez-Rodríguez, C., Porthault, A. & de Vries, W. (2006) Distribución de los anfibios del Parque Nacional de Doñana en función de la abundancia y densidad de los hábitats de reproducción. *Revista Española de Herpetología*, **20**, 17–30.
- Díaz-Paniagua, C., Fernández-Zamudio, R., Florencio, M., García-Murillo, P., Gómez-Rodríguez, C., Porthault, A., Serrano, L. & Siljeström, P. (2010) Temporary ponds from the Doñana National Park: A system of natural habitats for the preservation of aquatic flora and fauna. *Limnetica*, **29**, 41–58.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Engler, R., Guisan, A. & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, **41**, 263–274.
- Fielding, A.H. (2002) What are the appropriate characteristics of an accuracy measure? *Predicting plant and animal occurrences: issues of accuracy and scale* (ed. by M. Scott, P.J. Heglund, M. Morrison, J.B. Haufler, M.G. Raphael, W.B. Wall and F. Samson), pp. 271–280. Island Press, Washington.
- Foody, G.M. (2011) Impacts of imperfect reference data on the apparent accuracy of species presence–absence models and their predictions. *Global Change Biology*, **20**, 498–508.
- Fortuna, M., Gómez-Rodríguez, C. & Bascompte, J. (2006) Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1429–1434.
- Gibbons, J.W. (2003) Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. *Wetlands*, **23**, 630–635.
- Gibson, L., Barrett, B. & Burbidge, A. (2007) Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. *Diversity and Distributions*, **13**, 704–713.
- Gómez-Rodríguez, C., Bustamante, J., Koponen, S. & Díaz-Paniagua, C. (2008) High-resolution remote-sensing data in amphibian studies: identification of breeding sites and contribution to habitat models. *Herpetological Journal*, **18**, 103–113.
- Gómez-Rodríguez, C., Díaz-Paniagua, C., Serrano, L., Florencio, M. & Porthault, A. (2009) Mediterranean temporary ponds as amphibian breeding habitats: the importance

