Population size, abundance, habitat relationships and the result of a translocation programme in the Gran Canaria Blue Chaffinch *Fringilla polatzeki*

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Summary

The Gran Canaria Blue Chaffinch *Fringilla polatzeki* is a threatened, endemic, forest-dwelling bird species of the Canary Islands, whose core population at the end of the 20th century was restricted to the pine forests of Inagua Nature Reserve (38 km²). A translocation programme released birds from a breeding centre into the nearby (<3 km) pine forests of La Cumbre in the years following 2010. From 2015 to 2019 the La Cumbre population was reinforced by translocation of wild juveniles from the source population of Inagua. We estimate the population size, the spatial variation of abundance, and recent temporal changes in density of the species in Inagua and La Cumbre by means of line transects, distance sampling, and habitat suitability modelling using random forests. The average density of the Blue Chaffinch in Inagua Nature Reserve was 10.2 birds/km² in spring 2019, with a population estimated at 362 birds (95% CI: 257–489). The most important variables affecting the distribution of the Blue Chaffinch in Inagua were the amount of precipitation during the summer (July–September), the solar radiation in June, and the northern position in the reserve, highlighting the importance of abiotic factors related to thermal and hydric stress during the breeding season. The density was considerably lower in the translocated population inhabiting 21 km² of pine forests in La Cumbre (3.3 birds/km²), with an estimate of 68 Blue Chaffinches (35–141) breeding freely in the wild. The translocation programme successfully contributed to the establishment of a second viable nucleus, accounting for 16% of the total population within a time span of 10 years. This result reinforces the role of translocations in preventing extinctions of endangered species with very low population sizes restricted to only one isolated area.

Introduction

Island avifaunas include a very high proportion of endemic taxa (Johnson and Stattersfield 1990, Adler 1994) that have small ranges and low population sizes, traits that are related to extinction risk

(Gaston 1994, Mace and Kershaw 1997, Stattersfield *et al.* 1998; see review by Biber 2002), especially under high direct human impact through habitat destruction and the introduction of generalist predators (Wood *et al.* 2017). As a consequence, a very high proportion of bird extinctions has occurred on islands since 17th century (c.90%), and island birds tend to recover less robustly in islands than their mainland counterparts (Johnson and Stattersfield 1990, Suckling *et al.* 2016). Moreover, many threatened island birds are forest-dwelling, with a high proportion inhabiting temperate or seasonal forests (Johnson and Stattersfield 1990).

Conservation actions implemented to reverse unfavourable conservation status need to be evaluated over time to know their effectiveness (Pérez *et al.* 2012, Gerber *et al.* 2018, Berger-Tal *et al.* 2020, Resende *et al.* 2020, Nason *et al.* 2021), which in turn requires good information on the original baselines. These baselines should consider aspects of distribution and population size, habitat preferences, densities, and demographic parameters related to reproductive success, life expectancy and mortality rates. For those species restricted to a single location, an obvious management action is to establish new populations to reduce the risk of local environmental catastrophe, such as extreme weather events or large forest fires. Such conservation actions will be more effective if they promote connectivity between the source population and translocated ones (Berger-Tal *et al.* 2020). Therefore it is necessary to collect evidence about how the translocated individuals have contributed to establishing new viable populations which reproduce naturally, and how many individuals exist in the wild (Resende *et al.* 2020).

