Habitat suitability – density ~~link~~ relationship in an endangered woodland species: the case of the Blue Chaffinch (*Fringilla polatzeki*)

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Short Title: Habitat suitability and population density

ABSTRACT

Background. U~~The u~~nderstanding ~~of the~~ constraints to the distribution of threatened species may help to ascertain whether there are other suitable sectors for reducing the risks associated with their presence in only one protected locality, and to inform about the suitability of other areas for reintroduction or translocation programs.

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Methods. We study the Gran Canaria blue chaffinch (*Fringilla polatzeki*), a habitat specialist endemic of the Canary Islands restricted to the pine forest of Inagua, the only area where the species has been naturally present as a regular breeder in the last 25 years ~~as a regular breeder~~. A suitability distribution model using occurrences with demographic relevance (i.e., nest locations of successful breeding attempts) was built considering orographic, climatic and habitat structure predictors. By means of a standardized ~~census~~survey program we ~~have~~ monitored the yearly abundance of the species in 100 sectors since the declaration of Inagua as a Strict Nature Reserve in 1994.

Commented [TWE2]: A census is a complete count of a population or species. Given that not all birds were counted (not all birds could be detected), the authors conducted a survey rather than a census.

Results. The observed local abundance of the blue chaffinch in Inagua (~~census~~survey data) was significantly correlated with habitat suitability derived from modelling the location of successful nesting attempts. The outcomes of the habitat suitability model were used to quantify the suitability of other natural, historic, pine forests of Gran Canaria, being Tamadaba the forest that provides more suitable woodland patches for the species. We estimated a population size of 195–430 blue chaffinches in Inagua since 2011 (95% CI), the smallest population size of a woodland passerine in the Western Palearctic.

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Discussion. Habitat suitability obtained from modelling the location of successful breeding attempts is a good surrogate of the observed local abundance during the reproductive season. The outcomes of these models can be used for the identification of

potential areas for the reintroduction of the species in other suitable pine forests and to inform forest management practices.

INTRODUCTION

Habitat suitability is usually ~~established considering~~determined by the relationship between environmental predictors and species occurrence or abundance ~~, or the characteristics of localities where a species is found compared to those where it has not been detected or obtained at random from the environmental background~~ (Acevedo et al., 2016). ~~The second option~~Using species occurrence to understand the suitability of habitat is commonly employed when studying very scarce and spatially restricted species. In the case of very mobile species, such as birds, the localities where they have been observed may include areas that are important for their existence (e.g., space around nesting places), as well as other marginal areas used while dispersing or foraging outside the core home range. Thus, the utility of species occurrence models rests on the availability of good data on local species distribution, which will be all the better as the localities are linked to processes directly related to survival or breeding success. On the other hand, ~~the~~ analysis of the spatial variation of abundance may pose problems, since several authors have warned that density could be a misleading indicator of environmental quality if it is negatively correlated with other demographic variables via Ideal Pre-emptive Distribution processes (Van Horne, 1983; Pulliam & Danielson, 1991; Brawn & Robinson, 1996). For example, in environmentally restrictive areas, dominant individuals could displace other young or subordinate individuals to marginal areas where they become abundant, not as a consequence of habitat tracking considering foraging success, survival or successful reproduction, but according to mere habitat displacement. Therefore, in order to obtain good predictions about habitat suitability for selecting areas to protect ~~the~~ remnant populations of endangered species, or for ~~helping in the~~ defining~~tion~~ ~~of~~ habitat for translocation~~ programs~~, it is necessary to maximize data quality related to survival or breeding success. Furthermore, it is also necessary to know if habitat quality inferred

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from local abundance is associated with other independent measures related to suitability linked with demography (Vickery et al., 1992). The "habitat suitability – abundance" equivalence is a subject of intensive research~~,~~ because independent tests are needed to ascertain the validity of predictions of species occurrence models, considering that presence data are much easier to obtain than local measures of density (Jiménez-Valverde, 2011; Weber et al., 2016).

Natural reserves are established to protect biodiversity, both as a whole and considering those threatened species that have conservation problems. Nevertheless, their effectiveness may vary if phenomena outside the borders of the protected areas affect populations inside them (e.g., global warming and changes in rainfall regime, emergent diseases, invasive species), a worrying concern if species are restricted to only one protected area. This concern is a relevant question contributing to knowing whether it is advisable to place the emphasis on the conservation of an endangered species in only the protected area where it is relegated, or if more efforts should be directed towards translocations to other areas (Pérez et al., 2012; Rummel et al., 2016). To identify those other potential areas it is necessary to know ~~the~~ constraints to the distribution of species restricted to only one protected area, in order to know if there are other suitable sectors for reducing the risks associated with the presence of an endangered species in only one locality (an IUCN criteria for cataloging threat; IUCN, 2012).

The blue chaffinch of the Gran Canaria island (*Fringilla polatzeki*, Canary Islands) is a recently established species on the basis of genetic, morphological and behavioural data (Pestano et al., 2000; Lifjeld et al., 2016; Sangster et al., 2016), mainly restricted to the Strict Nature Reserve of Inagua-Ojeda-Pajonales (Inagua, hereafter; 39.2 km^2; Moreno and Rodríguez, 2007). It inhabits mature pine forests, where nests are placed in tall trees; breeding success is very low for a Fringillidae, with only ca. 1.5

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fledglings per successful nesting attempt, and 1.4 clutches per breeding season (Rodríguez & Moreno, 2008; Delgado et al., 2016). The estimated population size of the Gran Canaria blue chaffinch (guessed at around 300 birds with no recent estimation in its whole area of distribution, BirdLife Inernational, 2016a) lies within the left tail of the distribution of minimum viable population (MVP) estimates for many species, far away from the average MVP of 3,750 individuals for birds (Brook et al., 2006; Traill et al., 2007). This is most notable if we take into account the small size of the species (approx. 30 g), since body mass in birds is usually negatively correlated with abundance or maximum ecological densities in ~~the~~ preferred habitats (Carrascal & Tellería, 1991; Gaston & Blackburn, 2000). Surprisingly, and in spite of its low population size and smaller distribution area in comparison with the also endemic blue chaffinch from Tenerife island (*Fringilla teydea*; Rodríguez & Moreno, 2004; Moreno & Rodríguez, 2007), it has a higher haplotype diversity of the mitochondrial DNA control region (Pestano et al., 2000).

The main goals of this study are twofold. Firstly, to build a species occurrence distribution model ~~in order to disentangle the habitat preferences of the species~~ considering orographic, climatic and habitat structure predictors. This goal is carried out relying on ~~high~~ high-quality occurrence data, using the location of successful breeding attempts. The results of this model are used to contrast the habitat preferences of the Gran Canaria (*F. polatzeki*) and Tenerife (*F. teydea*) blue chaffinches considering the available literature, and to predict the habitat suitability of the natural and historic pine forests of Gran Canaria located within the same altitudinal range of Inagua. An applied utility of this aim is to understand if there are important environmental restrictions limiting the natural presence of the blue chaffinch outside of Inagua, and to quantify the suitability of other historic pine forests on Gran Canaria (?) as candidates for future translocations of birds. And secondly, to test if habitat suitability modelling, considering the location of successful nesting attempts, is related to independent measures of bird abundance during the breeding season using a different methodological approach. This exercise would cast light on the usefulness of occurrence distribution models, using labour-intensive occurrences with demographic relevance, forecasting the spatial variation of habitat suitability, and the validity of ~~census~~survey programs to derive ~~estimations~~ estimates of environmental quality.

MATERIAL AND METHODS

Study areas and environmental data

The study areas are located in several pine forests of Gran Canaria (27º58'N, 15º35'W), an island of volcanic origin (1560 km^2, maximum altitude of 1950 m.a.s.l.; for more details on the vegetation of the island see Santos, 2000). The canary pine forests are dry and monospecific stands of *Pinus canariensis*, very heterogeneous regarding the size and cover of trees and undergrowth (mainly composed by Leguminosae shrubs *Adenocarpus spp.* and *Chamaecytisus proliferus*, and the Ericaceae shrubs *Erica arborea* and *E. scoparia*), ~~that~~ occupying semi-arid hilly terrains ~~with~~ comprised of a predominance of high slopes and rugged terrain~~-~~ (González et al., 1986).

