1   **Small ponds support high terrestrial bird species richness in a Mediterranean**

2   **semiarid region**

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15

16   **Abstract**

17   Ponds are among the world's most endangered freshwater ecosystems. A comprehensive knowledge of

18   pond biodiversity is urgently required to inform effective pond conservation actions. Most studies about

19   pond biodiversity focus on aquatic taxa, while the terrestrial biodiversity, especially of birds, has been

20   little studied. Moreover, the few studies existing on pond biodiversity do not account for different

21   detection rates of species, thus yielding biased results. Here, we apply a hierarchical Bayesian modelling

22   technique to data obtained from visual censuses to estimate bird richness associated to small ponds in a

23   semiarid region, considering the imperfect detection of species. The model incorporates specific

24   responses to site characteristics (pond typology), landscape (environmental heterogeneity) and at regional

25   scale (mean annual precipitation). Ponds were used by two thirds of the terrestrial breeding bird

26   community of the study region. Our modelling approach increased by an average of 7.5 species the

27   observed site-specific richness. Drinking troughs supported greater richness than other pond types.

28   Environmental heterogeneity was positively related with species richness, whereas no clear relation was

29   observed between richness and precipitation. In addition to their ecosystem services to human welfare,

30   our results suggest small ponds may act as key landscape elements for terrestrial birds in semiarid

31   regions.

32

33   Keywords: waterbodies, artificial pools, drinking troughs, cattle ponds, environmental heterogeneity,

34   precipitation

35

36   **Introduction**

37   Freshwater habitats host almost 9.5% of the species described to date, even though they cover only 0.01%

38   of the total water surface area of the Earth (Balian et al., 2008). However, inland waters are considered

39   among the most endangered ecosystems in the world and their associated biodiversity is declining much

40   faster than that of marine and terrestrial environments (Reid et al., 2019). Large aquatic ecosystems such

41   as rivers, lakes and reservoirs have traditionally attracted the attention of freshwater conservationists and

42   managers (Oertli et al., 2009). However, ponds and other small waterbodies can make collectively a non-

43   negligible contribution to the total freshwater area of the world, even higher than rivers and large lakes

44   (Downing et al., 2006; Downing, 2010), and making up 3-4% of some landscapes (Lehner & Döll, 2004).

45   Despite their contribution, these small isolated waterbodies are often neglected by wildlife managers and

46   policy makers (Céréghino et al., 2008).

47

48   Ponds are temporary or permanent water sources (both natural and man-made) with a size varying from 1

49   m^2 to 2 ha and no more than 8 m in depth (Oertli et al., 2005). In the last two decades, several studies

50   have highlighted the great potential of small ponds to support a high richness of aquatic species (Gómez-

51   Rodríguez et al., 2009; Oertli et al., 2010; Akasaka & Takamura, 2012; Biggs et al., 2016), including rare

52   and unique taxa (Lemmens et al., 2013; Ilg & Oertli, 2014; Fait et al., 2020). Moreover, the contribution

53   of ponds to biodiversity conservation is particularly important at regional scale, with a high proportion of

54   the regional species pool being present in ponds (Williams et al., 2004; Davies et al., 2008; Zamora-

55   Marín et al., 2021a). The role of ponds to provide key services for biodiversity may be even more

56   pronounced in arid and semiarid regions, where temporary or permanent waterbodies are in short supply

57   (Abellán et al., 2006; Sebastián-González et al., 2010; Lisón & Calvo, 2014). However, just as other

58   freshwater ecosystems, ponds are exposed to many pressures derived from human activities, such as land

59   drainage, nutrient loading, the decline of traditional farming and cattle raising, as well as the introduction

60   of invasive alien species (Declerck et al., 2006), most of these threats having increased in recent years.

61   Among these pressures, land-use changes related to intensive farming are particularly affecting temporary

62   ponds (Ferreira & Beja, 2013) and traditional drinking troughs (Buono et al., 2019), leading to infilling,

63   groundwater overexploitation or pond abandonment. As a consequence, many, if not most, ponds have

64   vanished from the farmlands of continental Europe, even the loss rate reaching as much as 90% in some

65   countries (Oertli et al., 2005). This is why studies aimed at providing robust knowledge on the role of

66   small ponds in biodiversity conservation are urgently required in order to establish pond management

67   strategies.

68

69   To date, pond biodiversity research has mainly focused on strict or facultative aquatic taxa, such as

70   macrophytes (Della Bella et al., 2008; Bubíková & Hrivnák, 2018), macroinvertebrates (Florencio et al.,

71   2014; Hill et al., 2016; Fait et al., 2020) and amphibians (Arntzen et al., 2017). However, recent studies

72   have pointed to the need to assess the importance of freshwater ecosystems for conserving not only

73   aquatic organisms but also terrestrial species (Soininen et al., 2015; Smit et al., 2019), including

74   pollinating insects (Walton et al., 2020), bats (Razgour et al., 2010), large mammals (Harper et al., 2019)

75   and farm birds (Lewis-Phillips et al., 2019a). In the case of terrestrial fauna, these habitats provide

76   essential cross-system services such as food (Davies et al., 2016) or drinking water (Abdu et al., 2018),

77   both extremely important resources for wildlife, especially during the breeding season (Lewis-Phillips et

78   al., 2020) or during hot periods (Lee et al., 2017). Until now, very few studies have analysed the role of

79   small ponds in providing services to protect terrestrial biodiversity. In the case of birds, Lewis-Phillips *et*

80   *al.,* (2019, 2020) found a greater bird abundance and richness in managed open-canopy ponds than in

81   unmanaged overgrown ponds, due mainly to the higher abundance of emergent insects in the former.

82   More generally, bird communities associated to small waterbodies have been described in some arid

83   regions (Bock, 2015; Abdu et al., 2018; Smit et al., 2019), pointing to the moderate contribution of

84   services made by ponds to terrestrial birds. However, these studies did not account for differences in

85   species detectability, which strongly affects occupancy estimates in birds (Einoder et al., 2018), thus

86   yielding biased results that may underestimate the true species richness associated with certain sampling

87   sites (MacKenzie & Bailey, 2004).

88

89   Species richness is the most commonly used biological measurement in ecological studies and monitoring

90   programs (MacKenzie et al., 2006; Kéry et al., 2009). However, determining species richness with

91   accuracy can be complicated because of variability in species-specific detection rates (Kéry & Schmidt,

92   2008). Previous approaches have traditionally ignored detectability by using raw species counts, leading

93   to questionable inferences with respect to species richness patterns (Kéry & Royle, 2008). Rare species

94   are frequently overlooked in community-level studies, mainly due to their limited detection rates, which

95   are influenced by low abundances (MacKenzie et al., 2005), despite the fact that most of them are

96   considered as species of conservation concern or even have poor conservation status. Nevertheless,

97   management and conservation strategies should consider all species inhabiting a particular site, not just

98   those species which provide enough data (Zipkin et al., 2010). Concern about the imperfect detection of

99   species in ecological studies has increased over recent years, and the rapid development of hierarchical

100 models has led to different approaches being used (Guillera-Arroita, 2017). Among the many advantages

101 of hierarchical models in comparison with other previous approaches (see Kéry & Royle, 2008) -e.g.

102 classical richness estimators- is the fact that they can incorporate habitat and sampling effects that

103 influence occupancy and detection processes, thus enabling the extensive evaluation of several features

104 that may modulate species richness and detectability (Maphisa, Smit-Robinson & Altwegg, 2019).

105　Moreover, richness estimation through hierarchical models allows to compute independently occupancy

106　and detectability estimates for each species within a community, thus accounting for the different

107　detection rates of species (Kéry & Royle, 2016). Furthermore, hierarchical occupancy models have rarely

108　been applied to aquatic ecosystems and are vastly underrepesented in the literature (Devarajan et al.,

109　2020). Indeed, very few studies apply hierarchical models to pond biodiversity data (Ferreira & Beja,

110　2013).

111

112　This study looks at the species richness of terrestrial breeding birds associated to 39 small ponds in the

113　most arid region of Europe (southeast of the Iberian Peninsula), using hierarchical Bayesian multi-species

114　occupancy modelling to account for differences in detectability across species. Our hierarchical modelling

115　incorporates three spatial scale covariates, which were expected to affect bird species richness in the

116　study ponds. Firstly, at pond site scale, we hypothesized that some pond attributes can promote the

117　terrestrial bird richness associated to ponds (Davies et al., 2016). For this reason, we explore differences

118　in species richness associated to three pond types that differ in their structural characteristics: artificial

119　pools, cattle ponds and drinking troughs. Secondly, we evaluate a measure of environmental

120　heterogeneity (hereafter, EH) as an environmental variable shaping bird richness associated to ponds at

121　landscape scale. Lastly, mean annual precipitation was incorporated in the model as one of the main

122　climatic factors shaping bird richness at regional scale. Based on previous studies (Qian & Kissling, 2010;

123　Stein et al., 2014; Lorenzón et al., 2016), we hypothesized that both environmental factors (EH and

124　precipitation) might be drivers of bird species richness associated to ponds. Therefore, our objectives

125　were to estimate species richness of terrestrial birds associated to three different pond types, and to

126　explore its relationship with EH and precipitation.

127

128　**Materials and methods**

129　Study area

130　The study was conducted in the province of Murcia, in the Iberian southeast, which is the most arid

131　region of continental Europe (Armas et al., 2011). The province of Murcia extends over an area of 11,317

132　km^2 and is characterized by a dry warm Mediterranean climate, with a strong water deficit during spring

133　and summer. Mean annual precipitation is 350 mm in most of the province and the average annual

134　temperature ranges from 18.5 ºC in the driest coastal areas –characterized by scarce precipitation- to 12.0

135　ºC in the coldest inland zones (Machado et al., 2011). However, during dry hydrological years, mean

136　annual precipitation usually does not exceed 200 mm, with rainfall being extremely unusual during late

137　spring and summer (mean monthly precipitation 11.5 mm). Despite the semiarid conditions, the existence

138　of a coast-inland climatic gradient promotes high ecosystem heterogeneity, which is even more

139　pronounced as a result of multiple environmental factors, which include weather conditions, intense

140　human pressure, topography and the availability of water resources. Three main different types of

141　ecosystem can be identified in the study area: semidesert zones, Mediterranean shrublands and coniferous

142　forests, mainly composed of *Pinus halepensis* Miller 1768 and *Pinus pinaster* Aiton 1789 (Esteve et al.,

143　2015). In general, the further one moves inland from the coast, the greater the presence of mountainous

144　areas, the more continental the climate (colder winters and higher mean annual precipitation) and the

145　lower the pressure of human occupancy. Indeed, mean annual precipitation can usually reach 680 mm in

146　some inland places, which is more than twice the 250 mm normally recorded in the most arid zones.

147

148　Regarding the principal land uses, rainfed and irrigated agriculture predominate in the lowlands and high

149　plateaus, whereas steeper areas are occupied by Mediterranean shrubland and pine forests. In recent

150　decades, intensive irrigated agriculture has expanded to almost half of the study area, which has involved

151　the excessive overexploitation of groundwater and surface water resources (Rupérez-Moreno et al., 2017).