The Gran Canaria Blue Chaffinch *Fringilla polatzeki* is an endemic taxon of the Canary Islands, recently separated from its former sister species, the Tenerife Blue Chaffinch (*Fringilla teydea*; Lifjeld *et al.* 2016, Sangster *et al.* 2016). While the species from Tenerife is classified on the IUCN Red List as 'Near Threatened' (BirdLife International 2017a), the one from Gran Canaria is assessed as 'Endangered' (BirdLife International 2017b). The core historical population survives in the pine forests of the Inagua Nature Reserve, Gran Canaria, where the species was discovered in 1905. Very few birds also inhabited the pine forests of Tamadaba, located about 5–6 km from Inagua, but this small population vanished in 1991, with a few occasional recent records of wandering individuals that do not reproduce (Moreno and Rodríguez 2007, Carrascal and Moreno 2020). Thus, there was only one population of the Gran Canaria Blue Chaffinch in 2000, restricted to an area of about 37.6 km² established as a Strict Nature Reserve. The protection offered by Inagua did not protect the species against a devastating wildfire in July 2007, which reduced its population density by half (Moreno *et al.* 2018). By 2008, some individuals had moved naturally from Inagua and were recorded in the nearby pine forests of La Cumbre (located c.3 km away), beginning shortly after a successful captive breeding programme that has released birds in that area since 2010 (Delgado *et al.* 2016). The captive breeding programme was reinforced by a new translocation programme from 2015 to 2019, using wild juvenile individuals from the source population of Inagua (LIFE+PINZÓN 2019). The population density of the Blue Chaffinch in Inagua has remained relatively stable at around 9–16 birds/km², the lowest recorded abundance for a small woodland passerine in the Western Palearctic (Moreno *et al.* 2018), with a tentative population size estimated by means of habitat suitability modelling of c.280 Blue Chaffinches for the years 2011–2016 (Carrascal *et al.* 2017). These very low numbers clearly contrast with the densities and population size recorded for the Tenerife Blue Chaffinch, with more than 5,000 mature individuals and more than 70 birds/km² (Carrascal and Palomino 2005, García-del-Rey *et al.* 2010, BirdLife International 2017a). Moreover, the population size of the Gran Canaria Blue Chaffinch is several times lower than that recorded for the other endangered, small-sized, woodland species of the Western Palearctic, such as *Pyrrhula murina* (1,000 individuals in c.100 km², 10.0 birds/km²; BirdLife International 2015), and *Sitta ledanti* (350–1,500 individuals in c.700 km², 0.5–2.0 birds/km²; BirdLife International 2017c).

The main goals of this paper are to estimate the population size, spatial variation in abundance, and recent temporal changes in density of the Gran Canaria Blue Chaffinch in its main area of distribution, the Inagua Nature Reserve. We also estimate the population size of the species in La Cumbre pine forest, in order to know how the 176 birds released during translocations from 2010 to

2018 have translated into a wild, free-living population. These first quantitative estimates of the population size of the Gran Canaria Blue Chaffinch, obtained by means of a broad census scheme and distance sampling, will set the baseline for future studies, and allow an assessment of the effectiveness of the translocation program at creating a stable wild population 10 years after it was launched.

Methods

Study areas

The study areas are located in the pine forests of Inagua Nature Reserve and La Cumbre on Gran Canaria Island (27°58'N, 15°35'W; 1,560 km², maximum altitude 1,950 m asl. See González *et al.* (1986) and Santos *et al.* (2000) for details of vegetation cover and landscape characteristics). The pine forest of Inagua (37.6 km²) is mainly composed of dry and monospecific stands of *Pinus canariensis* occupying semi-arid rugged terrain of steep slopes, in a mountainous area spanning 850–1,575 m. It harbours the main breeding population of the Blue Chaffinch since the beginning of the 20th century (Moreno and Rodríguez 2007), after the species became extinct in Tamadaba pine forest in 1991 (Carrascal and Moreno 2020). For more details on the habitat and environmental characteristics of Inagua pine forest see Carrascal *et al.* (2017). The pine forest of La Cumbre (20.7 km²) is characterised by pine plantations of *Pinus canariensis*, with scattered vegetable gardens and shrublands (*Teline microphylla*, *Adenocarpus foliolosus* and *Chamaecytisus proliferus*), mainly ranging between 1,180 and 1,950 m. One breeding pair of Blue Chaffinch naturally established in La Cumbre in 2008, and a translocation programme began in 2010, first releasing birds from captive breeding and then from translocations of juveniles from the core population of Inagua. For more details on the Blue Chaffinch and environmental characteristics of La Cumbre pine forest see Delgado *et al.* (2016). See Figure 1 for the location of the two study areas in Gran Canaria and the Canary archipelago.

