Predicting regional densities from bird occurrence data: validation and effects of species traits in a Macaronesian Island

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ABSTRACT

Aim Quantifying species abundances is costly, especially when many species are involved. To overcome this problem several studies have predicted local abundances (at the sample unit level) from species occurrence distribution models (SODM), with differences in predictive performance among studies. Surprisingly, the ability of SODM to predict regional abundances of an entire area of interest has never been tested, despite the fact that it is an essential parameter for species conservation and management. We tested whether local and regional abundances of 21 terrestrial bird species could be predicted from SODMs in an exhaustively surveyed island, and examined the variation explained by species-specific traits.

Location La Palma Island, Canary Islands.

Methods We firstly assessed two types of algorithms representing the two main families of SODMs. We built models using presence/absence (with boosted classification trees) and presence/background (with MaxEnt) data as a function of relevant environmental predictors, and tested their ability to predict the observed local abundances. The predicted probabilities of occurrence (P_i) were translated into animal numbers (n') using the revisited equation $n_i' = - ln (1-P_i)$, and we obtained regional abundances (for the whole island).

Results Predictive ability of presence/absence models was superior than that ofMaxEnt. At the regional level, the observed average densities of all species were highly predictable from occurrence probabilities (R^2=93.5%), without overall overestimation or underestimation. Interspecific variation in the accuracy of predicted regional density was largely explained (R^2=73%); with habitat breath and variation in local abundance being the traits of greatest importance.

Main conclusions Despite uncertainties associated with local predictions and the idiosyncrasies of each species, our procedures enabled us to predict regional abundances in an unbiased way. Our approach provides a cost-effective tool when a large number of species is involved. Furthermore, the influence of species-specific traits on the prediction accuracy provides insights into sampling designs for focal species.

Keywords

Biodiversity monitoring, species abundance, species distribution modelling, boosted classification trees, MaxEnt, birds, island biogeography.

INTRODUCTION

Organism abundance and richness are recognised as two of the most important components of biological diversity. Measures of species abundance for biodiversity assessments provide useful information, from aspects of population dynamics and biotic interactions to ecosystem functioning (e.g. Estes *et al.*, 1998; Yamamoto *et al.*, 2007). Moreover, human-mediated changes in biodiversity are detected more quickly using abundance measurements than accounting for other biodiversity components (Chapin *et al.*, 2000). However, quantifying species abundances is challenging because it is costly in terms of time, and human and economic resources. In contrast, the number of studies analyzing variables derived from species presences is becoming disproportionately higher than those making use of measures of abundance (Guisan & Thuiller, 2005; Rodríguez *et al.,* 2007). To overcome this problem several studies aimed to predict species abundance from Species Occurrence Distribution Models (SODMs; e.g., Conlisk *et al.*, 2009 and references therein). Thus, linking successfully distributional occurrence data with abundance through relevant factors should provide a useful tool since species presence data are easier to obtain, which opens the possibility of coordinating volunteer programs in field survey designs.

However, the extent to which SODM outputs are able to precisely predict local abundances or densities remains controversial (Pearce & Ferrier, 2001; Nielsen *et al.,* 2005; Jiménez-Valverde *et al.,* 2009; Estrada & Arroyo, 2012; Van Couwenberghe *et al.,* 2013; Thuiller *et al.,* 2014; Bean *et al.,* 2014; Yañez *et al.,* 2014; Russell *et al.,* 2015). Despite potential limitations of SODMs to account for local abundances (Pearce & Ferrier, 2001; Nielsen *et al.,* 2005), their ability to predict the total count of individuals in the whole study area (hereafter regional abundance) is unknown. When

59 the central limit theorem holds (Grinstead & Snell, 1997) local overpredictions and
60 underpredictions can be counteracted because they are randomly, and equally
61 distributed. In this case, regional abundances could be accurately predicted even in
62 cases of moderate ability of SODMs to predict local abundances.
63 Among the SODM types there are also differences regarding the difficulty of
64 obtaining distributional data, mainly depending on whether they makes use of
65 presence/absence or only true presences. Recording presence/absence data requires
66 greater survey effort than presence-only data since uncertainties associated with
67 absences are greater (Jiménez-Valverde *et al*., 2008). Moreover, part of the variability
68 regarding the ability of SODM to predict abundances might be influenced by whether or
69 not true absences are assumed (Nielsen *et al.,* 2005, VanDerWal *et al.,* 2009).
70 Therefore, elucidating the extent to which obtaining absence data merits additional
71 survey efforts needs to solve the trade-off between feasibility and effectiveness when
72 predicting abundances from SODMs. Comparisons between SODM outputs,
73 considering they include or not reliable absence data, may help to examine the
74 variability in the relationships between probability/suitability values and abundance
75 estimations.
76 In the same way, species-specific traits linked with natural history are also sources
77 of variability in model accuracy to predict species' distributions and abundances. This
78 interspecific variability limits the predictive power of modelling exercises, a limitation
79 that cannot be always overcome by mere statistical refinements (Seoane *et al.,* 2005).
80 Several studies have shown that ecological and natural history traits of species may
81 predict the errors in SODMs (Boone & Krohn, 1999; Kadmon *et al.,* 2003; Carrascal *et*
82 *al.,* 2006). For example, modelling success is inversely related to spatial variability

(mobility and nomadism) and niche breadth, although the observed patterns are not consistent across all biological groups (Pearce & Ferrier, 2000; Pearce *et al.,* 2001). Similar species-specific variations in modelling success have been found considering the positive effects of commonness, abundance and detectability (Boone & Krohn, 1999; Kadmon *et al.,* 2003). Therefore, the analysis of the association between species' biological traits and model accuracy is useful because if we know the effect of specific traits on modelling results, we can improve the sampling design for multi-species studies (Seoane *et al.,* 2005).

In this study we examined whether local and regional abundances of a group of terrestrial bird species can be predicted from SODMs in La Palma, a Macaronesian island in the Canary archipelago. An exhaustive field survey was carried out to record presence/absence data and abundances of twenty one bird species throughout a representative sample of transects encompassing the spatial and environmental range of the island. First, for each species we built distribution models for La Palma Island using presence/absence or presence/background data as a function of relevant environmental predictors. Second, we compared the ability of these two types of models to predict the observed local abundances of the studied bird species. Third, we used the type of SODM that derived better local predictions to obtain estimations of regional abundances. For this purpose SODM outputs were converted to abundances by means of a previously proposed and well founded procedure in the early seventies, the binomial sampling to estimate average densities (Gerrard & Chiang, 1970). This conversion has been rarely applied for organisms other than arthropods but merits further evaluation, because it does not require complex parameterizations. Our predictions of regional abundances were then evaluated using total number of birds

recorded in the field. Fourth, we performed an analysis including all species to elucidate species-specific traits that can potentially explain an inter-specific variation in the regional abundance estimations. To our knowledge this is the first time that the ability of SODM to predict species regional abundances has been examined.

METHODS

Study area

The study area is located in La Palma (28º42' N, 17º50' W; 706 km^2) a young (1-2 My) oceanic island of the Canary archipelago located 417 km from the African coast. It is a high island (2,426 m a.s.l.), with extensive areas with annual precipitation higher than 600 mm, and with a widespread representation of native shrublands and pine and evergreen '*laurisilva'* forests (although natural cover has been much reduced since humans occupied the islands: de Nascimento *et al.,* 2009). A considerable proportion of island area below 1,100 m a.s.l. has been highly transformed by agricultural activities and urban sprawl. See Juan *et al.* (2000) and Fernández-Palacios and Martín-Esquivel (2001) for more details on island characteristics.