152　In addition, traditional livestock grazing has experienced a sharp decline over the last decades, thus

153　leading to the lack of maintenance of cattle ponds and drinking troughs. Moreover, some traditional

154　waterbodies are also exposed to some unsuitable practices such as piping or channelling (López

155　Bermúdez et al., 2016). Indeed, the loss rate of traditional ponds in the study area have been estimated in

156　36% for cattle ponds (Verdiell-Cubedo, 2012) and 23% for other types of small ponds in the last decades

157　(Ballester-Sabater et al., 2003). This situation has dramatically decreased the availability of water

158　resources (both groundwater fed or not) for wildlife (Valera et al., 2011), especially in periods with a

159　marked water deficit, usually spring and summer. Thus, the availability of water resources for wildlife is

160　considerably lower in natural or semi-natural zones of the study area, where the main land uses are

161　rainfed agriculture and Mediterranean shrubland and forests, and no irrigation ponds appear in the

162　landscape. Consequently, due to the marked scarcity of rivers and streams, artificial pools and traditional

163　ponds (cattle ponds and drinking troughs) still present become the dominant waterbodies in these rural

164   landscapes and they can play an essential role in supporting terrestrial biodiversity (Lisón & Calvo, 2014;

165   Abdu et al., 2018).

166

167   Sampling sites: pond types and environmental variables

168   Study ponds were selected according to the following criteria: 1) easy pond access by birds, so that they

169   could drink safely from the pond shoreline or border; 2) size (up to 450 m^2), allowing the authors to

170   visually record bird activity along the whole pond shoreline from the same position; 3) a degree of

171   isolation from other water sources including wetlands, rivers, intermittent streams and other waterbodies

172   (average distance to nearest water source was 935 ± 728 m), which ensured that birds from the

173   surrounding area would use the particular pond; and 4) location in areas far from human settlements

174   (urban centres) in order to avoid biases from human influence -other than pond use- on the bird

175   community composition. As far as possible, ponds were selected along a coast-inland climatic gradient to

176   ensure representative information on the bird communities associated to ponds in areas under different

177   climatic conditions.

178

179   Overall, we selected 39 ponds spread over the study area (Fig. 1) and belonging to three different pond

180   types according to their structural features: 14 artificial pools, 12 cattle ponds and 13 drinking troughs

181   (see a representative picture for each pond type in Fig. 1). Artificial pools are permanent ponds with

182   cemented bottoms and a round or square structure, mostly located in forest or agroforestry landscapes,

183   where extensive agriculture and hunting are the main land uses. They are intermediate in size and depth

184   compared with the other two pond types. Most of them are directly fed from small natural springs, while

185   the rest are filled by farmers or rangers. Cattle ponds are temporal round waterbodies, which were

186   originally dug into Mediterranean farmlands to collect runoff water and provide drinking water for cattle.

187   They hold water at least during nine months per annual cycle. Cattle ponds are larger (270 ± 96 m) and

188   deeper (100 ± 37 cm) than the other two pond types. Although cattle ponds were dug artificially, they

189   appear natural because of their silt bottom and absence of artificial structures around them. They are

190   typically located in plateaus dominated by extensive grassland and tree farming. Lastly, drinking troughs

191   are lineal permanent artificial small waterbodies where cattle drink. In contrast to cattle ponds, drinking

192   troughs are exclusively located in mountain areas dominated by Mediterranean mature forests with small

193   scattered patches of extensive agriculture. Moreover, they are characterized by their small size and

194   shallowness, which limits the development of aquatic vegetation. Although fed from small natural

195   springs, all of them have been modified by lining with cement to ensure water permanence, thus adding to

196   their artificial appearance. Both permanent and temporary ponds held surface water during the study

197   period.

198

199   We considered environmental heterogeneity (EH) and mean annual precipitation to be the main

200   environmental variables affecting bird richness associated to study ponds at landscape and regional scale,

201   respectively. Regarding EH, a 1-km radius around each study pond enabled the land cover proportion

202   occupied by four main land use types to be calculated: tree crop (almond trees and vineyards), herbaceous

203   farming (cereal crops), Mediterranean shrubland and woodland (pine forests). This buffer size was

204   selected because bird community composition associated to ponds is markedly influenced by nearby land

205   uses (Sebastián-González & Green, 2014). To identify the land use types, the land cover mapping data

206   from the Spanish National Forestry Inventory (Dirección General de Desarrollo Rural y Política, 2012)

207   were used, along with the free software QGIS (version 2.18.19). Following Bain & Stevenson (1999),

208   standard deviation was calculated as a proxy of the land cover EH, using the cover proportion occupied

209   by each land-use type. A high standard deviation meant the dominance of a single land-use type (e.g. 1-

210   km radius fully occupied -100%- by woodland), thus indicating low habitat heterogeneity. Conversely,

211   the lowest standard deviation meant the four selected land-use types (tree crop, herbaceous farming,

212   shrubland and woodland) extend over a similar proportion of land cover (e.g. each land-use type covering

213   25% of land cover), thus indicating high habitat heterogeneity. Mean annual precipitation was extracted

214   from the climate atlas of the province of Murcia (Garrido et al., 2013) with a 1-km^2 grid size.

215

216   Bird surveys

217   We conducted three visits to 19 study ponds in 2017 and to 20 ponds in 2018. Visits were carried out in

218   early-mid spring (April), late spring (May-June) and early summer (July) to cover the whole breeding

219   season of the bird species in the study area. Intervals between visits to each pond were no longer than 40

220   days. As the ponds were far away from each other (average distance = 4.2 km), spatial autocorrelation in

221   our bird observations at the study ponds was unlikely. Home-range size in passerine birds is often

222   particularly reduced during the breeding season (Roldano, 2002), due to territoriality and brooding

223   activities, and it rarely exceeds 2 ha. (Morganti et al., 2017). Indeed, in a previous study using mist

224   netting to individually mark birds in some of the same study ponds (Zamora-Marín et al., 2021b), we

225   reported no recapture cases between different near ponds, despite most birds were caught twice at the

226   same pond. The order of the visits was constant throughout the study period to correct for the slightly

227   earlier phenology of bird species in warmer coastal areas (unpublished data). Each visit consisted of a 3-

228   hour census conducted by direct observation from within a portable hide, which was deployed in a

229   position (at least 10 m from the pond) that maximized the visibility of pond shoreline. As far as possible,

230   the hide was set up close to surrounding vegetation to avoid affecting bird behaviour. In addition,

231   conventional video cameras (Panasonic Handycam, HC-V180, Panasonic Corporation, Osaka, Japan)

232   were set in 14 out of the 39 study ponds during the 3-hour censuses with the aim of covering the entire

233   water surface at the largest ponds. Surveys began at sunrise (7:00-8:30 h), in good weather conditions

234   (rainless and windless days) and were always conducted by the same surveyors (JMZ-M and AZ-L). This

235   time of the day has been reported as being the period with greatest bird activity, after which species

236   detectability declines steeply (Lynch, 1989; Whitman et al., 1997). As far as was possible, surveys were

237   conducted during rainless periods because birds visit ponds much less in rainy conditions in arid regions

238   (Lynn et al., 2008; García-Castellanos et al., 2016). We recorded all birds seen or heard within a 10-m

239   buffer from the study pond. All birds were identified at species level, except crested lark (*Galerida*

240   *cristata* (L., 1758)) and Thekla´s lark (*Galerida theklae* (Brehm, 1858)), which were pooled at genus

241   level (*Galerida sp.)* to avoid misidentification (Guillaumet et al., 2005).

242

243   Modelling framework

244   We used a Bayesian multi-species occupancy model (Dorazio & Royle, 2005; Dorazio et al., 2006) to

245   evaluate the bird species richness associated to the study ponds, as well as to examine the influence of

246   pond typology, EH and mean annual precipitation on bird richness. This model is an extension of the

247   single species site occupancy model (MacKenzie et al., 2002), whereby the hierarchical structure

248   combines community and species level attributes within a single analytical framework (Zipkin et al.,

249   2010). The hierarchical model is composed of the ecological process (governed by occupancy

250   probability) and the observational process (governed by detectability probability). Data are compiled as a

251   2×2 matrix (**Y**) with i rows by k columns, corresponding to sites and species, respectively. The number of

252   temporal replicates or surveys j for each site i where the species k was observed is quantified in the

253   matrix. The ecological process assumes that site specific occupancy (i. e. 'true' presence⁄absence) for

254   species k at site i is denoted $z(i,k)$, where $z(i,k) = 1$ if species k occurs in site i and is zero otherwise. The

255   model for occurrence is specified as $z(i,k) \sim Bern(\psi_{i,k})$ where $\psi_{i,k}$ is the probability that species k occurs at

256   site i. The true occurrence is imperfectly observed, and we define the detection model for species k at site

257   i in survey j as $\mathbf{Y}(i,k) \sim Bern(p_{i,k} \cdot z(i,k))$ where $p_{i,k}$ is the detection probability of species k for the jth

258   temporal replicate at site i, given that species k is in fact present at site i (Zipkin et al., 2009). In the

259   simplest specification of the model, the occurrence and detection probabilities are composed of species-

260   specific effects and site-level effects (Dorazio et al., 2006; Kéry & Royle, 2016). Extensions of this basic

261   model have explicitly incorporated landscape characteristics into the probability of occupancy (Zipkin et

262   al., 2009; Jiménez-Franco et al., 2019; Maphisa et al., 2019). Following this approach, we modelled the

263   occurrence probability for species k at site i by incorporating the three above mentioned site-specific

264   covariates: pond type (artificial pool, AP; cattle pond, CP; drinking trough, DT), environmental

265   heterogeneity of the surrounding landscape (EH) and mean annual precipitation (PREC). Linear and

266   quadratic effects of EH and precipitation were included, and both quantitative covariates were

267   standardized. Therefore, the probability of occupancy was defined as follows:

268

269
$$\text{logit}\left(\psi_{i,k}\right) \sim Normal\left(\mu_{lpsi,i,k},\ \sigma^2_{lpsi,i,k}\right)$$

270
$$\mu_{lpsi,i,k} = \beta_{1,k}\text{AP}_i + \beta_{2,k}\text{CP}_i + \beta_{3,k}\text{DT}_i + \beta_{4,k}\text{EH}_i + \beta_{5,k}\text{EH}_i^2 + \beta_{6,k}\text{PREC}_i + \beta_{7,k}\text{PREC}_i^2$$

271

272   The coefficients from $\beta_{1,k}$ to $\beta_{7,k}$ are the effects of pond type, EH of the landscape (linear and squared)

273   and precipitation (linear and squared), for species k respectively. We assumed that detection probabilities

274   varied depending on the species but were not influenced by survey characteristics:

275     $\text{logit}(p_k) \sim Normal(\mu_{lp,k}, \sigma^2_{lp,k})$. The model was fitted using JAGS (Plummer, 2003) run in R version 3.6.3

276   (R Core Team, 2020) with the package *jagsUI* (Kellner, 2015), using uninformative priors, three chains,

277   15 000 iterations and a burn-in of 5 000 iterations and a thin rate of 2. Convergence was assessed by

278   examining the R-hat values for each parameter estimate (Brooks & Gelman, 1998). We present posterior

279   means and the 95% credible intervals (CRI), the Bayesian analogue to confidence intervals.