Bird census

Data on Blue Chaffinch abundance were obtained through distance sampling using line transects carried out in Inagua and La Cumbre during the breeding seasons of 2017, 2018 and 2019 (second fortnight in May and the first fortnight in June). We surveyed a fixed network of trails totalling 22.9 km in Inagua and 15.5 km in La Cumbre designed to monitor population changes of the Blue Chaffinch in both areas (since 1994 in Inagua –see Moreno *et al.* 2018– and 2016 in La Cumbre). The line transects were divided into 500-m contiguous units. They were repeated on three different occasions, and the numbers of birds detected in each 500-m unit were averaged to obtain more precise results. Bird censuses were carried out on rainless days, at a slow pace (1–3 km/h approximately), in the first four hours after dawn. For each bird heard or seen, we estimated the perpendicular distance to the observer's trajectory. Previous training helped to reduce between–observer variability in distance estimates. All censuses devoted to monitoring Blue Chaffinch abundance were performed by V.S. and A.D. For more details of the line transect census programme for the Gran Canaria Blue Chaffinch see Moreno *et al.* (2018). In addition, more line transects were carried out during the spring of 2019, in order to broaden the pine forests covered by the census programme, according to habitat characteristics and the whole area of Inagua and La Cumbre: 30 km in Inagua (by L.M.C.) and 4 km in La Cumbre (by A.D.).

Detectability models to estimate Blue Chaffinch density were built with the R packages {Distance} (Miller *et al.* 2019) and {mrds} (Laake *et al.* 2020). Maximum detection distance was established at 175 m on both sides of the line transect. Six models that are commonly used to explain the loss of detectability as a function of the distance from the transect line were fitted to estimate the probability of detection within the census belts of 175 m either side of the researcher: half–normal, hazard–rate and uniform, with the inclusion of polynomial or cosine adjustment
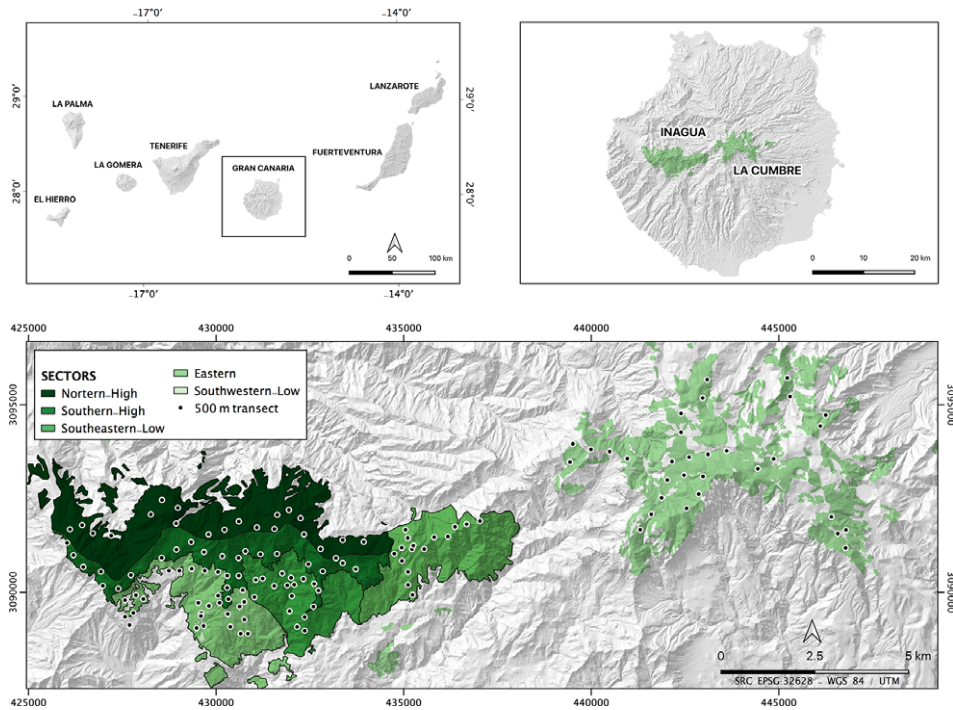
Figure 1. Study areas in Gran Canaria island. Black dots in the lower panel show the centre of 500-m length transects carried out to estimate the population size and habitat preferences of the Blue Chaffinch in the pine forests of Inagua nature reserve and La Cumbre.

terms (Buckland *et al*. 2007). Models were evaluated and averaged according to AICc to obtain weights for the six models.