Abundance estimations

Bird censuses, devoted to record presence/absence and abundance data, were carried out during the breeding season (April 2007). The survey method was the line transect, frequently used in extensive assessments of abundance, general distribution patterns and habitat preferences of birds (Bibby *et al.,* 2000). Fieldwork was designed as a broad-scale sampling for land birds. Thus, censuses were carried out across the whole island in

130 an attempt to sample the total range of vegetation types, land-use types and degrees of
131 slope (see Seoane *et al.*, 2011 for a detailed description on the sampling protocol). We
132 recorded all birds heard or seen without a detection limit distance, distinguishing
133 between those registered inside and outside the survey belt of 25 m at each side of the
134 progression line, in order to estimate a measurement of detectability (see below). All
135 censuses were carried out on windless and rainless days, at a low speed (ca. 1–3 km/h),
136 early in the morning (7:00–11:00 GMT) and late in the evening (16:00–17:30 GMT).
137 Transects were 0.5-km sample units of homogeneous habitat structure. They were
138 measured and georeferenced with portable GPS (precision of $\pm$2 m by means of the
139 average location function). The starting point of transects were randomly determined
140 and then the rest of 0.5-km samples were performed one after the other (n = 437
141 transects). We feel confident in assuming that these transects provide a representative
142 sample of broad habitat classes present in La Palma island (see Fig. 1).
143 A surrogate of detectability was built as the ratio between the birds belonging to
144 each species observed inside the transect belt of 25 m at both sides of the observer, and
145 the total number of birds detected (i.e., the ratio p of main belt to total belt
146 observations). This index reflects important species characteristics related to the
147 interaction with the observer, such as song or call intensity and audibility,
148 conspicuousness and mobility (Järvinen & Väisänen, 1975). Density estimations,
149 accounting for species-specific detectability, were calculated using the following
150 equation (Järvinen and Väisänen, 1975; Järvinen, 1978):
151 $$D = (N * k) / L$$
152 $$\text{being } k = (1-(1-p)^{0.5})/0.025$$

where D is the density in birds/km^2, N is the number of detected birds, k is a detectability coefficient, L is the transect length in km, and p is the ratio of main belt to total belt observations of each bird species (0.025 is transect belt of 25 m expressed in km). This is a convenient approach to account for differences in detection probabilities among species in highly vegetated environments, when measuring exact distances to each individual bird is not feasible because devices such as laser range-finders cannot be applied precisely to birds heard but not seen in densely vegetated habitats.

Environmental predictors

Models were built with environmental predictors that have been shown to play a role in shaping the distributions and/or abundances of birds at our spatial resolution, such as those expressing vegetation structure, primary productivity, topography and human impact (Seoane et al. 2005; Mcfarland *et al*. 2012). The vegetation structure categories were assigned to each transect based on an existing map of plant communities in the Canary Islands (Del Arco *et al.,* 2003). The following ten broad classes were identified: volcanic fields (‘*malpaíses’*), pasturelands, *Euphorbia* shrublands, scrublands, tall heathlands (‘*fayal-brezal*’), evergreen forests (‘*laurisilva*’), pine forests of *Pinus canariensis*, rocky slopes with scattered plants (‘*cerrillar*’), agricultural habitats and urban areas. For each transect, we also measured the minimum distance to these habitats using ArcGis. The altitude, cardinal direction and the terrain slope in the centre of each transect were obtained from a digital model (100 m spatial resolution). As an indicator of primary productivity, we quantified photosynthetic activity using a normalized difference vegetation index (NDVI). Raw NDVI data were ten-day synthesis obtained from the sensor VEGETATION onboard the SPOT satellite, averaging data for March

177 to June of the sampling year, and discarding cloudy pixels. Additionally, in order to
178 increase prediction capacity of models we also used UTM latitude and longitude in
179 meters to absorb potential remaining spatial variation not explained by vegetation and
180 topography. All these data were also obtained for the centre of all UTM 500 m x 500 m
181 squares of La Palma Island (n = 3263).
182
183 **Species occurrence distribution models**
184 Boosted Classification Trees (BCT) were employed to assess the probability of
185 occurrence (presence-1/absence-0) of each species in the sample of 437 transects of 0.5-
186 km using the 16 formerly mentioned predictor variables. The BCT algorithm builds a
187 number of regression trees (typically hundreds) in a stage-wise fashion on randomly
188 selected subsets of data and combines them to improve predictive performance (see for
189 details: De'Ath, 2007; Elith *et al.,* 2008). We used a five-fold approach in order to test
190 the accuracy of predictions of BCT models. As outputs from boosting are not well
191 calibrated, posterior probabilities predictions of BCT models were calibrated applying a
192 logit function to transform boosting predictions with a sigmoid function (Niculescu-
193 Mizil & Caruana, 2007).
194 To compare BCT predictions with those provided when accurate absence data does
195 not exist, occurrences for each species were also modelled using the MaxEnt algorithm
196 (Phillips *et al.,* 2006; Phillips & Dudik, 2008). We selected this modelling technique
197 because it is a widely used procedure when only presences are available, and is also a
198 machine learning method. As in the classic resource selection functions of use-
199 availability designs (Manly *et al.,* 2002), MaxEnt generates suitability outputs from
200 presence data and a pool of background absences selected at random from the study area

using a maximum entropy approach (Phillips *et al.,* 2006; Pearce & Boyce, 2006). In our case, these background absences were selected out of the UTM squares in which transects occur and equal in numbers to those used in BCT models for each species (range: 44 to 420; average=335). This approach has been chosen to i) avoid the use of true absences as background absences, and ii) to ease the comparison of model outputs using an identical number of true absences (in BCT) and background absences (in MaxEnt). Moreover, for MaxEnt the 5-fold data split into training and testing subsets was the same as for the BCT models within each species. Thus, our data arrangement will enable more direct inferences regarding the use of reliable absences in models while keeping other sources of inter-model variability as fixed as possible.

The discrimination ability of BCT and MaxEnt models to predict each species' distribution was compared through the area under the curve (AUC) of the receiver operating characteristic (ROC) plot of sensitivity against 1-specificity (Fielding & Bell, 1997). AUC values should not be interpreted uncritically, and one of the major misuses is relying on absolute values to compare among species with different prevalences (Lobo *et al.,* 2008). In spite of this, its use in a relative way may be useful to compare among modelling techniques within species with identical prevalences (Aragón & Sánchez-Fernández, 2013).

Predicting local and regional abundances from occurrence distribution models

Firstly, we aimed to assess the general ability of presence/absence models (BCT) and presence/background absence models (MaxEnt) to predict local abundances at the transect level. For this purpose, we estimated separately for each species the Pearson correlations of the relationships between observed abundances in transects and SODM

outputs (the predicted habitat suitabilities using MaxEnt or probabilities of occurrence using BCT). Sequential Bonferroni adjustment was applied to these analyses to control for type I errors (Benjamini & Hochberg 1995). Then, we used a paired *t*-test to compare between the Pearson correlation coefficients obtained for each species separately with BCT outputs and those obtained with MaxEnt outputs. In addition, we assessed the degree of triangularity in the relationships between observed local abundances and model outputs separately for each species (see Appendix S1 in Supporting Information).