- of preserving pond networks. *Aquatic Ecology*, **43**, 1179–1191.
- Gómez-Rodríguez, C., Bustamante, J. & Díaz-Paniagua, C. (2010a) Evidence of hydroperiod shortening in a preserved system of temporary ponds. *Remote Sensing*, **2**, 1439–1462.
- Gómez-Rodríguez, C., Díaz-Paniagua, C. & Bustamante, J. (2010b) *Cartografía de lagunas temporales del Parque Nacional de Doñana*. Agencia Andaluza del Agua, Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.
- Gómez-Rodríguez, C., Díaz-Paniagua, C., Bustamante, J., Portheault, A. & Florencio, M. (2010c) Inter-annual variability in amphibian assemblages: implications for diversity assessment and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 668–677.
- Gómez-Rodríguez, C., Guisan, A., Díaz-Paniagua, C. & Bustamante, J. (2010d) Application of detection probabilities to the design of amphibian monitoring programs in temporary ponds. *Annales Zoologici Fennici*, **47**, 306–322.
- Gu, W.D. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195–203.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized additive models*. Chapman and Hall, London.
- Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.-A.C. & Foster, M.S. (1994) *Measuring and monitoring biological diversity. Standard methods for amphibians*. Smithsonian Institution Press, Washington and London.
- Jakob, C., Poizat, G., Veith, M., Seitz, A. & Crivelli, A.J. (2003) Breeding phenology and larval distribution of amphibians in a Mediterranean pond network with unpredictable hydrology. *Hydrobiologia*, **499**, 51–61.
- Junta de Andalucía (2003) *Ortofotografía Digital de Andalucía*. Junta de Andalucía, Sevilla.
- Kéry, M., Gardner, B. & Monnerat, C. (2010) Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography*, **37**, 1851–1862.
- Lobo, J.M. (2008) More complex distribution models or more representative data? *Biodiversity Informatics*, **5**, 14–19.
- Lobo, J.M., Jiménez-Valverde, A. & Hortal, J. (2010) The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, **33**, 103–114.
- MacKenzie, D.I. (2006) Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management*, **70**, 367–374.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- MacKenzie, D.I., Nicholson, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy estimation and modeling. Inferring patterns and dynamics of species occurrence*. Elsevier, Amsterdam.
- Marsh, D.M., Fegraus, E.H. & Harrison, S. (1999) Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the tungara frog, *Physalaemus pustulosus*. *Journal of Animal Ecology*, **68**, 804–814.
- Martin, J., Chamaillé-Jammes, S., Nichols, J.D., Fritz, H., Hines, J.E., Fonesbeck, C.J., MacKenzie, D.I. & Bailey, L.L. (2010) Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. *Ecological Applications*, **20**, 1173–1182.
- Mazerolle, M.J., Desrochers, A. & Rochefort, L. (2005) Landscape characteristics influence pond occupancy by frogs after accounting for detectability. *Ecological Applications*, **15**, 824–834.
- Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J. & Nichols, J.D. (2007) Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology*, **41**, 672–689.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*. Chapman and Hall, London.
- Montes, C., Borja, F., Bravo, M.A. & Moreira, J.M. (1998) *Reconocimiento biofísico de espacios naturales protegidos. Doñana: Una aproximación ecosistémica*. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pinder, A.W., Storey, K.B. & Ultsch, G.R. (1992) Estivation and hibernation. *Environmental physiology of the amphibians* (ed. by M.E. Feder and W.W. Burggren), pp. 250–274. University of Chicago Press, Chicago and London.
- Pulliam, H.R. (1996) Sources and sinks: empirical evidence and population consequences. *Population Dynamics in Ecological Space and Time* (ed. by O.E. Rhodes, R.K. Chesser and M.H. Smith), pp. 45–74. University of Chicago Press, Chicago and London.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- R Development Core Team. (2010) *R: a language and environment for statistical computing*. Vienna, Austria.
- Richter-Boix, A., Llorente, G.A. & Montori, A. (2007) Structure and dynamics of an amphibian metacommunity in two regions. *Journal of Animal Ecology*, **76**, 607–618.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rota, C.T., Fletcher, R.J. Jr, Evans, J.M. & Hutto, R.L. (2011) Does accounting for imperfect detection improve species distribution models? *Ecography*, **34**, 659–670.
- Siljeström, P.A., Moreno, A., García, L.V. & Clemente, L.E. (1994) Doñana National Park (south-west Spain): geomorphological characterization through a soil-vegetation study. *Journal of Arid Environments*, **26**, 315–323.

- Smith, M.A. & Green, D.M. (2005) Dispersal and the meta-population paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, **28**, 110–128.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Urban, N.A. & Swihart, R.K. (2009) Multiscale perspectives on occupancy of meadow jumping mice in landscapes dominated by agriculture. *Journal of Mammalogy*, **90**, 1431–1439.
- Van Buskirk, J. (2005) Local and landscape influence on amphibian occurrence and abundance. *Ecology*, **86**, 1936–1947.
- Vicente, J., Alves, P., Randin, C.R., Guisan, A. & Honrado, J. (2010) What drives invasibility? A multi-model inference test of alien plant species richness patterns in Northern Portugal. *Ecography*, **33**, 1081–1092.
- Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.
- Wells, K.D. (2007) *The ecology and behavior of amphibians*. The University of Chicago Press, Chicago and London.
- Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2007) Amphibian species richness across environmental gradients. *Oikos*, **116**, 1697–1712.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Model selection and model evaluation results for each species.

**Table S2** Model-averaged estimates of parameters obtained for species distribution models accounting for absence data reliability (anuran species).

**Table S3** Model-averaged estimates of parameters obtained for species distribution models accounting for absence data reliability (urodele species).

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## BIOSKETCH

**Carola Gómez-Rodríguez** (PhD, University of Salamanca) is interested in freshwater ecology and monitoring biases. She is especially interested in potential biases in diversity assessments and species distribution models attributed to species and habitats temporal dynamics.

Author contributions: C.G.-R. conceived the ideas and analysed the data; C.G.-R., J.B., C.D.-P. and A.G. wrote the paper.

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