Population size estimates

The estimation of population size was carried out considering Blue Chaffinch density and area of La Cumbre, and the bird density and five geographic strata in Inagua. The confidence intervals of the population estimates were obtained by applying a randomization procedure. First, we generated 10,000 random values of probability of detection within the confidence intervals obtained separately for the two study areas. Second, we generated 10,000 random samples of the number of transects within each stratum by bootstrapping (Davison and Hinkley 1997) in order to obtain 10,000 average figures of the number of Blue Chaffinches recorded per 500-m transect. With these values of probability of detection and number of birds per transect we calculated the density of each one of the 10,000 random samples. Finally, we obtained 95% confidence intervals for the density within each stratum (one in La Cumbre and five in Inagua), using the bias corrected accelerated (BCa) percentile method (DiCiccio and Efron 1996). The average density for Inagua was obtained by means of the weighted average of 10,000 bootstrapped densities in the five strata, considering the area covered by each geographic stratum (Figure 1); its 95% confidence interval was calculated using the BCa method. The population size of the Blue Chaffinch in La Cumbre and Inagua was calculated by multiplying the estimated densities (mean, lower and upper 95% confidence intervals) by their areas. The analyses were carried out using the R package {bootstrap} (S Original *et al*. 2019).

Relationship between local abundance and habitat suitability for successful breeding

Carrascal *et al.* (2017) modelled the habitat suitability for successful breeding using the nest locations of successful breeding attempts of the Blue Chaffinch in Inagua and 12 orographic, climatic, and habitat structure predictors. The model predicted the habitat suitability of the whole Inagua Nature Reserve at a 50 x 50 m resolution. Cardinal orientation, slope of the terrain, and altitude were obtained from a digital elevation model built from a contour map with 5-m equidistant topographic curves (*Infraestructura de Datos Espaciales de Canarias*, http://www.idecanarias.es/). Rainfall in July–September was obtained from the "*Clima-Impacto*" project (http://climaimpacto.eu/) at a raster resolution of 50*50 m. Solar radiation in June was obtained from the photovoltaic potential maps in the Canary Islands (http://www.idecanarias.es/). Finally, vegetation structure variables (pine cover, shrub cover, and heights) were obtained from precision laser LiDAR measurements, provided at a raster resolution of 25*25 m by the project "*Enriquecimiento de la Cartografía de las islas forestales de Canarias a partir de datos LIDAR*". Using those data, we calculated the average habitat suitability for successful breeding of each of the 106 500-m transects considering a circular buffer of 250 m around their centres. The relationship between the Blue Chaffinch counts in the sample of the 106 transects was regressed upon habitat suitability for successful breeding using quantile regression at 50, 75 and 90 percentiles; ({quantreg} package; Koenker 2020).