The main study area is located in the pine forest of Inagua Integral Natural Reserve surrounding areas (3759 ha with nearby pine stands; Special Protection Area of the European Union since 1979), which harbours the main extant breeding population of the blue chaffinch (Moreno & Rodríguez, 2007; a new established small population, mainly derived from translocations is located in La Cumbre at a considerably higher altitude of 1600-1800 m a.s.l.; Delgado et al., 2016; Rodríguez, 2016). Location of nests and yearly monitoring of blue chaffinch abundance were carried out in Inagua. For

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evaluating the habitat suitability of other mature pine forests within the environmental span of Inagua, we also considered the pine forests of Tamadaba (2812 ha), Pilancones (3167 ha) and Tauro (470 ha). Fig. 1, Table S1 and Figures S1, S2 and S3 of the supplementary material show the geographical location of the study areas and their environmental characteristics. The four pine forests show a broad overlap in orographic attributes, with all cardinal orientations represented: altitudinal range of the studied pine forests is 250 – 1550 m a.s.l., slopes of the terrain varies between 0% and 260% (with very steep averages of 45%-55%). Pine canopy cover ranges between 0% (clearings) and 99%, with Tamadaba forest being the area with the largest cover (43%). Pine height also shows a large overlap among the four pine forests, with the tallest pines reaching 40 m in Inagua. The shrub layer shows similar structural characteristics in the four pine forests, with average covers ca. 10% (maximum of 75%) and heights ca. 0.7 m (maximum values of 1.25 m). Climatic variables considerably overlap among the study areas, with high levels of average incident sun radiation during April-August (ca. 7000 kWh/m^2; minimum of 4567 and maximum of 7515), high average temperatures in May (ca. 19 ºC; minimum: 17.0 ºC; maximum: 21.2 ºC) and July (ca. 24.5 ºC; minimum: 23.6 ºC; maximum: 25.9 ºC), and low summer rainfall (July-September) ranging from 0 mm to 34 mm (Tamadaba is the pine forest with the highest rainfall~~—~~, mainly horizontal precipitation~~–~~, while Pilancones ~~was~~ is the driest pine forest).

A severe fire occurring in July 2007 badly affected the Inagua Reserve, Pilancones and Tauro, but not the Tamadaba forest (see Fig. 1 in Suárez et al., 2012). The Canary Pine has the remarkable characteristic of being able to survive and grow after fire. In most places the pine foliage was partially recovered by June 2008, and the tree foliage showed full growth by the breeding season of 2010.

The geographic information was managed using the GRASS 6.4 (GRASS Development Team, 2015). The cartographic information employed to generate the digital terrain model comes from the "*Infraestructura de Datos Espaciales de Canarias*" (http://www.idecanarias.es/). The digital elevation model was built from a contour map with 5-m equidistant topographic curves which it was converted to a raster map of 50x50 m resolution, with module *{v.to.rast}* and *{r.surf.contour}*. From the digital terrain model, raster maps of slopes of the terrain, and cardinal orientations of the hillsides, were elaborated at 50×~~x~~50 m resolution by means of the module *{r.slope.aspect}*. Climatic variables were obtained from the "*Clima-Impacto*" project (http://climaimpacto.eu/), developed by the Gobierno de Canarias and funded by the European Regional Development Fund of the European Union, at a raster resolution of 50×~~x~~50 m. Vegetation structure variables (pine and shrubs covers and heights) were obtained from precision laser LiDAR measurements. Data was provided at a raster resolution of 25×~~x~~25 m by project "*Enriquecimiento de la Cartografía de las islas forestales de Canarias a partir de datos LIDAR*" (GESFORMAC -Gestión y Planificación Forestal en la Macaronesia-, funded by European Regional Development Fund and by Dirección General de Protección de la Naturaleza del Gobierno de Canarias). These vegetation LiDAR measurements were upscaled to a resolution of 50×~~x~~50 mm using the module *{r.resample}*. Finally, solar radiation data were obtained from the photovoltaic potential maps in the Canary Islands (http://www.idecanarias.es/), partially funded by the Spanish Ministery of Industry, Tourism and Commerce, and by the European Regional Development Fund.

Bird ~~census~~survey and nest location of blue chaffinches

D~~The d~~ata on bird counts was obtained ~~throughout~~ from ~~line~~ line-transect sampling in Inagua~~,~~ during the breeding season ~~of the species~~ (second fortnight of May and the first fortnight (?) of June; see Rodríguez and Moreno, 2008) from 1994 to 2016 in 15 different years. A fixed network of trails of a total length of 22.9 km has been surveyed using the same methodology since 1994 (see Fig. 1). From 1994 to 2006, ~~the~~ a transect of 22.9 km was ~~census~~surveyed ~~only~~ one time per year; from 2011 to 2016, the transect was repeated three times ~~in~~ on different days to ~~potentially~~ obtain ~~more stable~~ average results. Transects were carried out on windless and rainless days, walking along single tracks at a low speed (1–3 km/h approximately), during the first four hours after dawn. Different persons carried out the ~~census~~surveyes: A.C.M. from 1994 to 2004; V.S and A.D, in 2006, 2011-2016. To account for inter-personal and between-year variation~~s~~ in detectability while ~~doing the monitoring program of the blue chaffinch~~collecting counts, we employed distance sampling methods (Buckland et al., 2007). For each bird heard or seen, the perpendicular distance to the observer's trajectory was estimated. Previous training helped to reduce inter-observer variability in distance estimates. Detection distances were right-truncated, excluding 5% of birds recorded far away (i.e. beyond 125 m). Detectability estimations were as follow; Years 1994-2004: probability of detection (pDET) = 0.64, se = 0.12, sample size (N) = 345 bird contacts; Years 2006, 2013-2016: pDET = 0.56, se = 0.09, N = 385. The total length of transects were divided in 100 contiguous units of equal length (229 m), to which the detected blue chaffinches were averaged across years, accounting for detection probability.

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Intensive ~~prospections~~ surveys of the Inagua pine forest during 2011 to 2016 allowed the location of active nests (carried out by V.S., A.D. and D.T.). We restricted ~~the~~ sample nests used in ~~data~~ analyses to those years when the pine forest had recovered after the forest fire of July 2007. Although searches were mainly carried out around the area covered by the fixed network of trails where the monitoring ~~census~~ program was conducted, other sectors covering the whole Inagua reserve were surveyed while moving around to access those trails (by foot and by vehicles on dirt tracks). Nests were located by following individuals during the prelaying and incubation period (mainly by females), by means of audible begging calls by nestlings, or by observing parents feeding bouts to chicks (see Rodríguez & Moreno, 2008 for more details on nest location and the breeding biology of the blue chaffinch in Inagua). Nests were monitored every 3–~~-~~5 days in order to establish the successful reproduction of each breeding pair. We considered a successful breeding attempt when at least one fledgling was produced in the focal nest. ~~Fifty~~ Fifty-nine successful nests were recorded: 16 in 2011, 12 in 2013, 16 in 2014, 15 in 2016. They were found within an area of 24.2 km^2 (2.6×~~ x ~~9.2 km in latitude and longitude geographical dimensions). Altitudinal range of nest locations was 860~~–~~–1485 m a.s.l., within a broad spectrum of orographic conditions regarding the cardinal orientation and the slope of the terrain (see Table S1 of the supplementary material). The Consejería de Medio Ambiente del Cabildo de Gran Canaria gave permisión to carry out all the field work under the LIFE14 NAT/ES/000077.

Data analyses

Detectability models for the blue chaffinch were built with the R packages *{Distance}* (Miller, 2016a) and *{mrds}* (Miller, 2016b) under R version 3.1.2 (R Core Team, 2014). Population density of the blue chaffinch in Inagua was calculated considering the counts of birds in the 22.9 km transect and the effective strip width (ESW) derived from the probability of detection.

Breeding habitat suitability for the blue chaffinch in Inagua was modelled using boosting classification trees with the occurrence of the species ~~in the~~denoted as nest locations ~~with~~ where successful breeding ~~attempts~~occurred. Boosting trees are a statistical learning method that attains both accurate predictions and good explanations for regression and classification problems, dealing with many types of response and predictor variables (numeric or categorical) and loss functions (Gaussian, binomial, Poisson), and managing parsimoniously complex interactions among predictors (De'Ath, 2007; Elith et al., 2008). Boosting trees algorithm aims to improve model accuracy by fitting several trees in a stage-wise process in which the first tree focuses on the raw data, the second tree on the residuals from the first tree, and so on. Final predictions are made through model averaging.