280

281   **Results**

282   We recorded a total of 80 bird species associated to the 39 surveyed small ponds of different types (Table

283   S1, Supporting Information). The observed species corresponded to 34 different avian families, with

284 flycatchers (Muscicapidae) and finches (Fringillidae) being the richest families (nine and eight species,

285 respectively), whereas finches were also the dominant family in terms of abundance (64% of the total

286 abundance). European serin (*Serinus serinus* L., 1766), common chaffinch (*Fringilla coelebs* L., 1758)

287 and common linnet (*Linaria cannabina* (L., 1758)) were the most frequent species in general, occurring

288 in 97.4%, 87.2% and 76.9% of the study ponds, whereas 16 species were occasional and were only

289 recorded in a single pond site. Detection probability estimates ranged from 0.10 to 0.84 (median = 0.35)

290 which illustrates the high variability in detectability among recorded species. Interestingly, our multi-

291 species model revealed that eight or more species were undetected at 12 out of our 39 study ponds.

292 Indeed, richness estimation increased by an average of 7.5 species over observed richness (Fig. 2).

293

294 Almost full occupancy estimates in artificial pools and drinking troughs were revealed for rock bunting

295 (*Emberiza cia* L., 1766), red crossbill (*Loxia curvirostra* L., 1758), great tit (*Parus major* L., 1758),

296 European serin, common chaffinch and Eurasian blackbird (*Turdus merula* L.,1758), indicating the

297 widespread use of small ponds by these species (Fig. S1, Supporting Information). Common linnet, larks

298 (*Galerida* sp.) and European serin were the most frequent species in cattle ponds.

299

300 The multi-species occupancy model revealed the important effect of pond type on associated bird richness

301 (Fig. 3), with a higher visually estimated local richness in drinking troughs (median = 31.8, range = 25.9,

302 45.2) than in the other pond types. Cattle ponds supported the second highest estimated richness (median

303 = 22.7, range = 15.4, 33.3), whereas artificial pools were the poorest pond type in terms of estimated

304 richness (median = 21.0, range = 13.8, 33.1). Some 29 bird species were exclusively associated to a single

305 pond type, with differences between the typologies, cattle ponds supporting more exclusive taxa (16

306 species) than drinking troughs and artificial pools (10 and 3 exclusive species, respectively). Considered

307 as a whole, drinking troughs represented the pond type with the highest observed bird richness (61

308 species), followed closely by cattle ponds (55), whereas artificial pools were the species-poorest, with 41

309 taxa. On the other hand, EH was positively related to bird richness after controlling for differences in

310 detectability across species (Fig. 4). However, no clear relation was observed in the case of mean annual

311 precipitation (Fig. 5), even though the wettest sites seemed to support the highest bird richness.

312

313 **Discussion**

In addition to their widely reported contribution to freshwater biodiversity, small ponds can also play an essential role in providing ecological services for terrestrial wildlife (Lisón & Calvo, 2014; Sutherland et al., 2018; Lewis-Phillips et al., 2019a). Our study supports the importance of small ponds for maintaining terrestrial bird communities in semiarid regions, which is highlighted by the high terrestrial bird richness associated to the study ponds. Interestingly, two thirds of the species composing the entire community of terrestrial breeding birds in the study region, which comprises 120 species (Calvo *et al.*, 2017), were observed visiting these small isolated aquatic ecosystems. This richness value is similar to reported from pond-uninfluenced line transects conducted through the province of Murcia (73 species, see Jiménez-Franco et al., 2019), thus suggesting study ponds were used by a large proportion of the bird assemblage breeding in terrestrial habitats of the study area. Indeed, 1-km line transects conducted in terrestrial habitats adjacent to study ponds revealed that 71% ($\pm$14.5% SD) of the bird species composing the local breeding bird community were recorded making use of the study ponds (authors´ unpublished data). However, this proportion of species may have been even higher because of our multi-species occupancy model yielded a median detection probability of 0.35 among all species. In this sense, several factors have been shown to affect detectability in bird species (Rigby & Johnson, 2019), including the effects from survey design, species behaviour, environmental conditions and observer performance (Jarzyna & Jetz, 2016; Guillera-Arroita, 2017; Jiménez-Franco et al., 2019). In our case, the use of a non-remote survey method may have underestimated the occurrence of elusive and large species, such as raptors and crows, which have been reported to make use of waterbodies through remote cameras (Votto et al., 2020). Even though our sampling method was deemed suitable for the study aims and some large or medium-sized bird species were occasionally detected (e. g. *Accipiter gentilis* (L., 1758), *Columba palumbus* L., 1758 and *Corvus corone* L., 1758), this survey technique may trigger avoidance behaviour in some elusive species due to the hide's presence. However, a methodological study recently conducted at the same ponds showed direct observation as the most efficient sampling method for detecting bird species associated to ponds, being even more effective than other traditional techniques such as mist netting (Zamora-Marín et al., 2021b). Indeed, direct observation (e.g. point counts and line transects) is a suitable survey method for community-level studies based on bird richness and abundance data, because of it allows to efficiently record different avian guilds (including gregarious and large birds), thus providing representative data on the whole community (Whitman et al., 1997; Faaborg et al., 2004). Furthermore, conversely to other survey methods, direct observation demands less human and economic resources

344 (Poulin et al., 2000). In our case, it should be noted we only surveyed a representative subset of the total

345 number of small waterbodies in the study area, meaning that the bird richness associated to small ponds in

346 the study area could be even greater than reported here.

347

348 The studied ponds accounted for a greater proportion of the regional bird species pool (80 out of 120

349 terrestrial breeding bird species, 67%, in the study area) than reported for small waterbodies from arid

350 regions, although comparisons must be considered with care due to the different sampling designs. For

351 instance, less than 50% of the local bird communities were recorded as using artificial waterholes in the

352 Kalahari desert (Abdu, Lee & Cunningham, 2018a; Smit *et al.*, 2019) and about 36% using natural ponds

353 from Western Cape, South Africa (Lee et al., 2017). These differences in the use of ponds by terrestrial

354 birds may be explained by the dissimilar physiological responses of bird species inhabiting different

355 aridity scenarios. In arid regions, the availability of water resources is naturally scarcer (or even totally

356 absent) compared with semiarid zones, meaning that avifauna from arid regions have been under greater

357 selection pressures to become independent of drinking water (Smit et al., 2019), for example, by

358 obtaining water from the diet (Smit, 2013). In semiarid study areas like ours, several natural springs and

359 other small waterbodies (farm ponds, cattle ponds and drinking troughs, among others) have traditionally

360 been present (López Bermúdez et al., 2016), providing water and other resources for wildlife. For this

361 reason, most bird species from semiarid regions have not developed physiological responses to become

362 independent of drinking water, since they have evolved in landscapes with certain availability of free-

363 water resources. These standing water resources were originally represented by natural springs, rock

364 pools and pools in intermittent or ephemeral streams (Sánchez-Montoya et al., 2016), and more recently

365 by artificial waterbodies such as cattle ponds and drinking troughs. Therefore, bearing in mind the

366 scarcity of natural water resources in semiarid regions, small traditional ponds seem to have become

367 essential for supporting terrestrial biodiversity, particularly bird communities.

368

369 Importantly, higher terrestrial bird richness was observed in drinking troughs than in the other pond types.

370 In our opinion, two factors seem to be responsible for the patterns of species richness associated to our

371 study pond types. On the one hand, vegetation cover is a local factor (i.e. pond attribute) that has been

372 reported to negatively affect terrestrial bird richness associated to ponds (Lewis-Phillips et al., 2019b).

373 Most of the artificial pools we studied were encroached upon or overgrown by emergent vegetation,

374   making the water less visible and accessible for birds, while decreasing food availability as a result of the

375   development and emergence of aquatic insects, consequently decreasing the associated bird richness

376   (Lewis-Phillips et al., 2020). Moreover, habitats overgrown by emergent vegetation may also increase the

377   predation risk perceived by small passerines (Whittingham & Evans, 2004), thus promoting an avoidance

378   behaviour. In our study, drinking troughs showed a pond shoreline discontinuously covered by bush

379   vegetation, thus allowing diversified bird use. Most of the observations for foliage gleaners in our study

380   (e.g. Sylviidae and Phylloscopidae families) corresponded to birds accessing pond shoreline through

381   adjacent bushes, as a behavioural response from their feeding habits. However, ground-foraging bird

382   species (e.g. Fringillidae and Columbidae families) were often observed accessing pond shoreline from

383   non-vegetated open areas. Thus, the occurrence of contrasting structural features within a given pond (i.e.

384   high within-pond heterogeneity) seems to play an important role in promoting the use by a diversified

385   bird community, as previously suggested (Davies et al., 2016). On the other hand, regional factors may

386   directly influence the likelihood of species inhabiting a given pond site. These regional factors include

387   large-scale environmental conditions that affect all systems in a region (e.g. land-use patterns), thus

388   determining the regional species pool (De Meester et al., 2005). Previous studies have reported the strong

389   influence of land uses on terrestrial bird richness (Waltert et al., 2004; Allen et al., 2019). In our case, it

390   was expected that land uses around the ponds would directly affect the regional pool of bird species, and

391   consequently the number of bird species using small ponds. Drinking troughs were mainly situated in

392   mature forests with small scattered patches of extensive tree crops. On a global scale, forest and

393   agroforest areas have been shown to support more bird species than agricultural landscapes (Sekercioglu,

394   2012). This pattern is explained by the high food availability (both fleshy fruits and insects) and complex

395   vegetation of mature forests (Waltert et al., 2004), factors which promote the occurrence of high diversity

396   of insectivorous and frugivorous bird species. Moreover, mature forests and tree plantations provide

397   suitable sites for nesting and roosting, as well as microclimatic refugia for several bird species

398   (Sekercioglu, 2007). Therefore, within-pond heterogeneity and land-uses patterns may act synergistically

399   in favour of drinking troughs for promoting the use by high terrestrial bird diversity, but further studies

400   are needed to assess this relationship. The lower bird richness recorded at cattle ponds may be explained

401   by the fact that cereal farming was the dominant land use type around these ponds, thus promoting the

402   occurrence of a species-poor and highly specialized community dominated by granivorous birds such as

403   larks or sparrows (Mahiga et al., 2019; Vaccaro et al., 2019). This pattern is attributed to the great

404   amounts of weed seeds and other food-grain resources provided by cereal crops for granivorous species

405   (Ndang'ang'a et al., 2013). Moreover, cattle ponds often show a non-vegetated open pond shoreline, thus

406   precluding pond use by foliage gleaners, as highlighted by the fact that species from Sylviidae and

407   Phylloscopidae families were poorly detected (or even undetected) at cattle ponds (Fig. S1, Supporting

408   Information).

409

410   Understanding how species richness differs among pond types can provide useful information for

411   improving the effectiveness of management strategies; for instance, by prioritizing conservation actions in