Spatial variation of the Blue Chaffinch abundance in Inagua

Spatio-temporal variation in Blue Chaffinch numbers along 500-m length transects was analysed using regression random forests (RRF; Cutler *et al.* 2007). RRF is an ensemble learning method that builds multiple regression trees on different training datasets, by means of bootstrapping the sample units and randomly choosing a subset of predictors. The outputs of those models (weak learners with low bias but high variance) are averaged to generate robust predictions about data (with low bias and low variance), thus avoiding overfitting, reducing the variance, and improving the performance of de-correlated decision trees. Each regression tree was built using one-third of 12 predictors and a bootstrap sample from the data comprising 106 500-m length transects. We ran RRF using 1,000 trees. On average, each transect was not considered in 36.79% of the trees (i.e. Out-Of-Bag sample); those instances were used in computing the OOB error estimate and variable importance of the whole RRF model. The overall OOB error rate was used to measure the performance of the model (i.e. the percentage of variance explained by the model on those transects not used in building the RRF model). We used three measures of variable importance: the overall contribution of each variable to the reduction of the mean square error in OOB data (IncMSE), the increase of node purity in OOB data (IncPurity), and the average node depth of each predictor (lower figures of this parameter denote a higher importance, as predictors appeared in more basal, important, tree splits). Partial dependence plots were built to show the graphical representation of the regression of each predictor on the response, while averaging over all other predictors. Considering the figures of each one of the twelve predictors in each 500 x 500 m UTM cell of Inagua, we generated a map of the spatial variation of the abundance of the Blue Chaffinch per 25 ha, taking into account the probability of detection of the species in this study area. The RRF was carried out using {randomForest} (Liaw and Wiener 2002).

The 12 environmental predictors in the RRF model were: latitude and longitude coordinates, altitude, terrain slope, north-south and east-west cardinal orientation of the hillsides, summer rainfall, solar radiation in June, cover of the canopy (pine) and shrub layers, and average pine and shrub heights. Other climatic variables such as monthly solar radiation, spring and summer temperatures or spring rainfall were considered, but they were highly correlated across the sample of 106 500-m transects. Thus, and in order to avoid multicollinearity in data analysis, we selected summer rainfall and solar radiation in June as the two least correlated measurements with a clear functional meaning related to thermal and hydric stress during the breeding season. Full details on these variables and their sources are extensively presented in Carrascal *et al.* (2017).

Results

Recent population trends in Inagua and La Cumbre

Probability of detection of Gran Canaria Blue Chaffinches along line transect censuses from 2017 to 2019 in Inagua was 0.653 up to 175 m distance from the observer (SE = 0.063), with an effective strip width (ESW) of 114 m (SE = 11 m; 95% CI = 92–135 m; n = 414 contacts). For the same period in La Cumbre, the probability of detection was 0.535 up to 175 m distance from the observer (SE = 0.112), with an ESW of 94 m (SE = 20 m; 95% CI: 51–136 m; n = 83). These high ESW figures could be explained by the complex orography of the terrain, with deep ravines that facilitate the spread of sound between nearby steep slopes.

The average density of Blue Chaffinches in Inagua over 22.9 km of the fixed transect network showed strong variation from 2017 to 2019: 12.7 birds/km² in 2017 (95% CI: 9.3–16.9), 8.3 birds/km² in 2018 (95% CI: 6.0–11.1), and 17.7 birds/km² in 2019 (95% CI: 12.9–23.6). For the La Cumbre population, average density over 15.5 km of the fixed transect network ranged from 2.5 birds/km² in 2017 (95% CI: 1.0–5.5), to 3.3 birds/km² in 2019 (95% CI: 1.7–6.8), with an intermediate figure of 2.7 birds/km² in 2018 (95% CI: 0.8–6.8). Thus, average population density in favourable areas for the Gran Canaria Blue Chaffinch was 3x to 5x higher in Inagua than in La Cumbre pine forests.

Population sizes in Inagua and La Cumbre in spring 2019

The average number of Blue Chaffinches per 500-m transect in each of the five sectors of Inagua Nature Reserve and in La Cumbre, along with their CI, are shown in Table 1. For Inagua, the Northern-High sector had more Blue Chaffinches than the two Southern-Low and the Eastern sectors (i.e. 95% CI not overlapping). The Southern-High sector had more Blue Chaffinches per transect than the Southwestern-Low and Eastern sectors. Blue Chaffinch abundance in La Cumbre was significantly lower than in the best sectors of Inagua where the census monitoring programme is carried out (Northern-High and Southern-High sectors), but was similar to the abundances measured in the Eastern and Southern-Low sectors of Inagua. Nevertheless, this last similarity could be the result of very different processes: a low habitat quality in the Eastern and Southern-Low sectors of Inagua, and because Blue Chaffinches are still in the process of colonising a new habitat in La Cumbre.