As use-availability models, such as MaxEnt, are unable to predict the probability of occurrence (Hastie & Fithiam, 2013), BCT probabilities of occurrence were subsequently used to obtain regional abundance estimations. For this purpose, we firstly converted the probabilities of occurrence to bird numbers applying a procedure that has been shown to be appropriate for the case of outputs from presence/absence models. The predicted probabilities of occurrence for each transect (P_i) derived from BCT models were converted to predicted bird numbers for each species (n_i') using the following expression under the assumption of random distributions with Poisson distributed populations (Gerrard & Chiang 1970, Gerrard & Cook 1982):

$$n_i' = - \ln (1-P_i)$$

The summation of the predicted n_i' figures for each species ($\sum n_i'$) was used to estimate its resemblance to the true number of birds counted in the whole sample ($\sum n_i$) of 437 transects that equal 218.5 km. These numbers were transformed in regional densities (DENREG; birds / km^2) considering the above mentioned formula by Järvinen and Väisänen (1975). Finally, we performed a Pearson correlation to estimate the relationship between predicted and observed regional densities for the 21 bird species

249 recorded. Additionally, we used t-tests to assess whether this predicted regression line
250 deviated significantly from the equality between the observed and predicted densities.
251
252 **Interspecific variation in prediction accuracy of regional density**
253 Interspecific variation in the prediction accuracy of densities using BCT models was
254 characterized by calculating the percentage difference between predicted and observed
255 regional densities in relation to observed regional density (hereafter % change). The
256 thus obtained % change was then related to several autoecological traits of the species:
257 species prevalence in the whole sample of transects (range: 0.04 – 0.90), coefficient of
258 variation in bird numbers when each species was present (30 – 167 %), a surrogate of
259 detectability (as measured by the ratio p of main belt to total belt observations of each
260 bird species -see above-; range: 0.22 – 0.89), body mass (5.8 – 480 g; obtained from
261 Perrins 1998 as the mean weight of males and females, or as the average value of body
262 weight range in spring and summer), and habitat breadth (0.14 – 0.74) and ecological
263 density (3.5 – 248.1 birds/km^2) estimated for the most preferred habitat (these two last
264 variables obtained from Appendix B of Seoane *et al.,* 2011).
265 All possible subsets of the predictors using General Linear Models were estimated
266 (64 models), and were compared with Akaike's second-order AIC corrected for small
267 sample sizes (AICc; Burnham & Anderson, 2002) to assess their weights of evidence.
268 The strength of evidence of models was obtained using weights (Wi) derived from *AICc*
269 figures, using all possible models (R package glmulti). Parameter estimates
270 (standardised regression coefficients, β; R^2 of models) were averaged using model
271 weights (Wi; Arnold, 2010).
272

RESULTS

Accuracy of species distribution models

Since AUC values were obtained by five-fold cross-validation, predictions of bird distributions from both BCT and MaxEnt models can be considered excellent or good according to usual performance criteria (Swets 1988) (n = 21; mean AUCs ± SD: BCT = 0.835 ± 0.118; MaxEnt = 0.792 ± 0.128; Table 1). AUCs for BCT and MaxEnt models were significantly and positively correlated (Pearson's correlation: r = 0.693; P = 0.0005) although BCT figures were slightly higher than those obtained with MaxEnt (paired t-test = 2.073, P = 0.051, Table 1).

Predicting bird local and regional abundances from distribution models

Probabilities of occurrence (from BCT) and habitat suitability values (from MaxEnt) were positively and significantly associated with their corresponding observed abundances for nearly all species using transects as sample units (see Pearson's correlation coefficients in Table 1). The exceptions were *Phylloscopus canariensis* and *Streptopelia turtur* for MaxEnt outputs, where relationships with abundance were not significant after sequential Bonferroni corrections. The strength of association between model predictions and observed abundances was considerably higher for BCT than for MaxEnt models (paired t-test = 10.792; $P < 0.001$; n = 21 species). On the other hand, the triangular relationship assessed with quantile regressions was always present and was not different between BCT and MaxEnt results (see Appendix S1).

296 At the regional level (i.e., using the whole sample of transects in the island), the
297 observed average densities per species were highly correlated with those predicted by
298 BCT occurrence probabilities (P_i) when converted to regional densities (*i.e.* $\sum$-ln[1-P_i]
299 for transects $i = 1$ to $i = 437$; $r = 0.967$; $P << 0.001$; Table 1; Fig. 2). Coefficients a and
300 b in the equation OBSERVED = $a + b \cdot$PREDICTED did not significantly differ from
301 zero and one respectively ($a = 3.5$, SE = 3.25; $b = 1.014$, SE = 0.061; $P > 0.2$ in both t-
302 tests; Fig. 2). Therefore, the observed and predicted regional densities are operatively
303 interchangeable. Moreover, % of difference between predicted and observed regional
304 density was close to zero (mean % difference = -0.076, SE = 7.97). Thus, there was no
305 overall bias toward either overestimation or underestimation of bird abundance at the
306 regional level.
307
308 **Interspecific variation in prediction accuracy of regional density**
309 Interspecific variation in the accuracy of predicted average density at regional scale
310 (*i.e.*, the average density in the whole sample of transects) was explained to a great
311 amount (73% of variance) by a weighted average model. The variability in bird counts
312 when the species was present, habitat breadth, prevalence in the sample of transects and
313 regional maximum density were the most influential variables ($\Sigma W_i \geq 0.4$; Table 2). The
314 variable most affecting the accuracy of predicted regional density was the variability in
315 bird counts measured by the coefficient of variation (CV%; $\Sigma W_i = 1$, with the largest
316 absolute value of the standardized regression coefficient; Fig. 3a). Habitat breadth had
317 also a similarly high importance, although its magnitude effect was lower (β coefficients
318 in Table 4; see Fig. 3b). Summarizing, predicted regional abundance tended to be
319 underestimated in those species which occupy a narrow range of habitats and show a

large variability in numbers when present. High prevalence in the sample and high density in the most preferred habitat also tended to underestimate regional estimates.

DISCUSSION

In this study we examined the extent to which the continuous predictions obtained from species' presence/absence (probabilities of occurrence from boosted classification trees) or presence/background (suitabilities from MaxEnt) models can predict species abundances, either at local (sampling units) or at a regional level (La Palma Island). To allow comparisons between presence/absence and presences/background models, prevalences and 5-fold partitions were kept identical in both modelling procedures for each species, while the only difference was the use of observed absences *vs*. background random data. Although the accuracy of presence/absence models was only slightly higher than that of presence/background models in predicting the occurrence of species, the ability to predict observed local abundances was clearly superior for presence/absence models using BCT. Since we designed an experimental protocol to rule out the influence of differences in the prevalence of training data, our results reveal that the differences found between MaxEnt and BCT were due to the algorithm used and/or to the nature of the non-presence data (absences/background) independently of the prevalence. Our results are robust since predicted occurrence probabilities derived from SODMs were obtained from five-fold cross-validations with data not used to build models.

An important difference between modelling with presence/absence and with presence-only data is that the latter operates with background data (a mixture of unrecorded absences and presences), inflating thus the number of false absences to an

unknown degree (Lobo *et al.,* 2008). As a consequence, the use of background data is less appropriate to estimate abundances from occurrence data. Our results support the use of presence/absence sampling protocols to predict animal abundance even at the local scale, although better results were obtained by combining these predictions to infer regional abundances (*i.e.* the total number of individuals per species recorded in the whole sample of line transects carried out in La Palma Island). Despite the fact that the relationships between SODM outputs and observed local abundances tended to be triangular (see Appendix S1), our estimations at the regional level turned out to be highly precise after applying the simplest transformation, assuming Poisson distributed populations, proposed by Gerrard and Chiang (1970). This is clearly shown by the fact that the regression line nearly represents the perfect equivalency between predicted and observed average bird densities in La Palma island (Table 1, Fig. 2).