BCT models were built and summarizing using the R packages *{gbm}* (Ridgeway, 2016), *{dismo}* (Hijmans et al., 2016), *{ROCR}* (Sing et al., 2015) and *{psych}* (Revelle, 2016). Model parameters were: bag fraction of 2/3, learning rate of 0.001, tree complexity of 5 (a maximum model complexity of 11 nodes-leaves and five splitting criteria), and minimum of 5 sampling units per inner node. We used a ten-fold approach in order to test the accuracy of predictions of BCT models. The discrimination ability of BCT models was estimated through the area under the curve (AUC) of the receiver operating characteristic (ROC) plot of sensitivity against 1-specificity.

The environmental characteristics of the cells of 50×~~x~~50 m in which the successful nests were located (n = 59; "breeding success", level 1 of a binomial distribution) were compared with those measured in an identical number of 50×~~x~~50 m cells randomly obtained from the background of Inagua (59 out of 15,037 cells obtained by means of resampling without replacement; "available habitat", level 0 of a binomial distribution). Moreover, ~~in order~~ to obtain a more robust approximation to the habitat occupancy during reproduction, bootstrapped samples of the ~~fifty~~ fifty-nine 50×~~x~~50 m cells with successful breeding were obtained (i.e., resampling with replacement ~~in order~~

Commented [TWE9]: I'm more familiar with this being 'boosted', boosted trees produced by a boosting algorithm to avoid outliers). This analytical approach is associated with the classic, and well-established, study of ~~the~~ habitat selection in which ~~the active~~ habitat used is compared against ~~the~~ habitat availability (Cody, 1985; Wiens, 1989)~~,~~ in such a way that the sample size of the availability records is determined by the sample size recorded for the individuals under study. Moreover, this approach shows good statistical properties in comparison with other presence-only analyses (Barbet-Massin et al., 2012; see also Warton & Aarts, 2013). BCT predictions (*p*) around 1 denote that the 50×~~x~~50 m cells have environmental characteristics very similar to those shown by the nest locations with blue finch successful reproduction. Conversely, BCT predictions around 0 are related to 50×~~x~~50 m cells with extremely different environmental characteristics for the successful reproduction of the species. And finally, when *p* = 0.5, the environmental characteristics of the 50×~~x~~50 m cells are similar to the average of the habitat use and habitat availability samples.

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We repeated the BCT models 20 times, using different bootstrap samples of the 50x50 m cells characterizing the habitat of the 59 breeding successful nests, and different random samples of 59 background cells of 50×~~x~~50 m. The values obtained with these 20 models were averaged (accuracy parameters, relative importance of the 12 predictor variables, partial effects of each variable, and predictions for all 50x50 cells in Inagua, Tamadaba, Pilancones and Tauro).

BCT predictions of habitat suitability for the successful breeding of the blue chaffinch in the one-hundred 229-m units, of the abundance monitoring transect, were obtained by averaging the nearest sixteen 50×~~x~~50 m cells. Habitat suitability in these 100 sample units were regressed upon the average number of blue chaffinch counted in those years ~~when~~ after the pine forest ~~have been~~ recovered from the forest fire of July 2007 (i.e., 1994-2006 and 2011-2016; 15 years considered). The spatial eigenvector mapping analysis (SEVM) was carried out to account for spatial autocorrelation in the 100 transect units (Diniz-Filho & Bini, 2005; Dorman et al., 2007). SEVM is based on the idea that spatial arrangement of sample locations can be translated into explanatory variables that capture spatial effects, by means of the eigenfunction decomposition of the spatial connectivity matrix among the 100 transect units of 229 m. SEVM produced three spatial filters that reduced the spatial autocorrelation in the residuals of the regression model of chaffinch abundance on predicted habitat suitability for successful breeding (i.e., the residuals showed nonsignificant figures of spatial autocorrelation according to Moran's I). SEVM was carried out using SAM package (v. 4.0; Rangel et al., 2010). Due to deviations from homoscedasticity of the residuals across the predictions of the SEVM model, we used the heteroscedasticity-corrected coefficient covariance matrix ~~in order~~ to obtain the proper significance of habitat suitability and the three spatial filters (Zeileis, 2004); the HC4m estimator suggested by Cribari-Neto (2004) was used to further improve the performance in significance estimations, especially in the presence of influential observations under small sample sizes (using the R package *{sandwich}*, Lumley and Zeileis, 2015). Quantile regression of bird abundance against habitat suitability was carried out using *{quantreg}* package (Koenker, 2016), applying the bootstrapping approach for estimating standard errors and significance.

RESULTS

Reproductive habitat selection and habitat suitability modelling

The boosted classification tree models (BCT) produced highly accurate results, considering sensitivity (0.999), specificity (0.979), 10-fold cross-validation AUC (0.905), and positive (0.979) and negative (0.999) predictive success figures (see Table 1 for more details regarding the results of the 20 randomized runs of the BCT models, each time with a different random sample of background 50×~~x~~50 m cells). The variables with the highest relative importance in the BCT models were pine height (relative importance = 26.4 units?), tree cover (19.2), altitude (13.7), and rainfall during the driest trimester (July-September; 11.7). The remaining eight predictors had relative importance lower than that expected considering the number of predictors (100/12 = 8.3). Table 2 shows the results for the relative importance of predictors in 20 runs of the BCT models, and Fig. 2 shows the partial dependence plots for the four most influential variables.

Habitat suitability for successful breeding steadily increased with pine height from 15 to 20 m (remaining stably high above the second value), with tree cover from 25% to 37% (the partial influence of tree cover was at random when cover was higher than 55%), with altitude from 1100 to 1280 m a.s.l. (remaining stably high above the second value), and from 13 to 20 mm of summer rainfall. Habitat suitability in Inagua was very low in sectors with ~~less than~~≤17 m of pine height, ≤30% of tree cover, at altitudes ~~lower than~~ ≤1100 m a.s.l. and at locations with ~~less than~~≤13 mm of precipitation during July-September. ~~Average~~ Mean habitat suitability in the forest patches with those characteristics was 0.029 (sd = 0.019, interquartile range: 0.018-0.030, n = 2285 cells~~ of 50x50 m~~). Conversely, habitat suitability reached the highest figures in woodland sectors located between 1200 and 1550 m of altitude, with pines taller than 20 m covering 37-50% of the area, and with a summer precipitation of 18-24 mm. Average habitat suitability in these favourable forest patches was 0.827 (sd = 0.083, interquartile range: 0.781-0.889, n = 261 cells~~ of 50x50 m~~).

The average BCT model obtained in Inagua has been applied to the environmental data of the pine forests of Gran Canaria island located within the altitudinal range of the study area in which the BCT models were built. The results of the predicted suitability for the pine forests of Inagua, Tamadaba, Pilancones and Tauro are presented in Fig. 3, and with more detail in the Figures S1-S3 of the supplementary material. Habitat suitabilities of pine forests are summarized in Fig. 4 according to the area in an increasing scale of suitability levels. Inagua is the pine forest with the largest surface for the successful breeding of the blue chaffinch (795 ha with a suitability >0.5), followed by Tamadaba pine forest (389 ha) and Pilancones (42 ha); Tauro forest lacks suitable habitat for the reproduction of the species. This pattern of among forests differences in habitat suitability becomes more skewed when considering higher levels of habitat suitability; e.g., with suitability >0.8, there are 209 ha in Inagua, 48 in Tamadaba and a complete lack of habitat in Pilancones and Tauro. Moreover, there is more contiguity of woodland patches with high levels of habitat suitability, and their sizes are larger, in Inagua than in Tamadaba (compare smoothed values of suitability >0.5 in Figures S1 and S2 of the supplementary material). Finally, the proportion of pine forest surface with very low habitat suitability (e.g., <0.2) decreased according to the following order: Pilancones (92.1%), Tauro (89.2%), Tamadaba (62.5%) and Inagua (57.5%). Summarizing, Inagua reserve, the classical pine forest with historic and continuous presence of the blue chaffinch, has the largest potential area of more favourable habitat for the successful breeding of the species, with larger and less fragmented suitable woodland patches, and with the lowest proportion of unfavourable breeding habitat. The pine forest of Tamadaba, with scarce presence of the blue chaffinch in the last 60 years, also provides suitable woodland patches for the species, although the amount of highly favourable habitat is lower, and its patchiness higher, than that obtained for Inagua. The pine forests of Pilancones and Tauro have an extremely low habitat suitability for the successful breeding of the species.