412   those kinds of pond supporting greater species diversity or those considered to have a rarity value. Global

413   conservation priorities are frequently based on bird endemisms or taxonomic uniqueness (among others)

414   rather than species diversity, since richness is generally driven by common and widespread species

415   (Brooks et al., 2006). In our case, drinking troughs were visited by a visibly higher number of bird species

416   than the other pond types, pointing to their greater potential for maintaining more diverse bird

417   communities. Interestingly, however, cattle ponds were visited by more exclusive species than the other

418   two pond types and most observations corresponded with species of conservation concern or threatened

419   taxa, such as calandra lark (*Melanocorypha calandra* L., 1766), greater short-toed lark (*Calandrella*

420   *brachydactyla* Leisler, 1814), lesser kestrel (*Falco naumanni* Fleischer, 1818) and black-bellied

421   sandgrouse (*Pterocles orientalis* (L., 1758)), all listed in the European Birds Directive (2009/14/CE), and

422   the locally endangered lesser short-toed lark (*Alaudala rufescens* (Veillot, 1820)) (Robledano, 2006). This

423   can be explained by the fact that cattle ponds are placed in steppe areas, which are considered among the

424   most threatened habitats in Europe, and leading to the poor conservation status of steppe birds (Burfield,

425   2005; Traba & Morales, 2019). Therefore, pond conservation and management priorities must consider

426   the importance of these small isolated habitats for supporting both bird richness and threatened species

427   (Davies et al., 2016; Lewis-Phillips et al., 2019a), and ensure the long-term protection of most species-

428   rich pond sites, but especially those that contribute to protecting threatened species. This conservation

429   goal can only be attained through the promotion of different pond types at regional scale (Oertli, 2018;

430   Zamora-Marín et al., 2021a), ensuring the continued presence of a wide variety of ponds with different

431   features that provide complementary ecological services. In this context, the potential role of some

432   management practices for game species (i.e. providing water points) should be considered because they

433   may also benefit threatened bird species (Estrada et al., 2015). In addition to the contributions of ponds to

434 biodiversity, their social and cultural values cannot be overlooked because of most traditional ponds in

435 the study area appear in association to livestock trials, which promote also landscape connectivity for

436 wildlife.

437

438 Here, EH was measured as the evenness of four types of land use in a 1-km radius around ponds. As

439 expected, EH showed a positive relation with bird richness. EH has been shown to be among the main

440 drivers of species richness for different biotic groups around the world (Qian & Kissling, 2010; Stein et

441 al., 2014), with particularly positive effects in the case of bird diversity (Lorenzón et al., 2016; Hung-

442 ming et al., 2020). This general pattern is related to the niche-based hypothesis, which states that different

443 species are associated with different habitat types (Hutchings et al., 2000). In our study, some habitat

444 specialist species were related to large habitat patches dominated by a single type of land use (e. g.

445 *Periparus ater* (L. 1758) and *Regulus ignicapilla* (Temminck, 1820)in woodlands; *Melanocorypha*

446 *calandra* and *Alaudala rufescens* in grasslands). Thus, a high EH around the study ponds indicates a

447 balanced proportion of the four land use types, which can promote the occurrence of high number of

448 habitat-specialist species when required habitat appears in a sufficiently large extension. However, other

449 ecological processes may also contribute to the high species richness as a result of the selection of

450 heterogeneous sites by individual species. For instance, some bird species show wide ecological

451 requirements and often need to use different habitat types simultaneously in order to meet their daily

452 requirements and tasks (i.e. roosting, feeding or nesting) (Camacho et al., 2014). This relationship stems

453 from the fact that a combination of habitat types can provide more resources for wildlife (Tews et al.,

454 2004) from different origins, thus complementing each other and allowing the coexistence of a wide

455 variety of species.

456 Finally, no clear effects of mean annual precipitation were observed on bird species richness. This

457 ambiguous relationship between precipitation and bird richness was also seem in an earlier study in the

458 same region (Jiménez-Franco *et al.*, 2019). However, precipitation has been widely shown to positively

459 influence bird richness in many places in the world (Cueto & De Casenave, 1999; Qian & Kissling, 2010;

460 Duclos et al., 2019), mainly through the increase in plant diversity, which ultimately implies more food

461 resources for birds (Rompré et al., 2007). Climate predictors of species richness are often believed to be

462 stronger at broader spatial scales (Field et al., 2009), so the relatively small size of our study area might

463 be masking the true effects of precipitation on bird richness. Indeed, the above-mentioned studies

464 supporting the precipitation-richness relationship were conducted in large regions (often at country or

465 continental scale).

466

467 In this study, we have applied a hierarchical approach, which is considered particularly useful for diverse

468 communities (Zipkin et al., 2010). This multi-species occupancy model integrates information from all

469 the sites surveyed, while accounting for the imperfect detection of species. This yields species-specific

470 occupancy probabilities, thus providing valuable information for monitoring program design. Similarly,

471 the model provides estimates of true species richness for each sampling site, enabling inferences about

472 richness distribution to be made for different habitat types. Indeed, the accurate estimation of total species

473 richness is considered to be extremely important for making conservation, management and policy

474 decisions (Guillera-Arroita et al., 2019). As recently reported, the potential contribution of farm ponds to

475 terrestrial wildlife has been greatly undervalued in conservation and management strategies (Lewis-

476 Phillips et al., 2019b). Even though small waterbodies are believed to provide key ecological services to

477 terrestrial biodiversity (Céréghino et al., 2014; Biggs et al., 2016), the contribution of these isolated

478 freshwater habitats to several non-aquatic animal groups remains largely unexplored and these cross-

479 system services have been rarely addressed in pond literature. According to our results, small ponds can

480 provide important ecological services for terrestrial bird communities, in addition to their role in

481 supporting freshwater biodiversity (Oertli, 2018). Two thirds of the breeding bird species inhabiting the

482 study area were observed using ponds. Thus, since birds are involved in several key services like pest

483 control, pollination and seed dispersal (Sekercioglu, 2006), small ponds can really act as critical habitats

484 at landscape scale for bird conservation and ecosystem functioning. Indeed, the installation of artificial

485 drinking troughs has been proven as a successful management tool for promoting the frugivore-mediated

486 restoration of old fields (e.g. abandoned lands) by attracting terrestrial birds in semiarid regions (García-

487 Castellanos et al., 2016; Martínez-López et al., 2019). The study ponds were visited by a representative

488 set of the local breeding bird communities inhabiting the landscape where the ponds were sited,

489 highlighting the potential of these small isolated freshwater habitats to provide services for terrestrial

490 birds, mainly related to drinking water provision or bath-related plumage care. These findings should

491 provide information on pond management strategies to effectively protect the ecological integrity of these

492 small isolated freshwater habitats, especially bearing in mind the wide variety of ecological services they

493 provide. Further studies are needed to explore the contribution of small ponds to the local bird species

494   pool with a focus on assessing their importance at community level, as well as to quantify and assess the

495   ecological services they provide for terrestrial birds.

496

507

508   **Author contributions**

509   J.M.Z.-M., J.F.C. and F.J.O.-P. conceived and supervised the entire study. J.M.Z.-M., A.Z.-L. and J.F.C. performed

510   the fieldwork. M.V.J.F. and J.F.C. conducted the statistical analysis. J.M.Z.-M. and M.V.J.F. wrote a first version of

511   manuscript. All authors reviewed and contributed to the manuscript, as well as approved the final version. The

512   authors declare no conflict of interest.

513

514   **Data availability**

515   The data that support the findings of this study are available from the corresponding author upon reasonable request.

516

517   **Conflict of interest**

518   The authors declare that they have no conflict of interest.

519

520   **References**

521   Abdu, S., A. T. K. Lee, & S. J. Cunningham, 2018. The presence of artificial water points structures an

522   arid-zone avian community over small spatial scales. Ostrich 89: 339–346.

523   Abellán, P., D. Sanchéz-Fernández, A. Millán, F. Botella, J. A. Sánchez-Zapata, & A. Giménez, 2006.

524   Irrigation pools as macroinvertebrate habitat in a semi-arid agricultural landscape (SE Spain). Journal of

525   Arid Environments 67: 255–269.

526   Akasaka, M., & N. Takamura, 2012. Hydrologic connection between ponds positively affects macrophyte

527   alpha and gamma diversity but negatively affects beta diversity. Ecology 93: 967–973.

528   Allen, D., H. Bateman, P. Warren, F. Suzart de Albuquerque, S. Arnett-Romero, & B. Harding, 2019.

529   Long-term effects of land-use change on bird communities depend on spatial scale and land-use type.

530   Ecosphere 10: e02952.

531   Armas, C., J. D. Miranda, F. M. Padilla, & F. I. Pugnaire, 2011. Special issue: The Iberian Southeast.

532   Journal of Arid Environments 75: 1241–1243.

533   Arntzen, J. W., C. Abrahams, W. R. M. Meilink, R. Iosif, & A. Zuiderwijk, 2017. Amphibian decline,

534   pond loss and reduced population connectivity under agricultural intensification over a 38 year period.

535   Biodiversity and Conservation 26: 1411–1430.

536   Bain, M. B., & N. J. Stevenson, 1999. Aquatic habitat assessment: common methods. American Fisheries

537   Society, Bethesda, Maryland.

538   Balian, E. V., H. Segers, C. Lévêque, & K. Martens, 2008. The freshwater animal diversity assessment:

539   an overview of the results. Hydrobiologia 595: 627–663.

540   Ballester-Sabater, R., M. Vidal-Abarca, M. Esteve-Selma, & M. Suárez-Alonso, 2003. Humedales y

541   ramblas de la Región de Murcia. Comunidad Autónoma de la Región de Murcia, Murcia, Spain.

542   Biggs, J., S. von Fumetti, & M. Kelly-Quinn, 2016. The importance of small waterbodies for biodiversity

543   and ecosystem services: implications for policy makers. Hydrobiologia 793: 3–39.

544   Bock, C. E., 2015. Abundance and variety of birds associated with point sources of water in southwestern

545   New Mexico, U. S. A. Journal of Arid Environments 116: 53–56.

546   Brooks, S. P., & A. Gelman, 1998. General methods for monitoring convergence of iterative simulations.

547   Journal of Computational and Graphical Statistics 7: 434–455.

548   Brooks, T. M., R. A. Mittermeier, G. A. B. Da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G.

549   Mittermeier, J. D. Pilgrim, & A. S. L. Rodrigues, 2006. Global biodiversity conservation priorities.

550   Science 313: 58–61.

551   Bubíková, K., & R. Hrivnák, 2018. Artificial ponds in Central Europe do not fall behind the natural ponds

552   in terms of macrophyte diversity. Knowledge and Management of Aquatic Ecosystems 419: 1–10.

553   Buono, V., A. M. Bissattini, & L. Vignoli, 2019. Can a cow save a newt? The role of cattle drinking

554   troughs in amphibian conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 29: 964–

555   975, https://doi.org/10.1002/aqc.3126.