Although several studies have focused on the ability of SODMs to predict local abundances (Nielsen *et al.,* 2005; Seoane *et al.,* 2005; Jiménez-Valverde *et al.,* 2009; Estrada & Arroyo 2012; Thuiller *et al.,* 2014; Bean *et al.,* 2014; Yañez *et al.,* 2014; Russell *et al.,* 2015), showing generally that they only allow for the demarcation of the upper-limit of the observed abundances (e.g. VanDerWal *et al.,* 2009; Tôrres *et al.,* 2012), little is known about the usefulness of occurrence data to predict regional abundances (i.e., number of individuals or densities). The advantage of the approach applied here at the regional level is that the same transformation is applied for all species, and hence it can be used as an alternative to specific parameterizations proposed in other studies for each species separately (*e.g.* VanDerWal *et al.,* 2009). We propose that this procedure is especially appropriate and cost-effective when the aim is to infer regional abundances of large sets of species under sampling restrictions, as often

368 occur in biodiversity studies. Thus, our procedure to predict average regional densities
369 can be a powerful tool in cases of biodiversity assessment in poorly known regions or
370 remote areas. Furthermore, we may be interested in examining the potential effect of an
371 ecological perturbation by comparing species abundances in the target area before and
372 after the perturbation occurred, or between the disturbed and other neighbouring areas.
373 In the same vein, this procedure can provide insights in the context of reserve design;
374 comparing predicted regional densities among contiguous areas with different
375 protection status would help to make decisions when reviewing their protection
376 capacity. It is remarkable that studies on reserve design selection are often based on
377 species representation (Araújo *et al.,* 2007), analogous procedures based on
378 probabilities of occurrence are scarce (Cabeza *et al.,* 2004), and there is a general lack
379 of approaches dealing with abundances in many organisms (apart from birds,
380 considering their attractiveness for citizen science projects). The high accuracy of the
381 procedure used here to predict regional densities from SODM outputs with true
382 presence/absences suggests its potential value when working with organisms for which
383 census programs dealing with abundances are not the norm or are not feasible.
384 At the regional scale, we found that the interspecific variation in prediction accuracy
385 of regional abundance can be explained by species-specific traits related to distribution
386 patterns and habitat preferences. This is in line with previous studies showing that
387 autoecological traits may affect model performance in predicting species distributions
388 from observed presences/absences (Hernandez *et al.,* 2006), abundances from observed
389 abundances (Seoane *et al.,* 2005; Carrascal *et al.,* 2006), and abundances from
390 occurrence probabilities (Nielsen *et al.,* 2005; Jiménez-Valverde *et al.,* 2009; Estrada &
391 Arroyo 2012; Russell *et al.,* 2015). Habitat breath and the coefficient of variation in bird

numbers were specific traits with higher relative importance in explaining the interspecific variation in predicting regional densities. Bird species with a greater habitat breadth, such as *Falco tinnunculus* and *Streptopelia turtur*, tended to be overestimated (Fig. 4b, see Appendix S2). Species inhabiting a greater number of habitat types can be associated to a greater range of environmental variation and hence predictions might be closer to the upper part of their potential. It is also plausible that species with broad niches are at lower numbers than the expected potential simply because other biologically relevant factors not included in the models might be also shaping subtle variations in their abundances. Thus, species with larger habitat breadths may be more sensitive to the exclusion of unknown relevant factors in models, which result in a greater mismatch between observed and predicted abundances. Whatever the processes involved, it appears that environmental tolerance governs both species occurrence distributions and abundances, since it has been shown to affect the accuracy of SODM and abundance models (Carrascal *et al.,* 2006; Hernandez *et al.,* 2006; Seoane *et al.,* 2005).

Species with higher coefficients of variation of local abundance when present, such as *Pyrrhocorax pyrrhocorax, Carduelis cannabina* and *Columba livia* (e.g., from 1 to 30 individuals as opposed to ranges of 1 to 3 individuals), tended to be underestimated. The coefficient of variation may be linked to the within-species variation regarding grouping behaviour or environmental fine-grained variables affecting animal abundance not included in the models (e.g., habitat structure, food availability, substrata for nesting). Estrada and Arroyo (2012) found that differences between two harrier species regarding the degree of association between SODM outputs and abundances could be explained by the degree of gregariousness and by the interspecific variation in the use of

social information for site selection. Thus, it is possible that the within and among-species variation in grouping behaviour affects abundance predictions intra- and inter-specifically. Finally, our results show that among the species traits considered, detectability had the lowest relative importance in explaining deviations from the observed regional density. In fact, it has been argued that presence/absence models are less affected by this trait than models built with presence-only data (Pearce & Ferrier, 2001).

To conclude, our results show that when predicting species abundances from occurrence data, presence/absence models outperformed presence/background models. If abundance or density information is essential to advise conservation decisions, such information should not be derived when reliable absences are lacking. The use of presence-only models with background data does not allow good predictions of local abundances. Moreover, the impossibility of estimating the probability of occurrence from these only-presence designs (Hastie & Fithiam, 2013) hinders the estimation of abundances by the conversion of probabilities to animal numbers. Our study shows that despite limitations of occurrence binary data (presence/absence) to predict precise local abundances, these local predictions may be combined to predict unbiased average regional abundance. This is because, although accuracies are not similar across species, overestimations and underestimations compensate each other within each species.

It is highly surprising that the procedure revisited here designed by Gerrard & Chiang (1970) to convert local probabilities of occurrence into numbers of individuals has rarely been used with vertebrates (but see Tellería & Sáez-Royuela 1986), considering that the accuracy of the predictions are very high as it has been demonstrated in this paper and previously with arthropods (e.g., Gerrard & Chiang

1970, Badenhausser *et al.*, 2007, Hall *et al.*, 2007). The only concern is to avoid the "dangerous zone" where the probability of occurrence (P_i) is higher than ca. 0.9. Over this probability, the observed and predicted abundances grow exponentially, so very small changes in P_i generate very large variations in abundance. Therefore, the obvious advice is to define sampling protocols where the size of the sampling unit (i.e., 0.5-km length transects in our study) produces probabilities or frequencies of occurrence below the "saturation point" of 0.9 (see also Gerrard & Chiang 1970). Further studies with heterogeneous taxa, scales and situations will likely reinforce the generality of this procedure.

Although obtaining good species' absences in a random sampling protocol is economically costly and time consuming, the costs associated to measure species' abundances are considerably higher and not always feasible. This study highlights the usefulness of surrogate measures of species abundances derived from distribution models built with presence/absence data. This approach can be a useful tool in applied ecology, especially when working in remote areas, under budget restrictions or with limited qualified personnel. Since the accuracies of predicted regional densities are similar across species, the approach is highly valuable in studies of biodiversity that deal with a large number of species. Moreover, analyses testing the potential influence of species-specific traits on prediction accuracy should be viewed as a valuable complement to gather further insights on the processes involved in the interaction between the sampling method and focus species.

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469

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SUPPORTING INFORMATION

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

Appendix S1 Degree of triangularity in the relationships between local observed and predicted abundances.

Appendix S2 Species-specific characteristics describing the distribution-abundance patterns of bird species.