Relationship between local abundance and predicted habitat suitability

There was a positive relationship between the predicted breeding habitat suitability of BCT models in 100 units of the same 22.9~~-~~-km ~~census~~survey trail in Inagua reserve, and the ~~average ~~mean number of blue chaffinches counted in the breeding season during 15 years in those units (1994-2006 and 2011-2016, considering those years when the pine forest was not affected by the devastating forest fire of July 2007; Fig. 5). The linear model obtained taking into account three spatial autocorrelation filters (that reduced the spatial autocorrelation in the residuals of the model -being nonsignificant according to Moran's I-) was highly significant: R^2 = 42.5%, $F_{4,95}$ = 17.55, p << 0.001. The partial contribution of the spatial filters (i.e., spatial component) to total variance in blue chaffinch counts was 19.2%, that attributable to predicted suitability was 15.3%, while 8% was the shared contribution of both sets of predictors. The partial effect of the habitat suitability on finch counts was highly significant (partial slope = 0.661, ~~heteroskedastic ~~heteroskedastic-corrected standard error = 0.151, p << 0.001). This relationship depicts a relatively triangular spread. In fact, a quantile regression analysis shows that the slope progressively increases from 10% to 50% to 90% percentiles (tau = 0.1, b = 0.367, se = 0.187, p = 0.053; tau=0.5, b = 0.491, se = 0.214, p = 0.0243; tau = 09, b = 0.760, se = 0.251, p = 0.003; taking into account the three spatial autocorrelation filters). Thus, two different sets of habitat preference measures were highly correlated, showing that for a passerine species with a low population density, such as the blue chaffinch in Gran Canaria, local estimations of abundance are positively related to habitat favourability for successful breeding.

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Considering the relationship between habitat suitability and local abundance of the blue chaffinch in 2011~~-~~–2016 (very similar to that depicted in Fig. 5; partial slope = 0.780, ~~heteroscedastic ~~heteroscedastic-corrected standard error = 0.194, p = 0.001), and its conversion to density (accounting for detectability in the period 2011–~~-~~2016), and the suitability map of Fig. 3, we ~~have~~ calculated the probable population size of the species in Inagua (using the 95% confidence interval of the predictions in 15037 cells of 50×~~x~~50 m^2). Although the topic merits an exhaustive census program, this assessment should be considered as a first approximation to the population estimation in Inagua. The ~~average~~ mean ~~estimation~~ estimate is 279 birds, with a 95% confidence interval of 195–~~-~~430 chaffinches.

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DISCUSSION

Relationship between local abundance and predicted habitat suitability

Studies aimed at predicting species abundance from species occurrence distribution models have yielded ~~a~~ mixed ~~bag of~~ results (e.g., Conlisk et al., 2009; Jiménez-Valverde et al., 2009; Yañez-Arenas et al., 2014; Carrascal et al., 2015; Basile et al., 2016). A recent meta-analysis (Weber et al., 2016) ~~concludes~~ concluded that occurrence data can be a reasonable proxy for abundance, especially if local environmental variables are considered when dealing with the abundance-suitability relationship. Our results show that the observed local abundance of the blue chaffinch in Inagua (~~census~~survey data) ~~correlates~~ correlated with habitat suitabilit~~i~~y derived from modelling the location of successful breeding attempts. The relationship was relatively triangular (Fig. 5), denoting the asymmetric relationship between these two parameters: unsuitable woodland sectors can only have low blue chaffinch abundances, whereas very favorable sites can have high or low abundances (see VanDerWal et al., 2009; Jiménez-Valverde, 2011). This suggests the existence of other important factors responsible for the emergence of the triangular positive relationship, such as the "unsaturation" of the available habitat (i.e., there are not enough blue chaffinches to occupy the favorable woodland patches) or other unmodelled habitat features. For example, García-del-Rey et al. (2009, 2010) have shown the importance of structure and species identity of the shrub layer during the breeding season, as well as pine seed availability on the ground for feeding habitat selection during winter in *F. teydea* of Tenerife island. On the other hand, ~~census~~survey counts at very small spatial scales may be accounting for the mere presence of floaters or breeders outside the core area of the nesting place, as chaffinches (especially males) spend a considerable amount of time outside the breeding territories (e.g., Hanski & Haila, 1988 with *Fringilla coelebs*). Conservation biologists are warned to be cautious when relying on abundance estimations as surrogates of habitat quality (Van Horne, 1983), which is more accurately described with labor-intensive demographic research (Johnson, 2007). Nevertheless, our results suggest that local abundance is a good surrogate of environmental quality for successful nesting in the blue chaffinch, which agrees with other previous studies showing that birds are usually more abundant in habitats where per capita reproduction is highest (e.g., review by Bock & Zach, 2004; Carrascal & Seoane, 2009).

Population size

In spite of the imperfect fit between habitat suitability for successful nesting and local bird abundance, regional abundance can be accurately predicted in an unbiased way from occurrence distribution models by the aggregation of local predictions, whose overpredictions and underpredictions can be counteracted (see Carrascal et al., 2015 for 21 terrestrial bird species in La Palma, Canary islands). Thus, the species occurrence distribution models can be used as a cost-effective tool to provide tentative population estimations when data from exhaustive census programs are not available. We ~~have~~ estimated an exiguous population size of ca. 280 blue chaffinches in Inagua, which is

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Commented [TWE13]: Love the word, but it is superfluous here consistent with its low population density and the small area of this pine forest (37.6 km^2). ~~Other~~ Another 38 blue chaffinches ~~have to be~~can be added to those low numbers (minimum estimation; Rodríguez, 2016), ~~considering~~ given the recently established small population located at higher altitudes in La Cumbre (from a captive breeding and translocation program; Delgado et al., 2016; Rodríguez, 2016). Therefore, with ~320 individuals during the breeding season, the Gran Canaria blue chaffinch is the ~~small~~ passerine ~~of the Western Palearctic~~ with the lowest population size in the Western Palearctic~~of around 320 individuals during the breeding season~~. This population size is several times lower than that recorded for the other three specialists species of marginal woodlands with very small populations: *Sitta whiteheadi* (5500 individuals in ca. 185 km^2; BirdLife International, 2016b), *Phyrrula murina* (1000 individuals in ca. 100 km^2; BirdLife International, 2016c), and *Sitta ledanti* (350-1500 individuals in ca. 700 km^2; BirdLife International, 2016d). Although the population size of the blue chaffinch is considerably lower than minimum viable population sizes suggested for birds (around 3500 individuals for a persistence probability of 99% in 40 generations; Brook et al., 2006; Traill et al., 2007), its persistence with relatively constant numbers in Inagua during the last several years probably shows its high resilience against demographic risk factors.

Commented [TWE14]: Or, it's just lucky

Breeding habitat selection

Habitat preferences for successful breeding of the Gran Canaria blue chaffinch are similar to those measured in its sibling species from the nearby Tenerife island, although ~~*Fringilla polatzeki*~~blue chaffinch show~~s~~s a remarkably lower altitudinal range and a higher preference for mature pine stands. *Fringilla teydea* ~~spreads~~ ranges from 1000 to 2060 m a.s.l., reaching in the 1500-2000 m belt an average abundance 3.4 times higher

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than that recorded at 1000-1500 m (Carrascal & Palomino, 2005). The BCT model for blue chaffinch ~~*F. polatzeki*~~ in Inagua shows a step increase of habitat suitability with altitude up to 1300 m where it stabilizes, a limit that can be understood considering that only 15.8% of Inagua is ~~above~~ >1300 m a.s.l. and 0.28% above 1500 m. Thus, Inagua ~~establishes~~ imposes an altitudinal restriction to blue chaffinch ~~*F. polatzeki* due to its~~based on orography, but the 1300 m a.s.l. threshold is not a true biological limit as the data of the recently established small population in La Cumbre demonstrates. The species is able to dwell at higher altitudes in this area (Delgado et al., 2016), and has shown a formidable increase in the number of breeding pairs from two in 2010 to 16 in 2016 (Rodríguez, 2016). Therefore, the altitudinal range of Gran Canaria probably imposes, *per se*, restrictions to the distribution of the blue chaffinch, assuming that *F. teydea* and blue chaffinch ~~*F. polatzeki*~~ share similar abiotic environmental preferences as sibling species.