The average population density of the Blue Chaffinch throughout Inagua Nature Reserve was 10.2 (95% CI: 7.2–13.7 birds/km²). The Inagua population in May–June 2019 was estimated at 362 (95% CI 257–489) birds. A large proportion of this population was concentrated in the Northern-High sector (73.4%), with 16.3% in the Southern-High sector, totalling 89.7% of the population, in spite of the fact that these two sectors account for only 55.6% of the entire area of Inagua Nature Reserve.

Table 1. Average number of Gran Canaria Blue Chaffinches detected per 500 m length transect in five sectors of Inagua Nature Reserve and in the pine forests of La Cumbre. n: number of 500-m transects. 95% CI: 95% confidence intervals obtained by means of bootstrapping using the bias corrected accelerated percentile method.

Area	Sectors	n	birds/500 m	95% CI
Inagua	Northern-High	20	2.15	1.55 − 2.80
Inagua	Southern-High	27	1.15	0.63 − 1.74
Inagua	Southwestern-Low	25	0.08	0.00 − 0.24
Inagua	Southeastern-Low	18	0.50	0.17 − 0.89
Inagua	Eastern	16	0.25	0.00 − 0.56
La Cumbre	Whole area	39	0.25	0.15 − 0.38

An average population of 68 (95% CI: 35–141) Blue Chaffinches was estimated for the 20.7 km² of pine forests of La Cumbre in June 2019. Thus, La Cumbre population accounts for 16% of the whole population size of the species on Gran Canaria, estimated at 430 (292–630) Blue Chaffinches in 2019.

Relationship between local abundance and habitat suitability for successful breeding

Carrascal *et al.* (2017) obtained a habitat suitability model of high explanatory and predictive power for the Inagua Natural Reserve using the location of successful nests from which at least one chick flew. The predictions of this model were applied at a very fine resolution scale of 50 x 50 m², to predict the probability of successful breeding in the area around the centre of each one of the 106 500-m length transects carried out in 2019 (within a circle of 250 m radius around the centre of each transect).

Figure 2 shows the relationship between the habitat suitability for successful breeding predicted by Carrascal's *et al.* (2017) model and the actual count of chaffinches on transects. The relationship is triangular, indicating that there is no uniform association between habitat suitability for successful breeding and bird numbers obtained by local census counts. Quantile regressions between both variables were obtained at percentiles 50% (i.e. median regression), 75% and 90%. The regression slope between the actual counts of birds on transects and the habitat suitability predictions increased with the percentile being considered: 50% percentile, slope-b = 2.56, SE = 0.91, P = 0.006, pseudo-R^2 = 0.12; 75% percentile, b = 6.25, SE = 1.13, P << 0.00001,
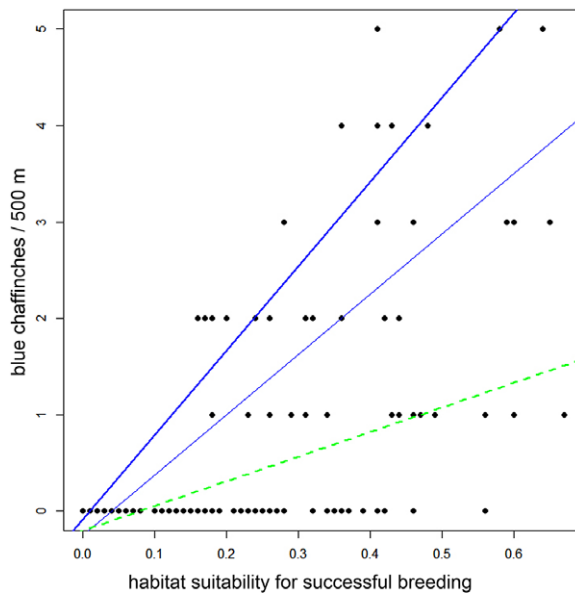