Biosketch

Luis M. Carrascal is a research professor at the Museo Nacional de Ciencias Naturales (CSIC, Spain). His current research interests are focused on macroecology, the biogeographical ecology of the avifauna of the South-western Palaearctic and on the study of habitat selection in birds for modelling patterns of species abundance/occurrence.

Table 1 Summary of model results for 21 bird species in La Palma Island (Canary Islands, Spain). **MaxEnt AUC**: AUC values from MaxEnt models; **BCT AUC**: AUC values from Boosted Classification Trees models; ***r* MaxEnt**: correlation coefficients from Pearson's correlations between MaxEnt outputs and estimated specie's abundances; ***r* BCT**: coefficients from Pearson's correlations between BCT outputs and estimated specie's abundances (significant correlations at $P < 0.05$ after sequential Bonferroni correction are shown in bold type); **DENREG pred**: average regional density (birds / km^2) predicted from transformed BCT probabilities in all transects; **DENREG est**: estimated regional density (birds / km^2) derived from all transects; **% change**: % difference between predicted and estimated regional densities in relation to estimated regional density. Predictions were obtained from five-fold cross-validations. Data on species presences/absences were obtained from 437 transects covering all habitats of the island.

Species	MaxEnt AUC	BCT AUC	*r* MaxEnt	*r* BCT	DENREG pred	DENREG est	% change
Alectoris barbara	0.796	0.709	**0.287**	**0.633**	2.5	2.6	-2.9
Anthus berthelotii	0.892	0.895	**0.624**	**0.818**	14.5	13.4	7.7
Carduelis cannabina	0.683	0.680	**0.141**	**0.714**	1.4	2.6	-45.9
Columba bolli	0.985	0.944	**0.754**	**0.853**	6.7	7.9	-16.2
Columba junoniae	0.954	0.868	**0.634**	**0.863**	14.0	12.0	16.5
Columba livia	0.707	0.780	**0.332**	**0.682**	23.7	74.1	-68.0
Erithacus rubecula	0.872	0.921	**0.550**	**0.864**	25.3	25.9	-2.3
Falco tinnunculus	0.594	0.647	**0.119**	**0.731**	6.4	3.8	68.1
Fringilla coelebs	0.862	0.922	**0.551**	**0.806**	31.6	37.4	-15.6
Motacilla cinerea	0.908	0.901	**0.472**	**0.847**	8.9	5.3	67.3
Parus caeruleus	0.757	0.815	**0.349**	**0.759**	25.5	22.9	11.2
Phylloscopus canariensis	0.580	0.932	0.091	**0.635**	188.1	186.5	0.9
Pyrrhocorax pyrrhocorax	0.599	0.643	**0.154**	**0.644**	7.3	15.4	-52.7
Regulus regulus	0.866	0.941	**0.576**	**0.823**	81.2	93.5	-13.1
Serinus canaries	0.668	0.890	**0.344**	**0.799**	78.5	89.4	-12.3
Streptopelia decaocto	0.940	0.965	**0.611**	**0.803**	11.5	17.7	-35.1
Streptopelia turtur	0.610	0.559	0.083	**0.751**	7.7	4.6	68.3
Sylvia atricapilla	0.864	0.904	**0.575**	**0.818**	36.5	40.3	-9.5
Sylvia conspicillata	0.789	0.847	**0.268**	**0.736**	5.4	4.4	22.2
Sylvia melanocephala	0.871	0.882	**0.561**	**0.831**	23.2	20.3	14.7
Turdus merula	0.834	0.908	**0.536**	**0.810**	70.4	74.1	-4.9

Table 2 Alternative models for interspecific variation in large-scale prediction accuracy of bird density in 21 species inhabiting La Palma island (Canary Islands, Spain). Accuracy is measured as the percentage of variation of predicted average densities with respect to estimated average densities of birds in the whole sample of the 437 0.5-km line transects (see % change in Table 1). Only models with ΔAICc <2 are shown for brevity. Multimodel inference (lower part of the table) has been obtained considering all the possible combinations of predictors (64 models), averaging the results according model weights (W_i). Figures for each variable are standardized regression coefficients (β) obtained in general linear models. For each variable, ΣW_i is the sum of weights of the models in which the variable appears, weighted average β is the weigthed average of standardized regression coefficients, and se β the unconditional standard errors. AICc: AIC corrected for small sample sizes. R^2: variance explained by each model (in %). CV%: coefficient of variation in bird numbers in transects where each species occurred; HB: habitat breadth considering 11 different habitats; PREV: prevalence of each species in the sample of 437 0.5-km line transects; DETECT: ratio of main belt (25 m) to total belt observations of each bird species (larger figures correspond to less detectable species); MASS: body mass of species (in log); DMAX: maximum density recorded in 11 different habitats. See Appendix S2 for more details on species characteristics. Models 1 to 5 are highly significant (P <0.001) using the classical frequentist approach.

	standardized regression coefficients (β)								
large-scale accuracy	PREV	CV%	DETECT	HB	DMAX	MASS	R^2 (%)	W_i	AICc
model 1		-0.718		0.280	-0.351		75.0	0.166	194.6
model 2	-0.450	-0.726		0.463			74.9	0.155	194.7
model 3	-0.607	-0.674		0.568		-0.224	78.6	0.111	195.3
model 4		-0.765			-0.242		68.5	0.081	196.0
model 5		-0.792					62.7	0.066	196.4
MULTIMODEL INFERENCE									
ΣW_i	**0.438**	**1.000**	**0.185**	**0.632**	**0.483**	**0.268**			
weighted average β	**-0.150**	**-0.737**	**-0.019**	**0.246**	**-0.165**	**-0.046**	**72.7**		
se β	**0.265**	**0.139**	**0.054**	**0.242**	**0.212**	**0.086**			