As for forest structure, the highest habitat suitability for the successful breeding of blue chaffinch ~~*F. polatzeki*~~ is attained in woodland stands with more than 21 m of pine height and tree cover between 35%-55%. Practical recommendations can be derived from these results for managing the dense and relatively young pine plantations located above 1300 m a.s.l. in other areas of Gran Canaria island (La Cumbre, Los Marteles, Moriscos-Galdar). The positive influence of pine height on habitat preferences has been also observed in *F. teydea* (see Carrascal and Palomino, 2005 at a broad scale, and García-del-Rey et al., 2009 at the habitat use level), while the species in Tenerife island is ca. three times more abundant in thinned (53% tree cover) than in unmanaged (86%) reafforestations (García-del-Rey et al., 2010). Nevertheless, the most remarkable difference between the habitat preferences of the two taxa is the ability of *F. teydea* to occupy young pine forests during the breeding season (e.g., Carrascal et al., 1992; García-del-Rey and Cresswell, 2005; García-del-Rey et al., 2010), even the non-native

Pinus radiata plantations (Carrascal, 1987), with densities ranging from 25 to 170 birds/km^2 in woodlands with pine height ranging from 7 to 15 m. Again, the preference for well-developed and open forests of blue chaffinch ~~*F. polatzeki*~~ in Inagua may be the consequence of the maturity of the pine forest in this area. This idea is supported by the fact that blue chaffinch ~~*F. polatzeki*~~ is able to thrive at higher altitudes in the less mature pine forests of La Cumbre, with a survival and reproductive success very similar to that recorded in Inagua (Rodríguez & Moreno, 2008; Delgado et al., 2016).

Habitat favourability outside the main distribution area

The favourable environmental conditions for the blue chaffinch identified in Inagua suggest other natural and historic Gran Canaria pine forests that are not suitable for the species, and should be discarded in the population management plans (i.e., habitat management-restoration or translocations of individuals). This is clearly the case of Tauro and Pilancones forests, for which the predicted very low habitat suitability maps (see Figure S3 of the supplementary material and Fig. 4) reinforces the lack of the species throughout the historical distribution of the species in Gran Canaria island (Martín & Lorenzo, 2001). On the other hand, Tamadaba forest has more favourable habitat for the species, especially in the upper part of the two main ridges. The existence of suitable habitat for the reproduction of the species agrees with the recorded historical presence in this area, although always in low numbers up to 1991 (Moreno and Rodríguez, 2007), and recent eventual sightings since 2010 (Pascual Calabuig and Felipe Rodríguez, pers. com.). Nevertheless, the antique photos available for the Tamadaba pine forests in the middle of the 20th century (little vegetation cover of a relatively young pine forest; www.fotosantiguascanarias.org), suggest that the species was not abundant in the past. The low amount of highly suitable habitat for the blue chaffinch in Tamadaba means that this area could foster a smaller population than Inagua (see woodland area with habitat suitability >0.7 in Fig. 4; 658 ha in Inagua for a population of ca. 280 individuals vs. 195 ha in Tamadaba). The potential area could be further reduced considering the fragmentation of highly suitable woodland patches (see Fig. 4 and Figure S2). This is a concern as woodland specialists usually require large patches of continuous well-preserved forests (e.g., Santos, et al., 2002; Fahrig, 2003; Devictor et al., 2008), and habitat fragmentation negatively affects the abundance and suitability of an area for birds (e.g., Basile et al., 2016). Nonetheless, Tamadaba should be considered as a potential area for translocations of blue chaffinches, especially those sectors located at higher altitudes, with tall~~est~~ pine trees and~~ with~~ higher summer rainfall. Even if in low numbers, this area would add to the two current distribution areas of the species in Gran Canaria.

CONCLUSIONS

Given the preference of this species for mature pine forests that are suffering forest dieback as a consequence of climate change (Martín et al., 2015), we may be witnessing the vanishing existence of an endemic woodland bird species in the eastern limit of the Canary forests. Nevertheless, the reintroduction of the species in other suitable pine forests (especially if they are located at higher altitudes), and forest management practices directed to reduce woodland fragmentation and modify habitat structure according to blue chaffinch habitat preferences, may ameliorate or counteract this vanishing trend. Our results demonstrate that habitat suitability obtained from modelling the location of successful breeding attempts is a good surrogate of the observed local abundance. Thus, ~~it~~ habitat suitability can be used for the identification of potential areas for translocations of blue chaffinches~~,~~ or as a cost-effective tool to provide tentative population estimates.

ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The authors declare there are no competing interests.

Author Contributions

LMC undertook the data analyses, conceived, wrote and oversaw the paper. ACM designed the ~~census~~survey program, conducted all data preparation and generated the figures with maps. ACM, AD, VS and DT obtained the field data. All authors read the final draft of the manuscript.

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Supplemental Information

Table S1. Environmental characteristics of the four studied pine forests.

Figures S1, S2 and S3: Contour line maps representing the habitat suitability for the successful breeding of the blue chaffinch in four pine forests of Gran Canaria island.

Table 1. Summary of the 20 randomized runs of the boosted classification tree (BCT) models analysing habitat suitability of the nesting location of successful breeding pairs (at least one fledgling per season). The BCT models compare the habitat characteristics in pixels of 50x50 m around nests (59 nests with breeding success recorded in six years from 2011 to 2016) against the same number of pixels of the same size randomly obtained from the pine forests of Inagua reserve. Twelve environmental variables were used in all BCT models (see Table 2).

	mean	sd	minimum	maximum
Number of boosted trees	4640	996.1	2800	6400
Ten-fold cross-validation AUC	0.905	0.024	0.869	0.938
Sensitivity	0.999	0.004	0.983	1.000
Specificity	0.979	0.015	0.932	1.000
Negative predictive value	0.999	0.004	0.983	1.000
Positive predictive value	0.979	0.015	0.937	1.000

Table 2. Average relative importance (in %) of 12 environmental variables in boosted classification trees models (for more details see Table 1). Results are for 20 randomized runs analysing habitat suitability of the nesting location of successful breeding pairs against the same number of pixels of the same size randomly obtained from the pine forests of Inagua reserve.

	mean	sd	minimum	maximum
Altitude	13.7	5.8	2.2	24.3
Slope	5.6	2.5	2.8	9.6
Northern orientation	4.4	1.7	2.1	7.9
Western orientation	2.6	0.8	1.6	4.8
Incident solar radiation	5.0	3.1	1.7	14.5
Average temperature in May	2.9	1.0	1.5	4.6
Average temperature in July	2.0	0.6	1.3	3.4
Rainfall in July-September	11.7	6.1	3.7	25.6
Cover of the canopy (pine) layer	19.2	7.9	7.7	37.5
Average pine height	26.4	9.2	10.2	49.2
Cover of the shrub layer	4.3	1.4	1.5	7.4
Average height of shrubs	2.2	1.3	0.5	5.3

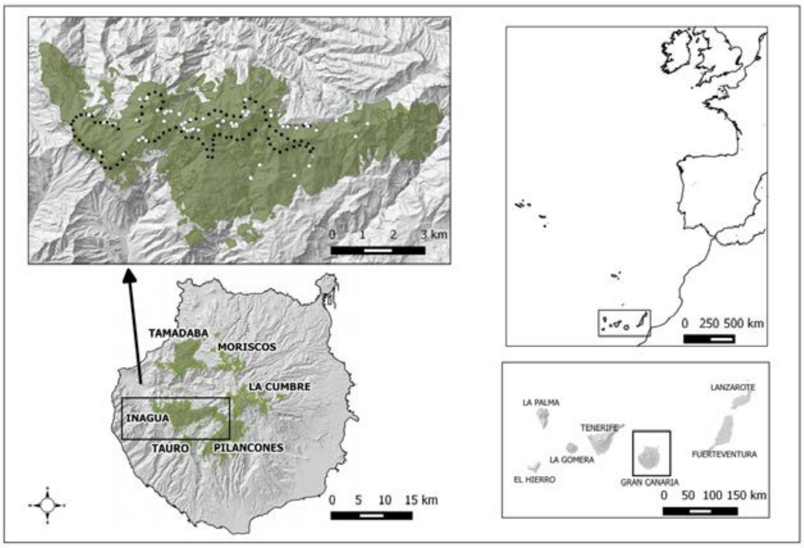


Figure 1. Study areas in Gran Canaria island. Other pine forests, outside the altitudinal range of the core distribution area of the blue chaffinch in Inagua, are also shown (Moriscos and La Cumbre; they are pine plantations mainly established after 1960). White dots in Inagua show the location of nests with successful breeding attempts (at least one chick fledged, and only one nest per breeding pair and year). Black dots show the centre of 100 units of 229 m in length of a ~~census~~survey trail of 22.9 km repeated from 1994 to 2016.