556   Burfield, I. J., 2005. The conservation status of steppic birds in Europe. In Bota, G., M. B. Morales, S.

Mañosa, & J. Camprodon (eds), Ecology and Conservation of Steppe-land Birds. Lynx Editcions: 119–140.

Calvo, J. F., A. J. Hernández-navarro, F. Robledano, M. Á. Esteve, G. Ballesteros, A. Fuentes, F. A. García-castellanos, C. González-revelles, Á. Guardiola, V. Hernández, R. Howard, J. E. Martínez, A. Zamora-López, & J. M. Zamora-Marín, 2017. Catálogo de las aves de la Región de Murcia (España). Anales de Biología 39: 7–33.

Camacho, C., S. Palacios, P. Sáez, S. Sánchez, & J. Potti, 2014. Human-induced changes in landscape configuration influence individual movement routines: Lessons from a versatile, highly mobile species. PLoS ONE 9: 1–9.

Céréghino, R., J. Biggs, B. Oertli, & S. Declerck, 2008. The ecology of European ponds: Defining the characteristics of a neglected freshwater habitat. Hydrobiologia 597: 1–6.

Céréghino, R., D. Boix, H. M. Cauchie, K. Martens, & B. Oertli, 2014. The ecological role of ponds in a changing world. Hydrobiologia 723: 1–6.

Cueto, V. R., & J. L. De Casenave, 1999. Determinants of bird species richness: Role of climate and vegetation structure at a regional scale. Journal of Biogeography 26: 487–492.

Davies, B., J. Biggs, P. Williams, M. Whitfield, P. Nicolet, D. Sear, S. Bray, & S. Maund, 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. Agriculture, Ecosystems and Environment 125: 1–8.

Davies, S. R., C. D. Sayer, H. Greaves, G. M. Siriwardena, & J. C. Axmacher, 2016. A new role for pond management in farmland bird conservation. Agriculture, Ecosystems and Environment 233: 179–191, http://dx.doi.org/10.1016/j.agee.2016.09.005.

De Meester, L., S. Declerck, R. Stoks, G. Louette, F. Van De Meutter, T. De Bie, E. Michels, & L. Brendonck, 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 715–725.

Declerck, S., T. De Bie, D. Ercken, H. Hampel, S. Schrijvers, J. Van Wichelen, V. Gillard, R. Mandiki, B. Losson, D. Bauwens, S. Keijers, W. Vyverman, B. Goddeeris, L. De meester, L. Brendonck, & K. Martens, 2006. Ecological characteristics of small farmland ponds: Associations with land use practices at multiple spatial scales. Biological Conservation 131: 523–532.

Della Bella, V., M. Bazzanti, M. G. Dowgiallo, & M. Iberite, 2008. Macrophyte diversity and physico-chemical characteristics of Tyrrhenian coast ponds in central Italy: Implications for conservation.

587   Hydrobiologia 597: 85–95.

588   Devarajan, K., T. L. Morelli, & S. Tenan, 2020. Multi-species occupancy models: review, roadmap, and

589   recommendations. Ecography 1–13.

590   Dirección General de Desarrollo Rural y Política, C., 2012. Cuarto Inventario Nacional Forestal: Región

591   de Murcia. Ministerio de Agriculgura, Alimentación y Medio Ambiente, Madrid.

592   Dorazio, R. M., & J. A. Royle, 2005. Estimating size and composition of biological communities by

593   modeling the occurrence of species. Journal of the American Statistical Association 100: 389–398.

594   Dorazio, R. M., J. A. Royle, B. Söderström, & A. Glimskär, 2006. Estimating species richness and

595   accumulation by modeling species occurrence and detectability. Ecology 87: 842–854.

596   Downing, J. A., 2010. Emerging global role of small lakes and ponds: little things mean a lot. Limnetica

597   29: 9–24.

598   Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P.

599   Kortelainen, N. F. Caraco, J. M. Melack, & J. J. Middelburg, 2006. Abundance and size distribution of

600   lakes, ponds and impoundments. Limnol. Oceanogr 51: 2388–2397.

601   Duclos, T. R., W. V. DeLuca, & D. I. King, 2019. Direct and indirect effects of climate on bird

602   abundance along elevation gradients in the Northern Appalachian mountains. Diversity and Distributions

603   25: 1670–1683, https://onlinelibrary.wiley.com/doi/abs/10.1111/ddi.12968.

604   Einoder, L. D., D. M. Southwell, J. J. Lahoz-Monfort, G. R. Gillespie, A. Fisher, & B. A. Wintle, 2018.

605   Occupancy and detectability modelling of vertebrates in northern Australia using multiple sampling

606   methods. PLoS ONE 13: 1–21.

607   Esteve, M. A., J. Martínez, I. Hernández, F. Robledano, M. A. Pérez, & L. F., 2015. Cambio climático y

608   biodiversidad en el contexto de la Región de Murcia In Victoria, F. (ed), Cambio climático en la Región

609   de Murcia. Evaluación basada en indicadores. Oficina de Impulso Socioeconómico del Medio, Murcia,

610   Spain: 105–132.

611   Estrada, A., M. Delibes-Mateos, J. Caro, J. Viñuela, S. Díaz-Fernández, F. Casas, & B. Arroyo, 2015.

612   Does small-game management benefit steppe birds of conservation concern? A field study in central

613   Spain. Animal Conservation 18: 567–575, http://doi.wiley.com/10.1111/acv.12211.

614   Faaborg, J., W. J. Arendt, & K. M. Dugger, 2004. Bird population studies in Puerto Rico using mist nets:

615   general patterns and comparisons with point counts. Studies in Avian Biology 29: 144–150.

616   Fait, P., E. Demierre, C. Ilg, & B. Oertli, 2020. Small mountain reservoirs in the Alps: new habitats for

617   alpine freshwater biodiversity?. Aquatic Conservation: Marine and Freshwater Ecosystems 1–14.

618   Ferreira, M., & P. Beja, 2013. Mediterranean amphibians and the loss of temporary ponds: Are there

619   alternative breeding habitats?. Biological Conservation 165: 179–186.

620   Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J.-F. Guégan, D. M. Kaufman,

621   J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, & J. R. G. Turner, 2009. Spatial species-

622   richness gradients across scales: a meta-analysis. Journal of Biogeography 36: 132–147,

623   http://doi.wiley.com/10.1111/j.1365-2699.2008.01963.x.

624   Florencio, M., C. Díaz-Paniagua, C. Gómez-Rodríguez, & L. Serrano, 2014. Biodiversity patterns in a

625   macroinvertebrate community of a temporary pond network. Insect Conservation and Diversity 7: 4–21.

626   García-Castellanos, F. A., F. Robledano-Aymerich, V. Zapata, V. Martínez-López, & G. González-

627   Barberá, 2016. Bebederos de aves: dinámica de uso y función en la dispersión ornitócora. Revista de

628   Anillamiento 35: 55–63.

629   Garrido, R., J. E. Palenzuela, & L. M. Bañón, 2013. Atlas Climático de la Región de Murcia. Agencia

630   Estatal de Meteorología.

631   Gómez-Rodríguez, C., C. Díaz-Paniagua, L. Serrano, M. Florencio, & A. Portheault, 2009. Mediterranean

632   temporary ponds as amphibian breeding habitats: The importance of preserving pond networks. Aquatic

633   Ecology 43: 1179–1191.

634   Guillaumet, A., P. A. Crochet, & B. Godelle, 2005. Phenotypic variation in Galerida larks in Morocco:

635   the role of history and natural selection. Molecular Ecology 14: 3809–3821,

636   http://doi.wiley.com/10.1111/j.1365-294X.2005.02696.x.

637   Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under

638   imperfect detection: advances, challenges and opportunities. Ecography 40: 281–295.

639   Guillera-Arroita, G., M. Kéry, & J. J. Lahoz-Monfort, 2019. Inferring species richness using multispecies

640   occupancy modeling: Estimation performance and interpretation. Ecology and Evolution 9: 780–792,

641   https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.4821.

642   Harper, L. R., L. Lawson Handley, A. I. Carpenter, M. Ghazali, C. Di Muri, C. J. Macgregor, T. W.

643   Logan, A. Law, T. Breithaupt, D. S. Read, A. D. McDevitt, & B. Hänfling, 2019. Environmental DNA

644   (eDNA) metabarcoding of pond water as a tool to survey conservation and management priority

645   mammals. Biological Conservation 238: 108225,

646   https://linkinghub.elsevier.com/retrieve/pii/S000632071930847X.

647 Hill, M. J., D. B. Ryves, J. C. White, & P. J. Wood, 2016. Macroinvertebrate diversity in urban and rural

648 ponds: Implications for freshwater biodiversity conservation. Biological Conservation 201: 50–59,

649 http://dx.doi.org/10.1016/j.biocon.2016.06.027.

650 Hung-ming, T., F. Meng-Wen, & K. Jerome Chie-Jen, 2020. Different habitat types affect bird richness

651 and evenness. Scientific Reports 10: 1221.

652 Hutchings, M. J., E. A. John, & J. A. Stewart, 2000. The ecological consequences of environmental

653 heterogeneity. Blackwell Science, Oxford, UK.

654 Ilg, C., & B. Oertli, 2014. How can we conserve cold stenotherm communities in warming Alpine

655 ponds?. Hydrobiologia 723: 53–62.

656 Jarzyna, M. A., & W. Jetz, 2016. Detecting the multiple facets of biodiversity. Trends in Ecology and

657 Evolution 31: 527–538, http://dx.doi.org/10.1016/j.tree.2016.04.002.

658 Jiménez-Franco, M. V., M. Kéry, M. León-Ortega, F. Robledano, M. A. Esteve, & J. F. Calvo, 2019. Use

659 of classical bird census transects as spatial replicates for hierarchical modeling of an avian community.

660 Ecology and Evolution 9: 825–835.

661 Kellner, K., 2015. jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses. R Package

662 Version1.3.7. Retrieved from http://CRAN.Rproject. org/package=jagsUI. .

663 Kéry, M., & J. A. Royle, 2008. Hierarchical Bayes estimation of species richness and occupancy in

664 spatially replicated surveys. Journal of Applied Ecology 45: 589–598.

665 Kéry, M., & J. A. Royle, 2016. Applied hierarchical modeling in ecology: Analysis of distribution,

666 abundance and species richness in R and BUGS: Volume 1: Prelude and static models. Cambridge, MA:

667 Academic Press.

668 Kéry, M., J. A. Royle, M. Plattner, & R. M. Dorazio, 2009. Species richness and occupancy estimation in

669 communities subject to temporary emigration. Ecology 90: 1279–1290.

670 Kéry, M., & B. Schmidt, 2008. Imperfect detection and its consequences for monitoring for conservation.

671 Community Ecology 9: 207–216.

672 Lee, A. T. K., D. Wright, & P. Barnard, 2017. Hot bird drinking patterns: drivers of water visitation in a

673 fynbos bird community. African Journal of Ecology 55: 541–553.

674 Lehner, B., & P. Döll, 2004. Development and validation of a global database of lakes, reservoirs and

675 wetlands. Journal of Hydrology 296: 1–22.