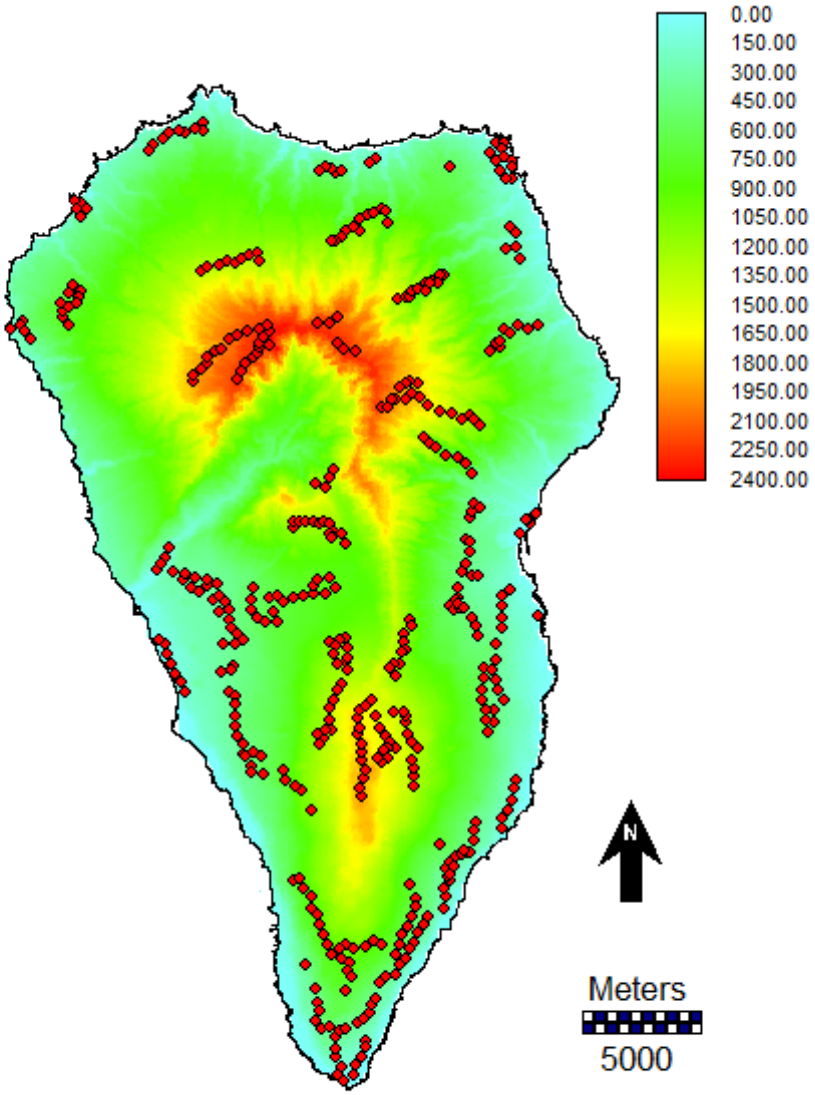
Figure legends

Figure 1 Location of 437 0.5-km transects in La Palma island. Each dot represents the center of the 0.5-km transects. The background map shows the topography of the island.

Figure 2 Linear relationship between predicted and estimated average regional densities for 21 species in La Palma Island (Canary Islands, Spain). Predictions were obtained from five-fold cross-validated boosted classification trees, whose outputs were converted to regional densities (through *-ln [1-f]*; see methods). Solid line denotes the regression line and dashed line denotes equality between the estimated and predicted densities.

Figure 3 Partial residual plots illustrating the influence of the coefficient of variation in bird numbers where they occurred (a), and habitat breadth (b) on the accuracy of predicted average regional densities measured as the percentage difference between predicted and estimated regional density respect to estimated regional density (% change in Table 1). $N = 21$ bird species from La Palma island (Canary Islands, Spain). Residual plots show the relationship between a given independent variable and the response given that the other independent variables in Table 2 are also in the model, therefore partialling out their effects.

Figure 1


0.00
150.00
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1200.00
1350.00
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1650.00
1800.00
1950.00
2100.00
2250.00
2400.00
N
Meters
5000

Figure 2

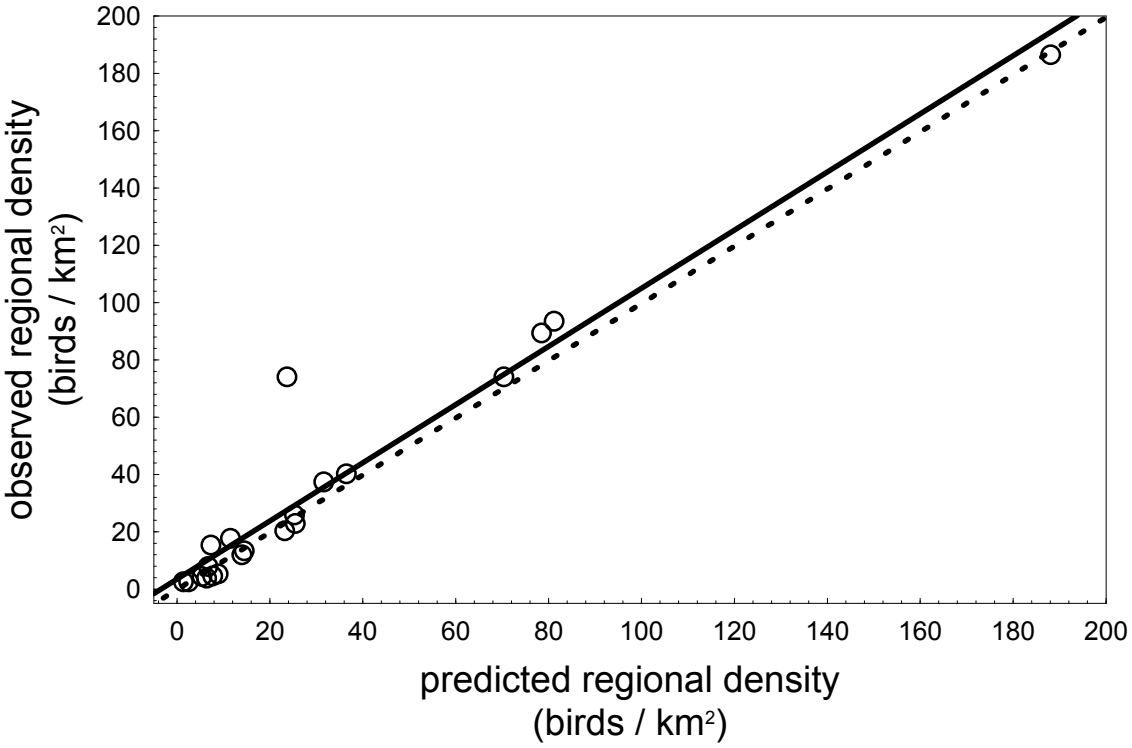
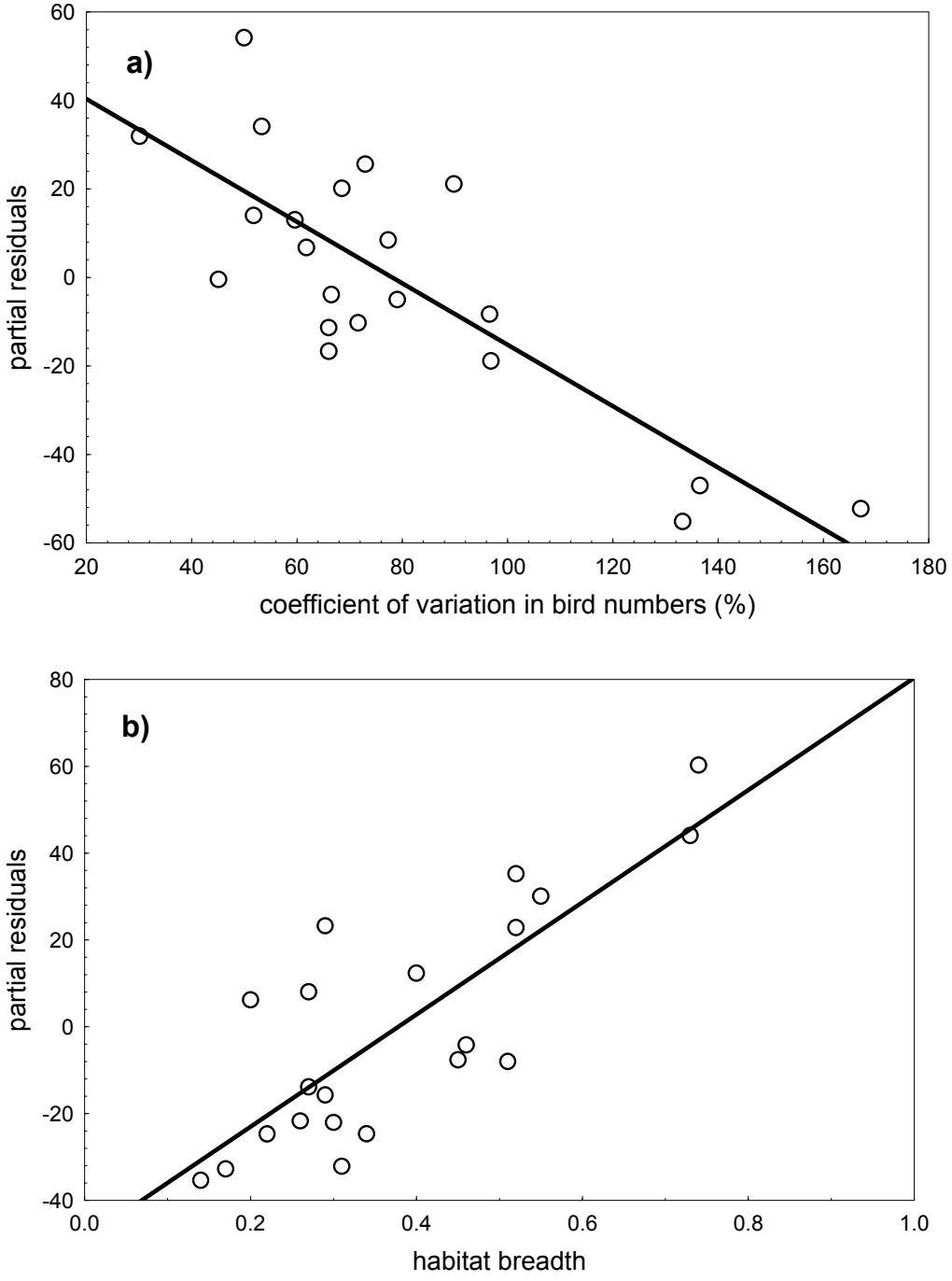