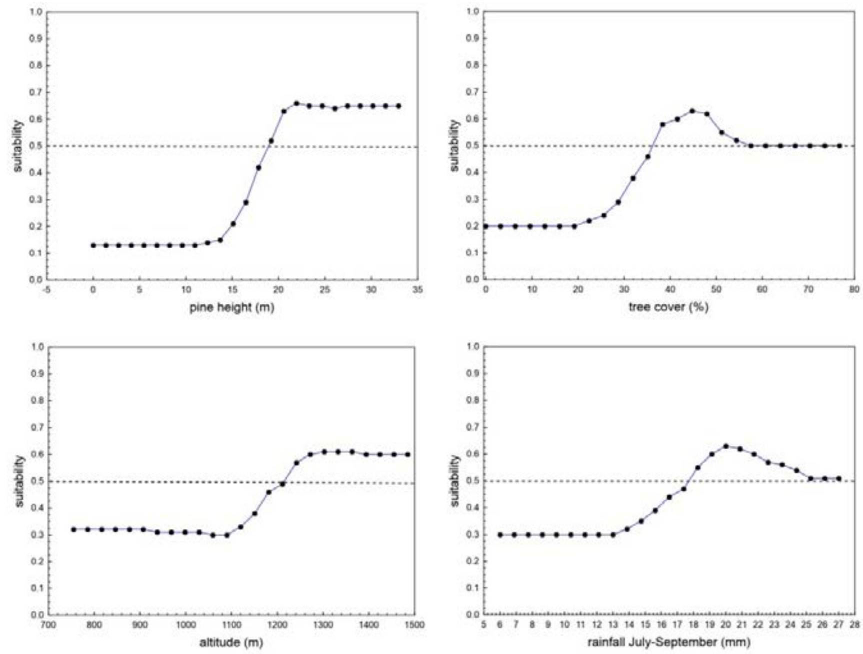


Figure 2. Average partial dependence plots for the four most influential variables in the 20 randomized runs of boosted classification trees models analysing habitat suitability of the nesting location of successful breeding pairs of blue chaffinches against the same number of pixels of the same size randomly obtained from the pine forests of Inagua reserve. Suitability value of 0.5 denotes random distribution according to each predictor (depicted by means of a dashed line). Values of the predictors with low suitability figures show that those environmental conditions are not favourable for the breeding success of the blue chaffinch in Inagua reserve. See Tables 1 and 2 for more details.

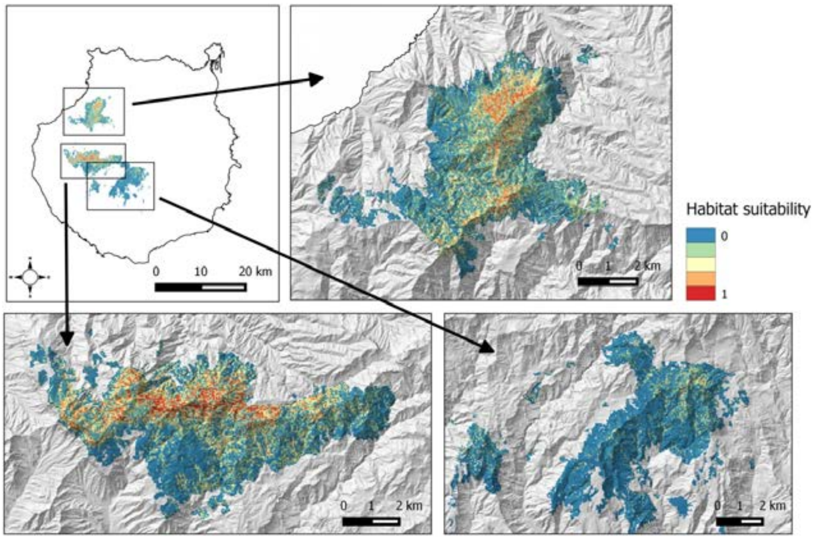


Figure 3. Habitat suitability map for the successful breeding of the blue chaffinch in four pine forests of Gran Canaria island located within the altitudinal range of Inagua. The map resolution is 50×~~x~~50 m^2 cells. Tamadaba in right upper panel; Inagua in left lower panel; Pilancones and Tauro in right lower panel.

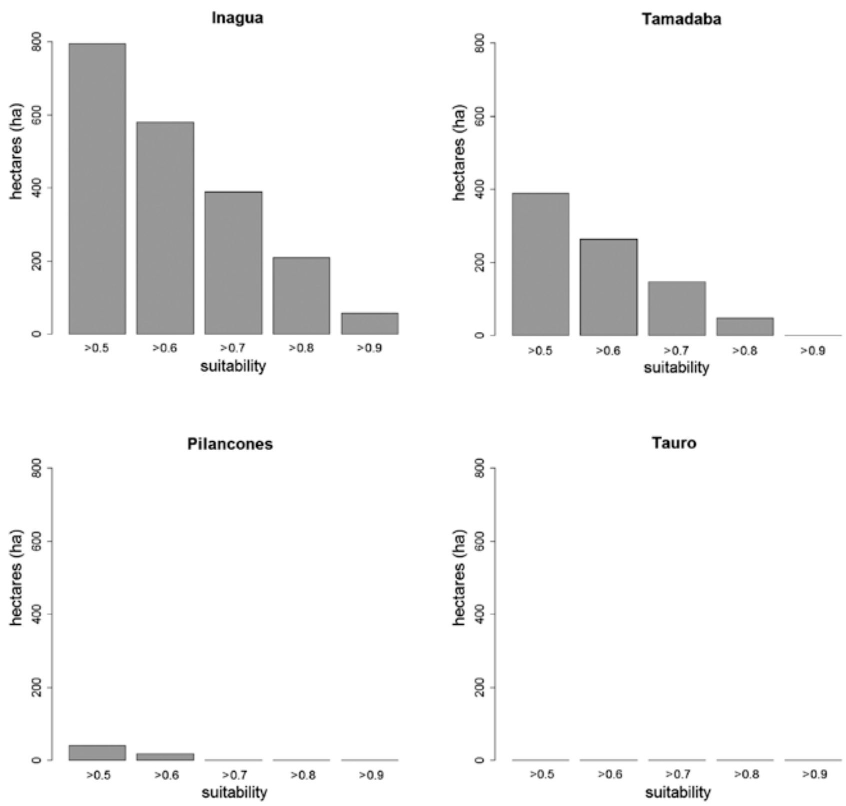


Figure 4. Surface of four pine forests of Gran Canaria Island with different levels of habitat suitability for the successful breeding of the blue chaffinch.

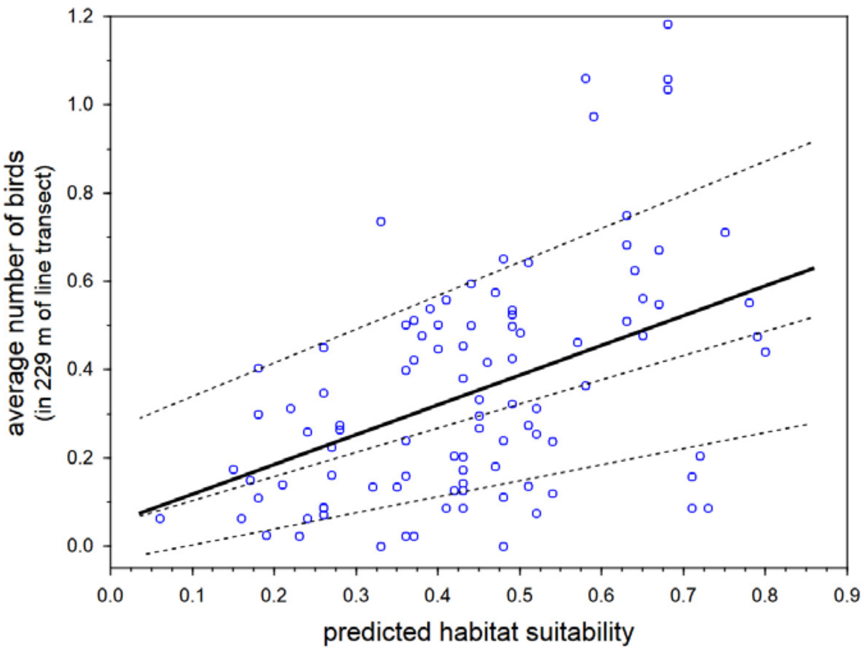


Figure 5. Relationship between the predicted breeding habitat suitability of BCT models and the average number of blue chaffinches counted during the breeding season in 100 transect units of 229 m along the same 22.9~~-~~km ~~census~~survey trail in Inagua reserve during 15 years (1994-2006 and 2011-2016 in those years when the pine forest was not affected by the devastating forest fire of July 2007). The thick line shows the partial OLS regression slope, and the three dashed lines the regression slopes for 90%, 50% and 10% quantile regressions, after controlling by three spatial filters obtained by means of spatial eigenvector mapping (i.e., the residuals of models do not manifest statistically significant spatial autocorrelation according to Moran’s I).