676 Lemmens, P., J. Mergeay, T. de Bie, J. Van Wichelen, L. de Meester, & S. A. J. Declerck, 2013. How to

677   maximally support local and regional biodiversity in applied conservation? Insights from pond

678   management. PLoS ONE 8: 1–13.

679   Lewis-Phillips, J., S. J. Brooks, C. D. Sayer, R. McCrea, G. Siriwardena, H. Robson, A. L. Harrison, & J.

680   C. Axmacher, 2019a. Seasonal benefits of farmland pond management for birds. Bird Study 66: 342–352,

681   https://doi.org/10.1080/00063657.2019.1688762.

682   Lewis-Phillips, J., S. J. Brooks, C. D. Sayer, I. R. Patmore, G. M. Hilton, A. Harrison, H. Robson, & J. C.

683   Axmacher, 2020. Ponds as insect chimneys: Restoring overgrown farmland ponds benefits birds through

684   elevated productivity of emerging aquatic insects. Biological Conservation 241: 108253.

685   Lewis-Phillips, J., S. Brooks, C. D. Sayer, R. McCrea, G. Siriwardena, & J. C. Axmacher, 2019b. Pond

686   management enhances the local abundance and species richness of farmland bird communities.

687   Agriculture, Ecosystems and Environment 273: 130–140.

688   Lisón, F., & J. F. Calvo, 2014. Bat activity over small ponds in dry Mediterranean forests: implications

689   for conservation. Acta Chiropterologica 16: 95–101,

690   http://www.bioone.org/doi/abs/10.3161/150811014X683309.

691   López Bermúdez, F., J. M. Quiñonero Rubio, R. García Marín, E. Martín de Valsameda Guijarro, C.

692   Sánchez Fuster, C. Chocano Vañó, & F. Guerero García, 2016. Fuentes y manantiales de la cuenca del

693   Segura: Región de Murcia. Fundación Instituto Euromediterráneo del Agua, Murcia (España).

694   Lorenzón, R. E., A. H. Beltzer, P. F. Olguin, & A. L. Ronchi-Virgolini, 2016. Habitat heterogeneity

695   drives bird species richness, nestedness and habitat selection by individual species in fluvial wetlands of

696   the Paraná River, Argentina. Austral Ecology 41: 829–841.

697   Lynch, J. F., 1989. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, I: general

698   patterns of occurrence. The Condor 91: 515, http://www.jstor.org/stable/1368104?origin=crossref.

699   Lynn, J. C., S. S. Rosenstock, & C. L. Chambers, 2008. Avian use of desert wildlife water developments

700   as determined by remote videography. Western North American Naturalist 68: 107–112.

701   Machado, M. J., G. Benito, M. Barriendos, & F. S. Rodrigo, 2011. 500 Years of rainfall variability and

702   extreme hydrological events in southeastern Spain drylands. Journal of Arid Environments 75: 1244–

703   1253.

704   MacKenzie, D. I., & L. L. Bailey, 2004. Assessing the fit of site-occupancy models. Journal of

705   Agricultural, Biological, and Environmental Statistics 9: 300–318.

706   MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, & J. E. Hines, 2006. Occupancy

707   estimation and modeling: inferring patterns and dynamycs of species occurence. Academic Press.

708   MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, & L. L. Bailey, 2005. Improving inferences in

709   population studies of rare species that are detected imperfectly. Ecology 86: 1101–1113.

710   MacKenzie, D., J. Nichols, & G. Lachman, 2002. Estimating site occupancy rates when detection

711   probabilities are less than one. Ecology 83: 2248–2255.

712   Mahiga, S. N., P. Webala, M. J. Mware, & P. K. Ndang'ang'a, 2019. Influence of land-use type on forest

713   bird community composition in Mount Kenya Forest. International Journal of Ecology 2019: 1–8,

714   https://www.hindawi.com/journals/ijecol/2019/8248270/.

715   Maphisa, D. H., H. Smit-Robinson, & R. Altwegg, 2019. Dynamic multi-species occupancy models

716   reveal individualistic habitat preferences in a high-altitude grassland bird community. PeerJ 7: e6276,

717   https://peerj.com/articles/6276.

718   Martínez-López, V., V. Zapata, P. De la Rúa, & F. Robledano, 2019. Uncovering mechanisms of bird

719   seed dispersal in semiarid environments to help to restore them. Ecosphere 10: 1–12.

720   Morganti, M., G. Assandri, J. I. Aguirre, Á. Ramirez, M. Caffi, & F. Pulido, 2017. How residents behave:

721   home range flexibility and dominance over migrants in a Mediterranean passerine. Animal Behaviour

722   123: 293–304, https://linkinghub.elsevier.com/retrieve/pii/S0003347216302706.

723   Ndang'ang'a, P. K., J. B. Njoroge, & M. Githiru, 2013. Vegetation composition and structure influences

724   bird species community assemblages in the highland agricultural landscape of Nyandarua, Kenya. Ostrich

725   84: 171–179, https://www.tandfonline.com/doi/full/10.2989/00306525.2013.860929.

726   Oertli, B., 2018. Freshwater biodiversity conservation: The role of artificial ponds in the 21st century.

727   Aquatic Conservation: Marine and Freshwater Ecosystems 28: 264–269,

728   https://doi.org/10.1002/aqc.2902.

729   Oertli, B., J. Biggs, R. Cereghino, S. Declerck, A. Hull, & M. R. Miracle, 2010. Pond conservation in

730   Europe. Springer, Dordrecht, the Netherlands.

731   Oertli, B., J. Biggs, R. Céréghino, P. Grillas, P. Joly, & J. B. Lachavanne, 2005. Conservation and

732   monitoring of pond biodiversity: Introduction. Aquatic Conservation: Marine and Freshwater Ecosystems

733   15: 535–540.

734   Oertli, B., R. Céréghino, A. Hull, & R. Miracle, 2009. Pond conservation: From science to practice.

735   Hydrobiologia 634: 1–9.

736   Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

737   In K. Hornik, F. Leisch, & A. Zeileis (Eds.), Proceedings of the 3rd International Workshop in

738   Distributed Statistical Computing (DSC 2003) Vienna, Austria: 20-22 pages.

739   Poulin, B., G. Lefebvre, & P. Pilard, 2000. Quantifying the breeding assemblage of reedbed passerines

740   with mist-net and point-count surveys. Journal of Field Ornithology 71: 443–454,

741   http://www.jstor.org/stable/4514507.

742   Qian, H., & W. D. Kissling, 2010. Spatial scale and cross-taxon congruence of terrestrial vertebrate and

743   vascular plant species richness in China. Ecology 91: 1172–1183, http://doi.wiley.com/10.1890/09-

744   0620.1.

745   R Core Team, 2016. R: A language and environment for statistical computing. Vienna, Austria: R

746   Foundation for Statistical Computing. Retrieved from https://www.R-project.org/. .

747   Razgour, O., C. Korine, & D. Saltz, 2010. Pond characteristics as determinants of species diversity and

748   community composition in desert bats. Animal Conservation 13: 505–513.

749   Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J.

750   MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D.

751   Dudgeon, & S. J. Cooke, 2019. Emerging threats and persistent conservation challenges for freshwater

752   biodiversity. Biological Reviews 94: 849–873.

753   Rigby, E. A., & D. H. Johnson, 2019. Factors affecting detection probability, effective area surveyed, and

754   species misidentification in grassland bird point counts. The Condor 121: 1–10.

755   Robledano, F., 2006. Libro rojo de los vertebrados de la Región de Murcia. Dirreción General del Medio

756   Natural, Consejería de Industria y Medio Ambiente. Comunidad Autónoma de la Región de Murcia,

757   Murcia, Spain.

758   Roldano, A., 2002. On the ecology of home range in birds. Revue de Écologie 57: 53–73.

759   Rompré, G., W. D. Robinson, A. Desrochers, & G. Angehr, 2007. Environmental correlates of avian

760   diversity in lowland Panama rain forests. Journal of Biogeography 34: 802–815.

761   Rupérez-Moreno, C., J. Senent-Aparicio, D. Martinez-Vicente, J. L. García-Aróstegui, F. C. Calvo-

762   Rubio, & J. Pérez-Sánchez, 2017. Sustainability of irrigated agriculture with overexploited aquifers: The

763   case of Segura basin (SE, Spain). Agricultural Water Management 182: 67–76,

764   http://dx.doi.org/10.1016/j.agwat.2016.12.008.

765   Sánchez-Montoya, M. M., M. Moleón, J. A. Sánchez-Zapata, & K. Tockner, 2016. Dry riverbeds:

766   corridors for terrestrial vertebrates. Ecosphere 7:, https://onlinelibrary.wiley.com/doi/10.1002/ecs2.1508.

767   Sebastián-González, E., & A. Green, 2014. Habitat use by waterbirds in relation to pond size, water depth

768   and isolation: lessons from a restorarion in Southern Spain. Restoration Ecology 22: 311–318.

769   Sebastián-González, E., J. A. Sánchez-Zapata, & F. Botella, 2010. Agricultural ponds as alternative

770   habitat for waterbirds: Spatial and temporal patterns of abundance and management strategies. European

771   Journal of Wildlife Research 56: 11–20.

772   Sekercioglu, C. H., 2006. Increasing awareness of avian ecological function. Trends in Ecology and

773   Evolution 21: 464–471.

774   Sekercioglu, C. H., 2007. Conservation ecology: area trumps mobility in fragment bird extinctions.

775   Current Biology 17: R283–R286, https://linkinghub.elsevier.com/retrieve/pii/S0960982207009967.

776   Sekercioglu, C. H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests

777   and agricultural areas. Journal of Ornithology 153: 153–161.

778   Smit, B., 2013. Taking the heat: integrating behavioural and physiological variables to predict avian

779   responses to climate change in the Kalahari Desert. University of Pretoria.

780   Smit, B., S. Woodborne, B. O. Wolf, & A. E. McKechnie, 2019. Differences in the use of surface water

781   resources by desert birds are revealed using isotopic tracers. The Auk 136: 1–13.

782   Soininen, J., P. Bartels, J. Heino, M. Luoto, & H. Hillebrand, 2015. Towards more integrated ecosystem

783   research in aquatic and terrestrial environments. BioScience 65: 174–182.

784   Stein, A., K. Gerstner, & H. Kreft, 2014. Environmental heterogeneity as a universal driver of species

785   richness across taxa, biomes and spatial scales. Ecology Letters 17: 866–880.

786   Sutherland, K., M. Ndlovu, & A. Pérez-Rodríguez, 2018. Use of artificial waterholes by animals in the

787   southern region of the Kruger National Park, South Africa. African Journal of Wildlife Research 48: 1–

788   15.

789   Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, & F. Jeltsch, 2004. Animal

790   species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal

791   of Biogeography 31: 79–92, http://doi.wiley.com/10.1046/j.0305-0270.2003.00994.x.

792   Traba, J., & M. B. Morales, 2019. The decline of farmland birds in Spain is strongly associated to the loss

793   of fallowland. Scientific Reports 9: 9473, http://www.nature.com/articles/s41598-019-45854-0.