observed regional density
(birds / km²)
predicted regional density
(birds / km²)
0
20
40
60
80
100
120
140
160
180
200

Figure 3


a)
partial residuals
coefficient of variation in bird numbers (%)
b)
partial residuals
habitat breadth

Appendix S1 Assessment of the degree of triangularity in the relationships between estimated local abundances and model outputs

The shape of the relationships between the estimated local abundances at the transect level and the SODM outputs were also analysed using quantile regression models (Cade & Noon, 2003), in order to test for changes in the slope of local abundance *vs*. suitability or probability derived from models in different subsets of data. We estimated the slopes of local abundances – SODM outputs at percentiles 50% (i.e., median regression, *tau* = 0.5) and 90% (*i.e.*, the maximum response of organisms attaining maximum ecological abundances; *tau* = 0.9). The changes of the slopes between percentiles 50% and 90% (b_{tau} = 0.9 – b_{tau} = 0.5) measure the unequal variation of local abundance with suitability or probability derived from models, indicating complex interactions between these two parameters that show solid, triangular, patterns instead of clearly linear relationships. Sequential Bonferroni adjustments were also applied to estimate the significance of slopes at the two selected percentiles, and the "triangularity" degree of the relationship between local abundances – SODM outputs, using BCT and MaxEnt, was tested by means of paired *t*-tests of the differences (b_{tau} = 0.9 – b_{tau} = 0.5).

We found that patterns of the relationship between estimated local abundances and predictions of bird distributions from both BCT and MaxEnt models were triangular (see Table S1 and an example with the endemic subspecies *Regulus regulus ellenthalerae* in Fig. S1): quantile slopes for percentile 90% were significantly higher than those for 50% both for BCT probabilities (paired *t*-test comparing slopes at *tau* = 0.9 *vs*. *tau* = 0.5: $t = 7.10$, 21 species, $P << 0.001$) and MaxEnt suitabilities ($t = 6.22$, 21 species, $P << 0.001$). Twenty out of 21 bird species have significant 0.9-quantile slopes

relating estimated local abundance to BCT predictions of probability of occurrence (established after sequential Bonferroni's correction for multiple *P* estimates); nevertheless, 0.9-quantile slopes for MaxEnt predictions attained the significance level for only 16 bird species. The triangularity of the relationship (estimated abundances – SDOM outputs), measured by the difference in the quantile slopes at *tau* = 0.9 and 0.5 (b_{tau} = 0.9 – b_{tau} = 0.5), was not different comparing BCT and MaxEnt models (paired *t*-test: *t* = -0.372, 21 species, *P* = 0.714).

The shape of the distribution (estimated local abundance – predicted probability or suitability) is triangular, in such a way that lower predicted probabilities remain associated to lower estimated abundances, whereas higher predicted probabilities remain associated to a higher variation in estimated abundances (see also VanDerWal *et al.,* 2009; Gutiérrez *et al.,* 2013). Several non-exclusive potential explanations underline these triangular distributions. First, it may be simply the asymmetric meaning of presence/absence data regarding animal abundance. The absence of a species in the area covered by the sampling unit, if true, has a unique possible value of zero individuals; but the presence of a species may have a very large span of figures ranging from one to many individuals (Comte & Grenouillet, 2013). This concern has been previously acknowledged in the analysis of spatial variation of binomial response variables, with an overall higher variability and bias of results for binary data (McCullagh & Nelder, 1989; Guisan & Zimmermann, 2000; Cushman & McGarigal, 2004). Second, the tendency of presence-absence data to derive triangular relationships with abundance might depend on the used resolution (see Bean *et al.,* 2014) and the aggregation of the focus species. Third, the local abundance of a species cannot change above some upper limit set by the measured environmental predictors included in the modelling tools

(BCT and MaxEnt in this paper), but might change below that upper limit according to some limiting unmeasured variables (Cade & Noon, 2003). Moreover, multiplicative interactions among unmeasured ecological factors might contribute to the residual variation in the estimated abundance when it is predicted from SDOM. Finally, there are limits to prediction accuracy unbeatable by methodological refinements (Seoane *et al.,* 2005), which are rooted on stochastic phenomena due to natural or anthropogenic factors (e.g., harsh weather, wildfires, hunting, poisoning), or to endogenous metapopulations' cycles unreachable by coarse grained environmental predictors obtained from GIS. In spite of this, the averaging of local abundance estimates over larger spatial scales compensates those components of random variation and generates precise projections of animal numbers at the regional level (i.e. La Palma island; see Table 1 and Fig. 2 in the main text).

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Table S1 Slopes of quantile regressions of estimated local abundances of species in 0.5-km length transects and outputs derived from BCT (boosted classification trees; probability) and MaxEnt (suitability) models at percentiles 50% (*tau* = 0.5) and 90% (*tau* = 0.9). Significant slopes at $P < 0.05$ after sequential Bonferroni correction are shown in bold type.