Supplemental Information

Table S1. Environmental characteristics of the four studied pine forests.

Figures S1, S2 and S3: Contour line maps representing the habitat suitability for the successful breeding of the blue chaffinch in four pine forests of Gran Canaria island.

Supplementary material.

Table S1. Environmental characteristics of the four studied pine forests (Inagua, 50×~~x~~50 m cells = 15,037; Tamadaba, 11,246; Pilancones, 12,667; Tauro, 1,880), the areas traversed by the ~~census~~survey trail in Inagua reserve (n = 100), and of the nests with successful breeding attempts in Inagua (n = 59).

		Inagua	Tamadaba	Pilancones	Tauro	~~census~~survey trail	nests
Altitude	mean	1115.50	1013.38	1008.15	911.99	1259.00	1264.92
(m)	min	250.00	360.00	300.00	295.00	1075.00	865.00
	max	1550.00	1435.00	1510.00	1215.00	1450.00	1485.00
	sd	168.13	198.93	178.15	167.79	95.07	142.43
Slope	mean	45.83	48.08	44.54	54.05	58.05	50.39
(%)	min	0.00	0.00	0.00	0.00	17.78	22.44
	max	183.75	260.19	155.72	219.95	120.20	118.25
	sd	23.44	24.95	22.78	32.90	23.10	15.96

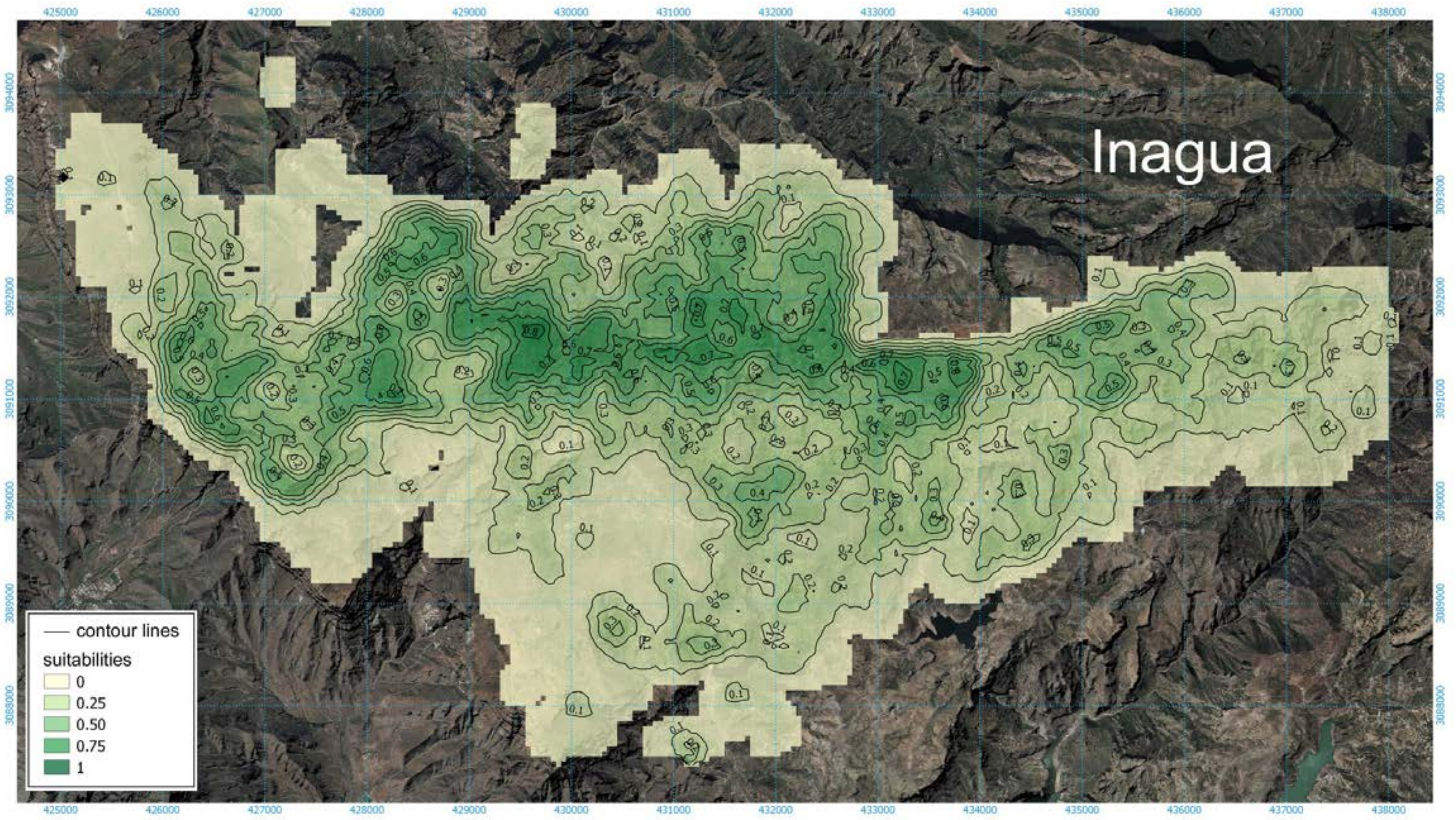
Western orientation	mean	-0.09	0.16	-0.05	-0.08	-0.07	0.01
(sin cardinal orientation)	min	-1.00	-1.00	-1.00	-1.00	-0.98	-0.97
	max	1.00	1.00	1.00	1.00	0.98	0.95
	sd	0.70	0.68	0.64	0.65	0.71	0.73
Northern orientation	mean	0.03	-0.06	-0.03	0.02	-0.03	-0.16
(cos cardinal orientation)	min	-1.00	-1.00	-1.00	-1.00	-0.98	-0.94
	max	1.00	1.00	1.00	1.00	0.99	0.97
	sd	0.70	0.71	0.77	0.76	0.58	0.57
		Inagua	Tamadaba	Pilancones	Tauro	~~census~~survey trail	nests
Cover of the canopy (pine) layer	mean	25.79	42.74	18.38	16.78	29.56	34.43
(%)	min	0.00	0.27	0.41	0.39	2.91	17.65
	max	97.26	99.29	82.00	80.49	46.69	52.64
	sd	13.87	20.10	10.33	11.32	8.46	5.86
Average pine height	mean	16.50	14.26	13.57	13.49	17.84	21.04
(m)	min	0.00	2.16	2.00	2.30	6.50	14.32
	max	40.23	36.66	31.64	29.96	26.64	25.95
	sd	6.38	4.66	4.15	4.88	4.96	2.41
Cover of the shrub layer	mean	8.83	13.42	6.05	8.67	8.47	9.81
(%)	min	0.00	0.00	0.00	0.00	0.67	0.71
	max	75.00	64.00	59.00	63.00	22.55	44.17

	sd	9.98	10.70	7.63	9.63	6.16	8.43
Average height of shrubs	mean	0.70	0.74	0.68	0.71	0.70	0.71
(m)	min	0.00	0.57	0.53	0.49	0.62	0.62
	max	1.25	1.22	1.21	1.25	0.83	1.01
	sd	0.09	0.10	0.07	0.09	0.06	0.07
Incident solar radiation	mean	7008.74	6796.56	6788.95	6972.34	7030.16	7062.41
(average April-August; kWh/m^2)	min	5230.27	4567.25	5260.99	5282.73	6197.41	6180.29
	max	7435.98	7221.65	7208.58	7514.96	7317.35	7268.68
	sd	264.54	280.17	252.71	400.39	238.69	171.37

		Inagua	Tamadaba	Pilancones	Tauro	~~census~~survey trail	nests
Average temperature in May	mean	19.42	18.54	19.35	20.28	19.62	19.44
(ºC)	min	17.89	16.98	17.82	18.80	18.53	17.94
	max	20.37	19.92	20.70	21.23	20.19	20.16
	sd	0.67	0.68	0.66	0.41	0.46	0.59
Average temperature in July	mean	24.48	23.85	24.98	24.55	24.47	24.44
(ºC)	min	23.95	23.61	24.44	24.25	24.25	24.07
	max	25.19	23.98	25.91	25.14	24.95	25.18
	sd	0.26	0.08	0.35	0.19	0.19	0.20
Rainfall in July-September	mean	15.87	23.88	8.36	14.48	20.02	19.57
(mm)	min	3.00	11.00	0.00	1.00	13.18	8.07

	max	28.00	34.00	17.00	20.00	27.00	26.85
	sd	6.44	4.63	4.04	4.31	3.91	4.45

Figures S1, S2 and S3: Contour line maps representing the habitat suitability for the successful breeding of the blue chaffinch in four pine forests of Gran Canaria island. The suitability level of 0.5 denotes random distribution of the species. The contour lines have been applied to a map of 50x50 m cells. The suitability of each cell was obtained after smoothing the original prediction of the boosted classification trees (BCT), considering a larger square of 5x5 cells where the cell of interest was located in its center. BCT models were carried out with the habitat characteristics in pixels of 50x50 m around nests (59 nests with breeding success recorded in six years from 2011 to 2016) against the same number of pixels of the same size randomly obtained from the pine forests of Inagua reserve.