794   Vaccaro, A. S., J. Filloy, & M. I. Bellocq, 2019. What land use better preserves taxonomic and functional

795   diversity of birds in a grassland biome ?. 14: 1.

796   Valera, F., C. Díaz-Paniagua, J. A. Garrido-García, J. Manrique, J. M. Pleguezuelos, & F. Suárez, 2011.

797   History and adaptation stories of the vertebrate fauna of southern Spain semiarid habitats. Journal of Arid

798   Environments 75: 1342–1351, http://dx.doi.org/10.1016/j.jaridenv.2011.05.004.

799   Verdiell-Cubedo, D., 2012. Inventario y estado de conservación de las charcas ganaderas en la Región de

800   Murcia (SE Península Ibérica). Anales de Biología 34: 1–8.

801   Votto, S. E., F. J. Dyer, V. Caron, & J. A. Davis, 2020. Thermally-driven thresholds in terrestrial avifauna

802   waterhole visitation indicate vulnerability to a warming climate. Journal of Arid Environments 181:

803   104217, https://doi.org/10.1016/j.jaridenv.2020.104217.

804   Waltert, M., A. Mardiastuti, & M. Mühlenberg, 2004. Effects of land use on bird species richness in

805   Sulawesi, Indonesia. Conservation Biology 15: 1339–1346.

806   Walton, R. E., C. D. Sayer, H. Bennion, & J. C. Axmacher, 2020. Open-canopy ponds benefit diurnal

807   pollinator communities in an agricultural landscape: implications for farmland pond management. Insect

808   Conservation and Diversity .

809   Whitman, A. A., J. M. Hagan, & N. V. L. Brokaw, 1997. A comparison of two bird survey techniques

810   used in a subtropical forest. The Condor 99: 955–965.

811   Whittingham, M. J., & K. L. Evans, 2004. The effects of habitat structure on predation risk of birds in

812   agricultural landscapes. Ibis 146: 210–220, http://doi.wiley.com/10.1111/j.1474-919X.2004.00370.x.

813   Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet, & D. Sear, 2004. Comparative

814   biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England.

815   Biological Conservation 115: 329–341.

816   Zamora-Marín, J. M., C. Ilg, E. Demierre, N. Bonnet, A. Wezel, J. Robin, D. Vallod, J. F. Calvo, F. J.

817   Oliva-Paterna, & B. Oertli, 2021a. Contribution of artificial waterbodies to biodiversity: A glass half

818   empty or half full?. Science of the Total Environment 753: 141987,

819   https://doi.org/10.1016/j.scitotenv.2020.141987.

820   Zamora-Marín, J. M., A. Zamora-López, J. F. Calvo, & F. J. Oliva-Paterna, 2021b. Comparing

821   detectability patterns of bird species in small ponds using multi-method occupancy modelling. Scientific

822   Reports 11: 22785.

823   Zipkin, E. F., J. Andrew Royle, D. K. Dawson, & S. Bates, 2010. Multi-species occurrence models to

824   evaluate the effects of conservation and management actions. Biological Conservation 143: 479–484,

825   http://dx.doi.org/10.1016/j.biocon.2009.11.016.

826   Zipkin, E. F., A. Dewan, & J. A. Royle, 2009. Impacts of forest fragmentation on species richness: A

827   hierarchical approach to community modelling. Journal of Applied Ecology 46: 815–822.

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829   **Electronic supplementary material**

830   The online version of this article contains supplementary material, which is available to authorized users.

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832

833   **Fig. 1**   Map of the study area and the location of the surveyed ponds. Coordinates are indicated as UTM

834   30S (metres). Elevation data and outline maps were obtained from public national data sources

835   (https://www.ign.es/web/cbg-area-cartografia). A representative picture of each pond type is provided

836   below: a) artificial pool; b) cattle pond; and c) drinking trough. Photo credits: José Manuel Zamora.
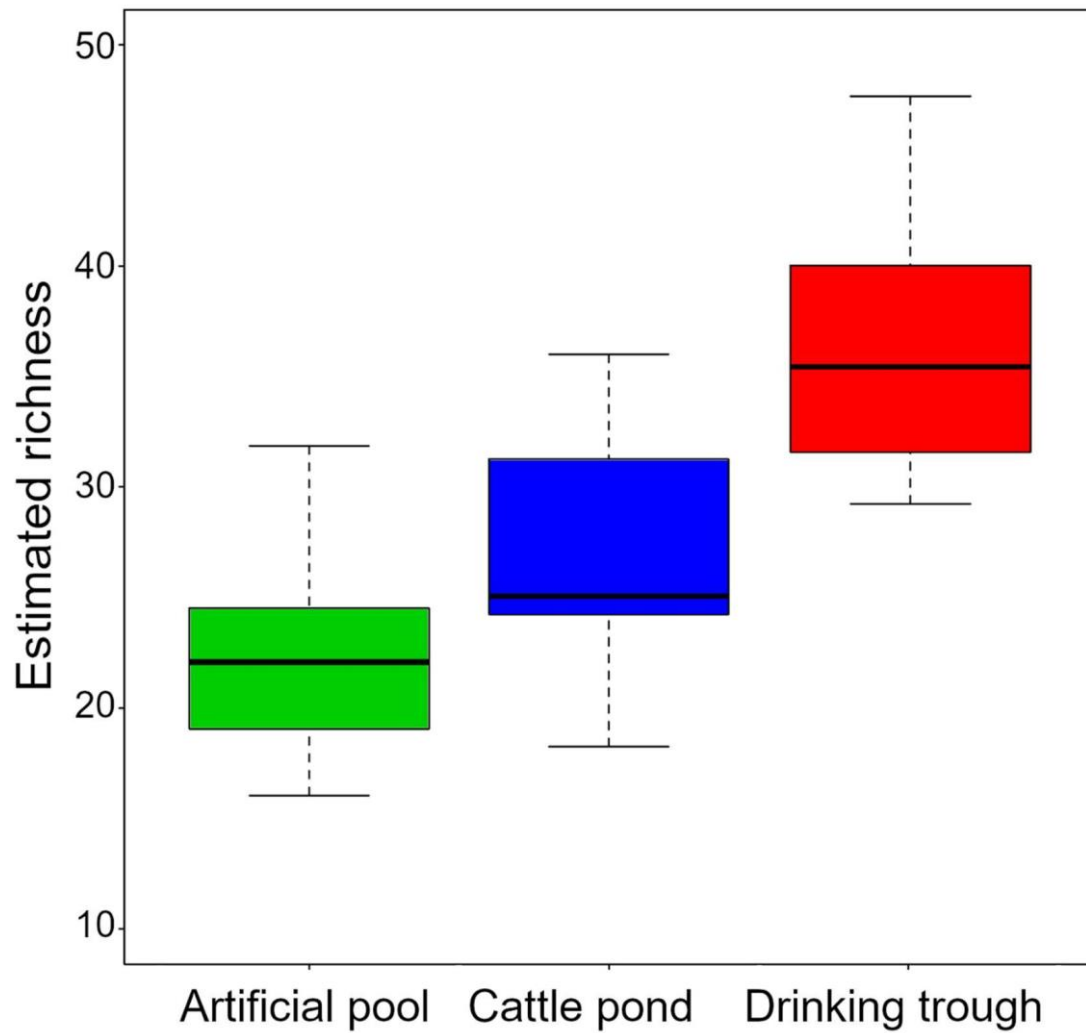
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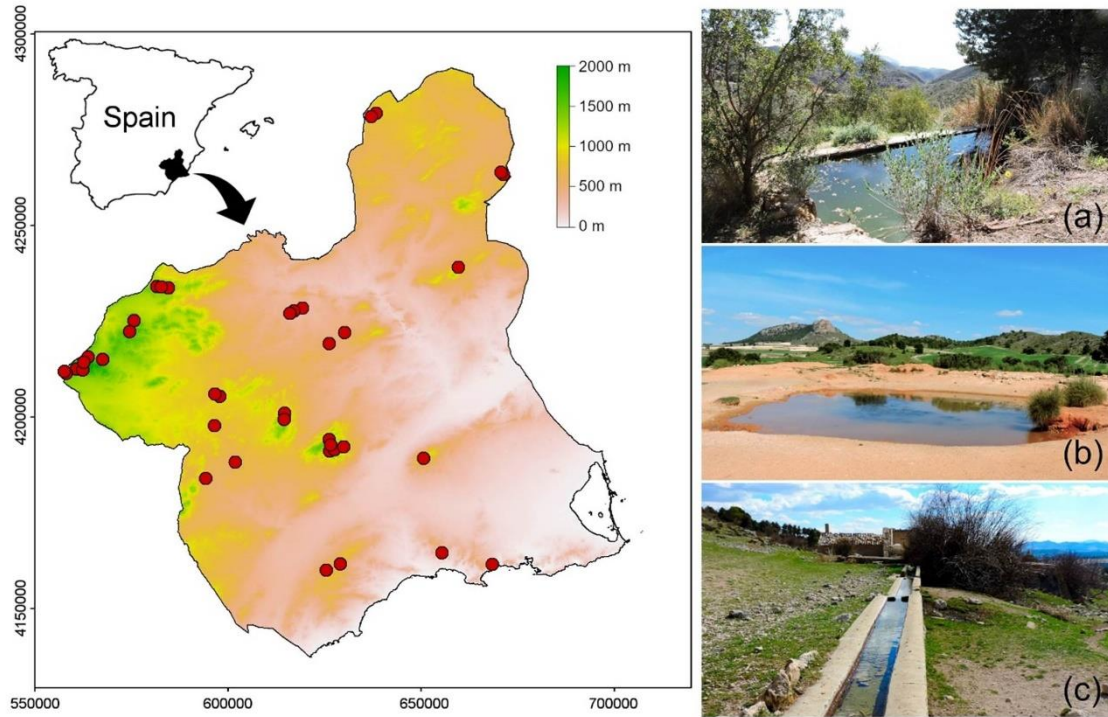
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840 **Fig. 2** Comparison of observed and estimated number of bird species in 39 ponds in the province of