	BCT		MaxEnt	
Species	*tau* = 0.5	*tau* = 0.9	*tau* = 0.5	*tau* = 0.9
Alectoris barbara	0.00	**10.72**	0.00	**5.23**
Anthus berthelotii	**1.16**	**3.72**	**0.99**	**4.90**
Carduelis cannabina	**1.09**	7.30	0.00	0.00
Columba bolli	**3.29**	**6.54**	**3.21**	**9.92**
Columba junoniae	**2.33**	**5.92**	**1.20**	**8.63**
Columba livia	**0.50**	**2.87**	0.00	**2.61**
Erithacus rubecula	**1.72**	**4.25**	0.00	**6.32**
Falco tinnunculus	**2.37**	**5.03**	0.00	0.00
Fringilla coelebs	**1.36**	**4.13**	**0.77**	**5.74**
Motacilla cinerea	**2.55**	**5.23**	0.00	**8.67**
Parus caeruleus	**1.11**	**4.00**	0.00	**3.47**
Phylloscopus canariensis	**1.17**	**2.73**	0.00	0.00
Pyrrhocorax pyrrhocorax	**0.41**	**2.69**	0.00	1.06
Regulus regulus	**1.36**	**3.71**	**1.22**	**5.20**
Serinus canaries	**0.90**	**2.52**	**0.68**	**3.02**
Streptopelia decaocto	0.92	**8.73**	0.00	**9.34**
Streptopelia turtur	**2.69**	**8.14**	0.00	0.00
Sylvia atricapilla	**1.18**	**3.34**	**1.30**	**4.24**
Sylvia conspicillata	**2.77**	**8.30**	0.00	**3.56**
Sylvia melanocephala	**2.18**	**4.45**	0.00	**5.75**
Turdus merula	**1.20**	**3.17**	**1.35**	**3.87**

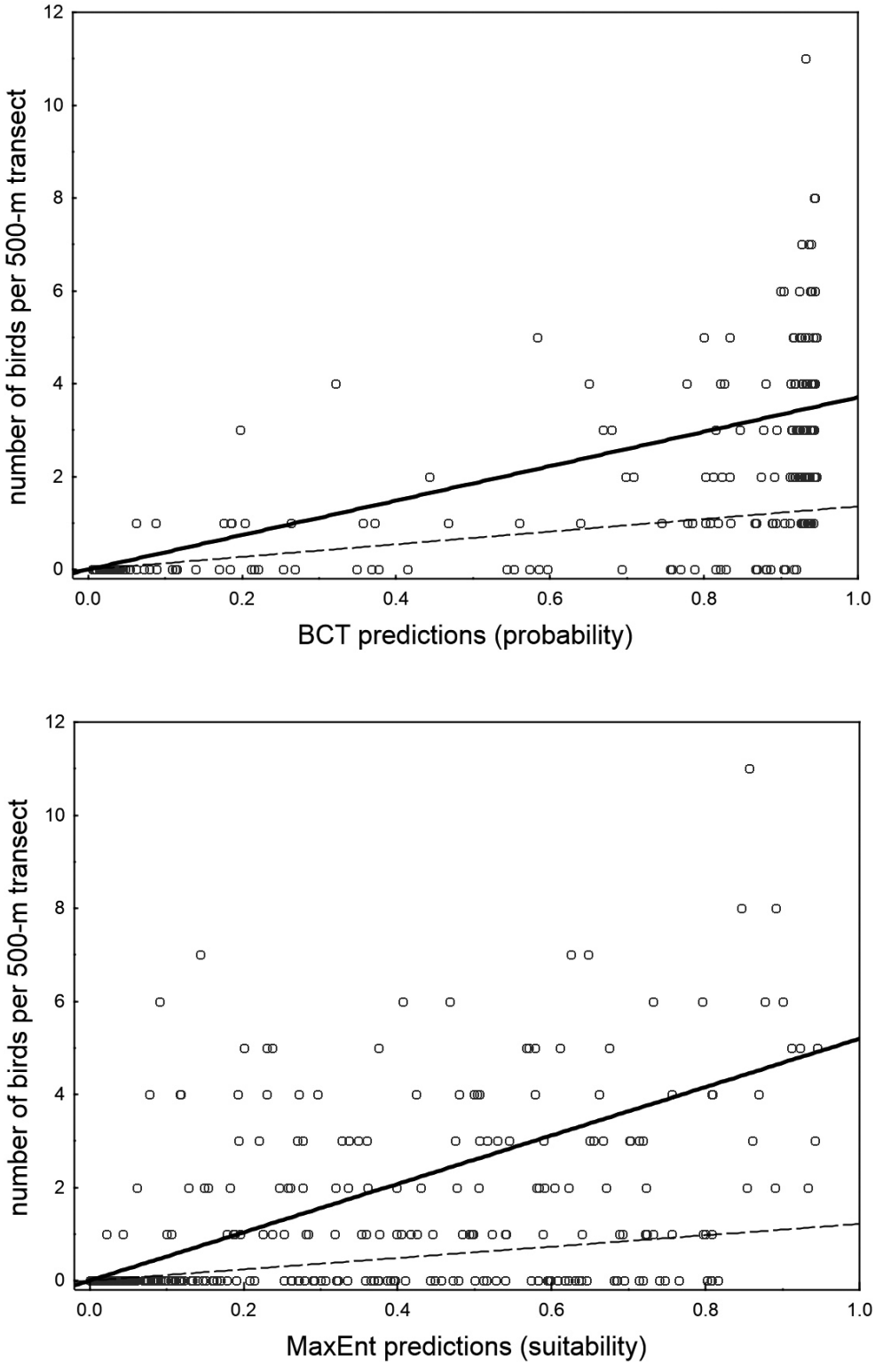

Figure S1 Shape of the relationship between estimated local abundance and predictions of probability of occurrence and suitability derived, respectively, from BCT and MaxEnt models. The panels show the relationships for the endemic subspecies *Regulus regulus ellenthalerae*. Regression lines show the quantile regressions for *tau* = 0.5 and *tau* = 0.9. *n* = 437 sample units (0.5-km length transects).

Appendix S2

Table S2 Species-specific characteristics describing the distribution-abundance patterns of 21 terrestrial bird species in La Palma island. PREV: prevalence of each species in the sample of 437 line transects; CV%: coefficient of variation in bird numbers in transects where each species occurred; p: ratio of main belt (25 m) to total belt observations of each bird species (larger figures correspond to less detectable species); HB: habitat breadth considering 11 different habitats; MASS: body mass of species (in log); DMAX: maximum density recorded in 11 different habitats. Data for DMAX and HB obtained from Appendix B of Seoane *et al.* (2011).

	PREV	CV%	p	HB	DMAX	MASS
Alectoris barbara	0.05	45.1	0.39	0.31	3.5	480.0
Anthus berthelotii	0.17	89.8	0.42	0.20	64.5	16.5
Carduelis cannabina	0.04	136.5	0.23	0.26	16.3	17.6
Columba bolli	0.06	61.8	0.59	0.14	58.3	286.0
Columba junoniae	0.10	73.0	0.59	0.27	42.9	328.7
Columba livia	0.33	133.2	0.45	0.45	117.9	216.0
Cyanistes caeruleus	0.25	71.6	0.55	0.46	29.2	11.3
Erithacus rubecula	0.19	66.5	0.61	0.30	60.6	16.7
Falco tinnunculus	0.19	30.1	0.22	0.73	3.6	174.5
Fringilla coelebs	0.25	79.1	0.63	0.29	112.0	23.0
Motacilla cinerea	0.08	50.0	0.53	0.29	12.5	18.0
Phylloscopus canariensis	0.90	68.5	0.47	0.74	248.1	7.7
Pyrrhocorax pyrrhocorax	0.14	167.1	0.32	0.40	21.6	321.5
Regulus regulus	0.31	66.0	0.89	0.34	146.5	5.8
Serinus canarius	0.50	96.6	0.52	0.52	124.8	15.3
Streptopelia decaocto	0.08	96.8	0.73	0.17	54.3	196.0
Streptopelia turtur	0.07	53.3	0.57	0.52	6.4	125.0
Sylvia atricapilla	0.39	66.1	0.42	0.51	48.4	22.3
Sylvia conspicillata	0.07	51.8	0.51	0.22	11.6	9.5
Sylvia melanocephala	0.19	59.6	0.60	0.27	52.5	11.2
Turdus merula	0.54	77.3	0.49	0.55	130.2	86.1