Inagua
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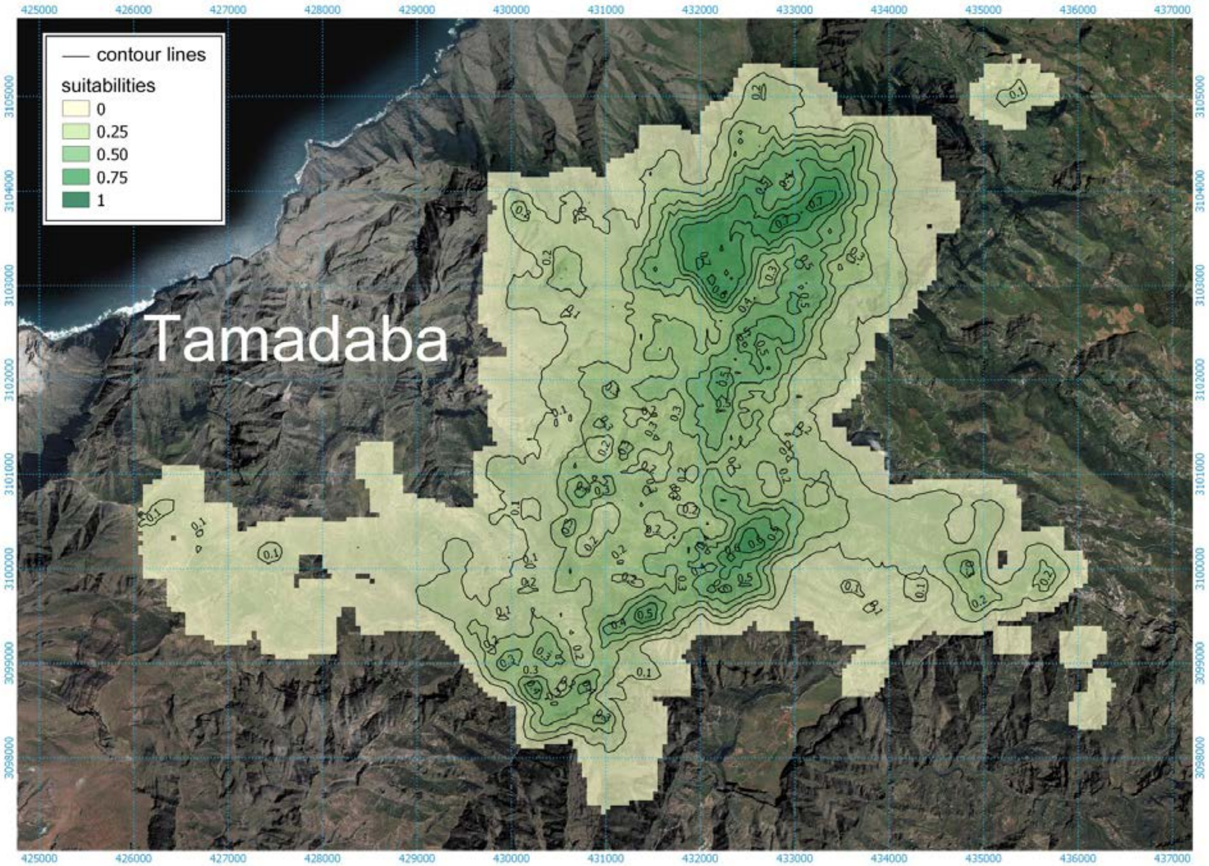

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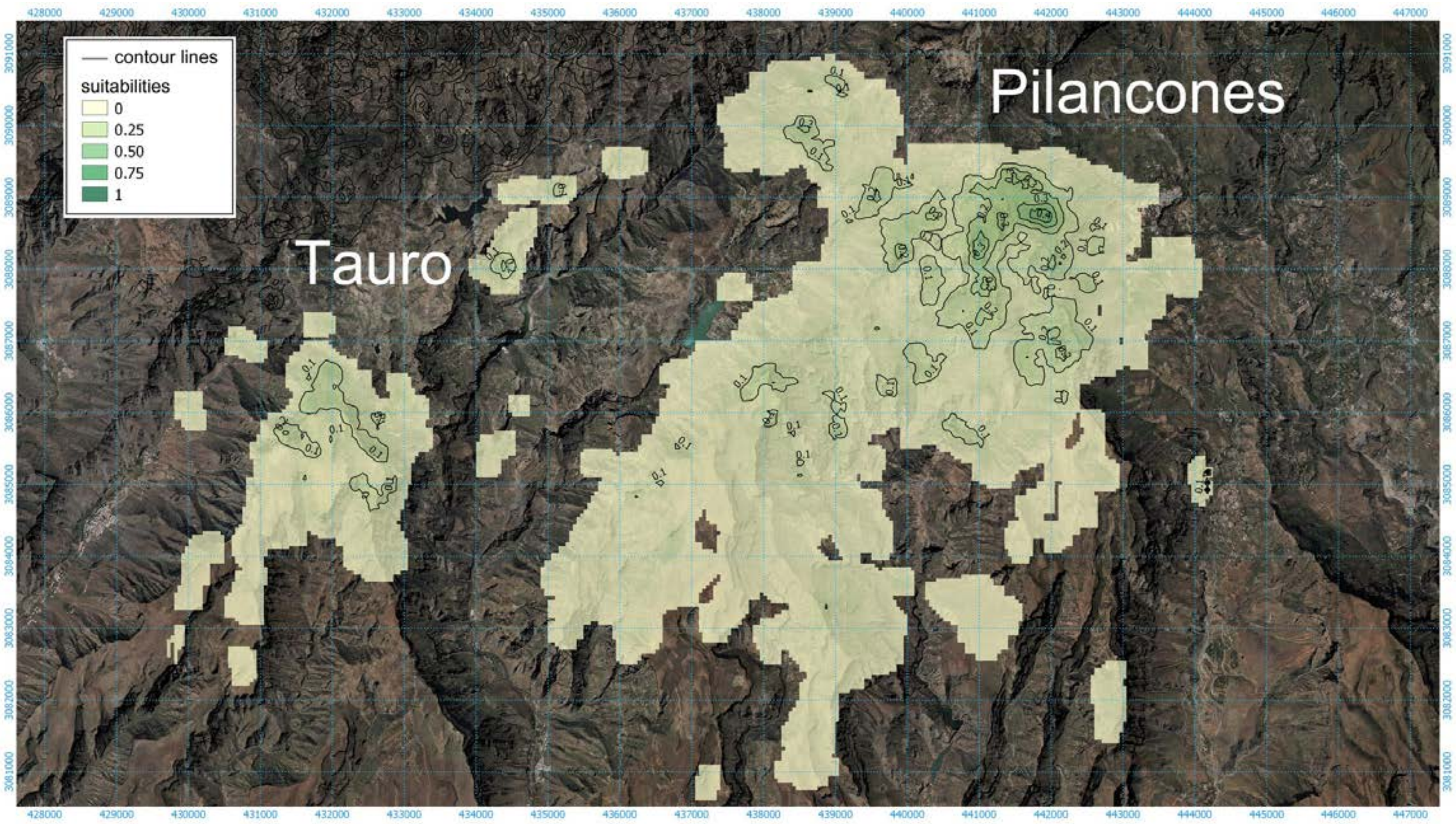
contour lines
suitabilities
0
0.25
0.50
0.75
1
Tauro
Pilancones