841 Murcia, south-eastern Spain. Vertical lines represent 95% credible intervals.

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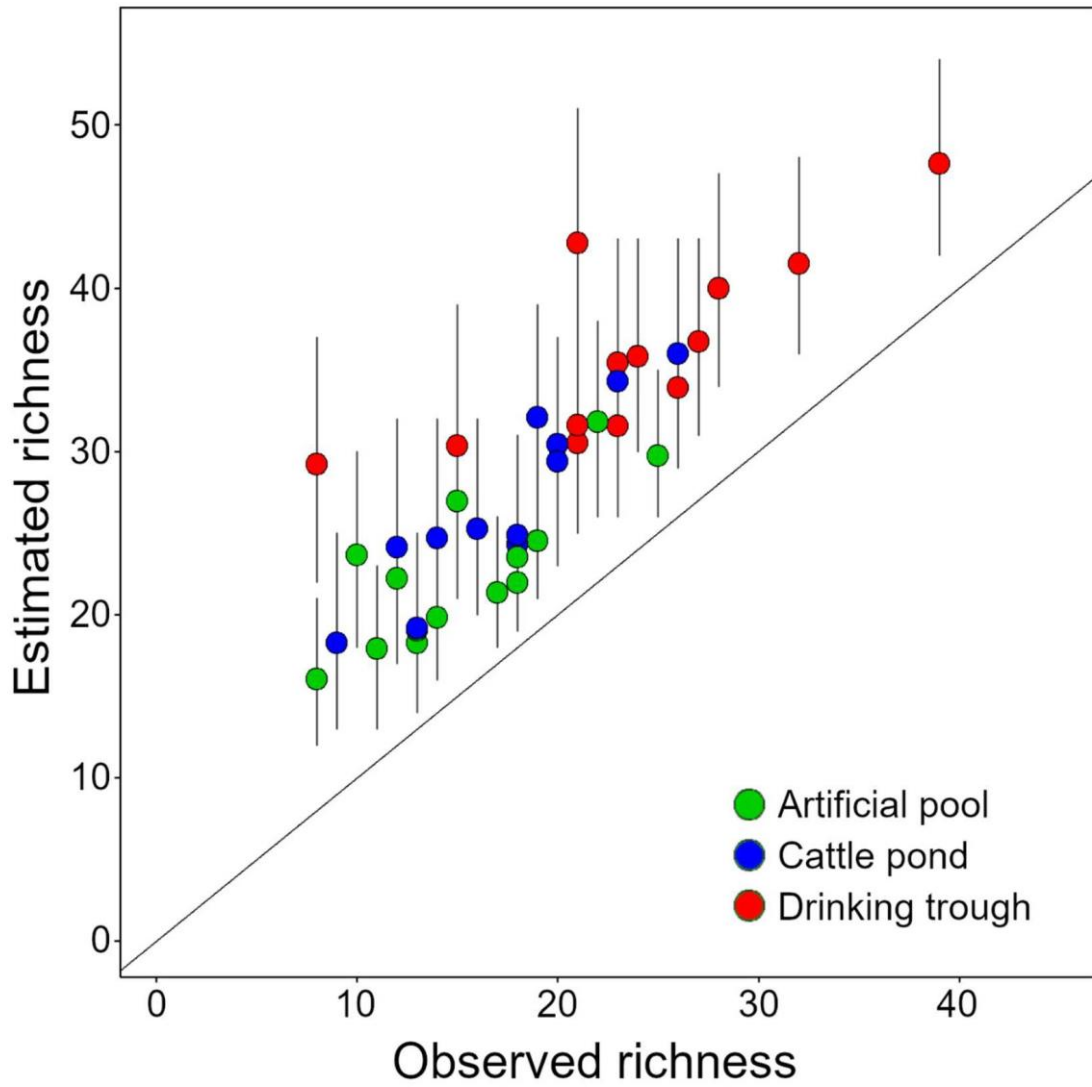
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845 **Fig. 3** Boxplots of estimated bird richness associated to the three investigated pond types in the

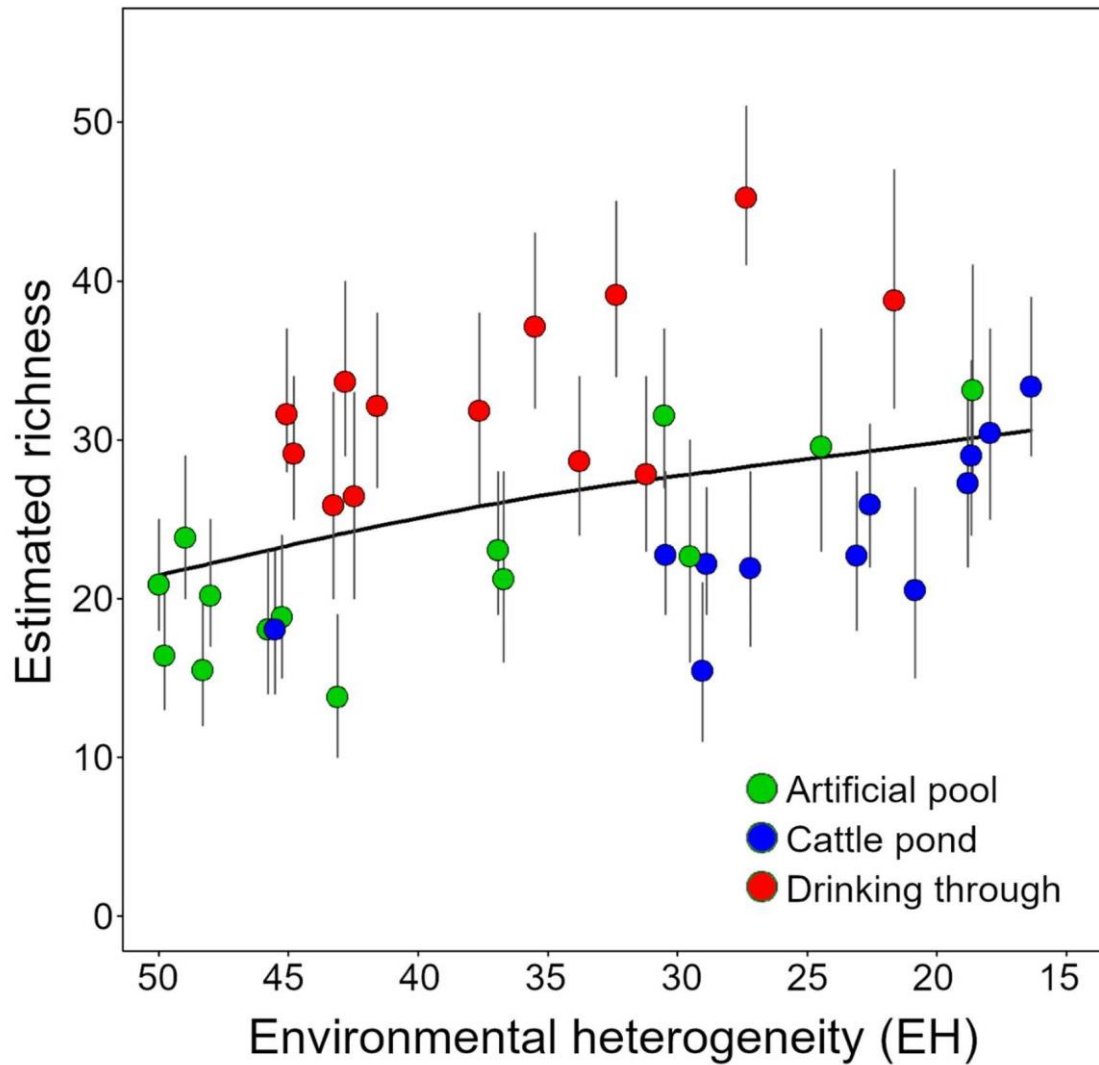846 province of Murcia, south-eastern Spain.
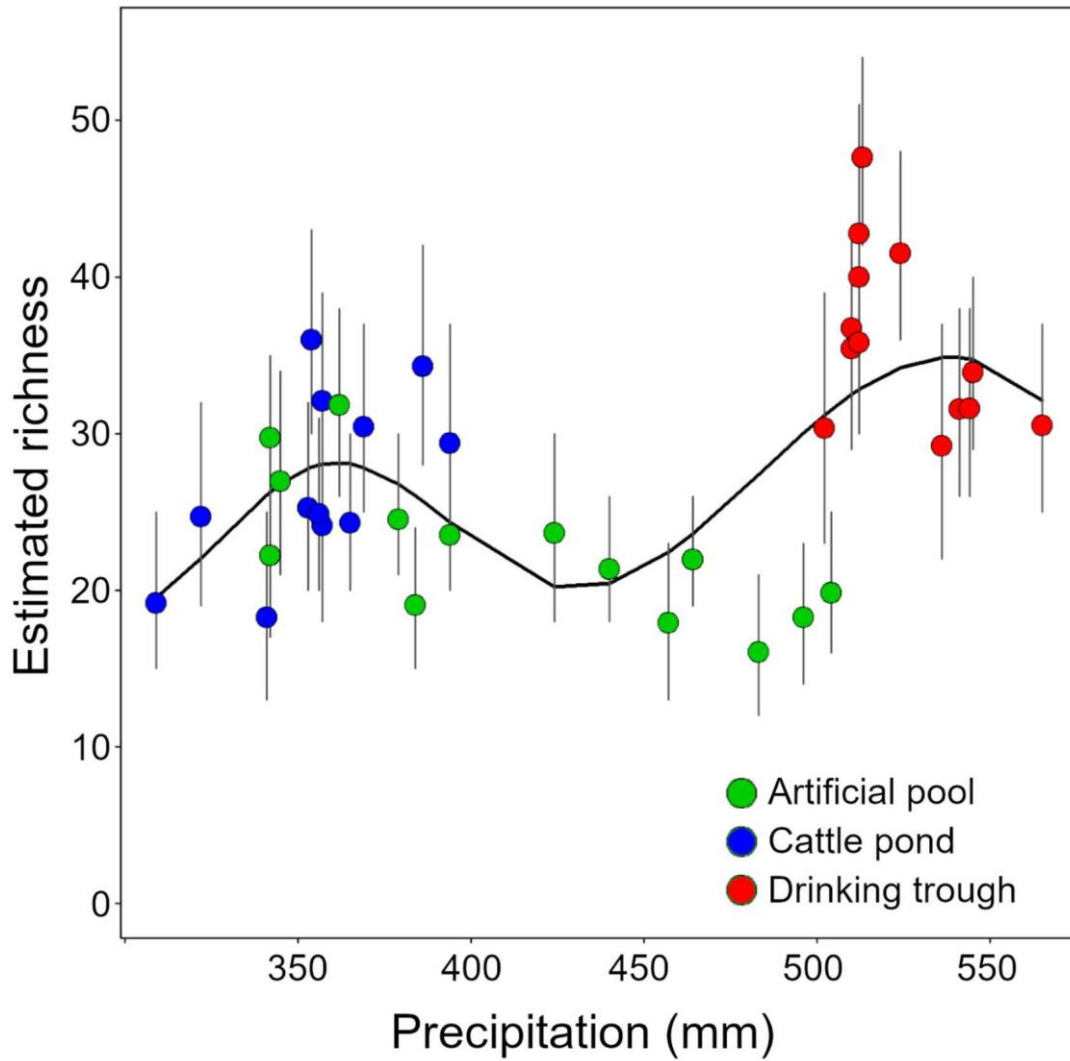
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849

850 **Fig. 4**   Relationship between the estimated number of bird species and the environmental heterogeneity

851   variable (EH) in 39 ponds in the province of Murcia, south-eastern Spain. Vertical lines represent 95%

852   credible intervals. The curve represents a cubic smoothing spline fitted to the data to show the general

853   trend. Note that low EH values indicate high environmental heterogeneity.

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857   **Fig. 5**   Relationship between the estimated number of bird species and the mean annual precipitation in

858   39 ponds in the province of Murcia, south-eastern Spain. Vertical lines represent 95% credible intervals.

859   The curve represents a cubic smoothing spline fitted to the data to show the general trend.

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