Figure 2. Relationship between the number of blue chaffinches per 500-m length transect in Inagua Nature Reserve during May-June 2019, and the predictions of a habitat suitability model for the successful reproduction of the species (model and predictions available in Carrascal *et al.* 2017). The dashed line defines the quantile regression slope at the 50% percentile (median regression), the thin line the 75% percentile regression line, and the thick line the regression at 90% percentile.

pseudo-R^2 = 0.30; 90% percentile: b = 8.77, SE = 1.05, P << 0.00001, pseudo-R^2 = 0.37. This increasing trend in the regression slopes and deviance accounted for by models suggests that the association between direct census counts and habitat suitability for successful breeding has a clear maximum: i.e. the highest bird counts during May–June are only possible in places of high habitat suitability for successful breeding (upper right corner of Figure 2; probability > 0.35). Nevertheless, null counts were recorded under a broad spectrum of habitat suitability ranging from zero to 0.55.

Habitat preferences and spatial variation in local abundance

Figure 3a shows the spatial variation of the abundance of the Blue Chaffinch in the 106 500-m length transects carried out in Inagua Nature Reserve. The random forest model (RRF) applied to the bird counts of the Blue Chaffinch in the sample of 106 transects of 500-m in length, using 12 environmental variables as predictors (Table 2), had a high explanatory power (R^2 = 93.8%); nevertheless, its predictive power was relatively low (R^2 = 34.8% in the Out Of Bag –OOB– sample).

The most important variables affecting the distribution of the Blue Chaffinch in Inagua were the amount of precipitation during the summer (July–September) and the latitudinal position of transects, both according to the large reduction of the residual variance, the increase in the node purity, and the average depth of those variables in the branching pattern of the regression trees of the random forest model (Table 2). Other important variables were solar radiation in June, the northern cardinal orientation of the slope and the longitude of the geographical position. Habitat characteristics related to the understorey and tree layers were of very little importance in affecting the spatial variation of abundance of the Blue Chaffinch in the Inagua pine forest. The relationship between the local abundance of Blue Chaffinches per 500-m length transect and the four most important predictors is shown in Figure 4. The abundance of the Blue Chaffinch was very low when summer rainfall was lower than 13 mm; abundance increased sharply from that amount of rain up to 17 mm, and then it continued to increase but at a lower rate. Blue Chaffinch local abundance increased with latitude (especially above 3090200) and attained the highest figures in the centre of the reserve according to the East-West component. Finally, Blue Chaffinch abundance decreased as solar radiation in June increased, especially above 7,450 kWh/m².

Repeating the previous random forest model with four different subsets of variables regarding their informative content (Table 3), the most important effects were related to the geographic position of transects within the Nature Reserve (31.1% of the variance predicted by the RRF model using only longitude, latitude), followed by the influence of climatic predictors (summer rainfall and solar radiation in June). Vegetation structure (four predictors) and orographic (another four predictors) factors had a considerably lower OOB predictive ability (8–9% of variance accounted for). Finally, Figure 3b shows the predicted abundance of the Blue Chaffinch in the 500 x 500 m² UTM cells of Inagua Nature Reserve, clearly showing the most important areas for the species.

Discussion

The total population size of the Gran Canaria Blue Chaffinch is estimated as 430 birds, restricted to a very small extent of occurrence of 60 km². The conservation efforts carried out by the Canary Islands government and the European Union through LIFE projects have successfully contributed to the establishment of a new viable nucleus, accounting for 16% of the total population and expanding the species' original distribution area by 50%, within 10 years. The new translocated population in La Cumbre breeds freely in the wild (LIFE+PINZON 2019), with frequent movements of birds between Inagua and La Cumbre (Delgado *et al.* 2020). This conservation outcome, together with the stable population trend in Inagua from 1994 to 2019 (Moreno *et al.* 2018 and this study) and the highest density ever recorded reached in 2019, allows us to be optimistic about the future of the species, despite its rarity. Nevertheless, the modelling of Blue Chaffinch density in
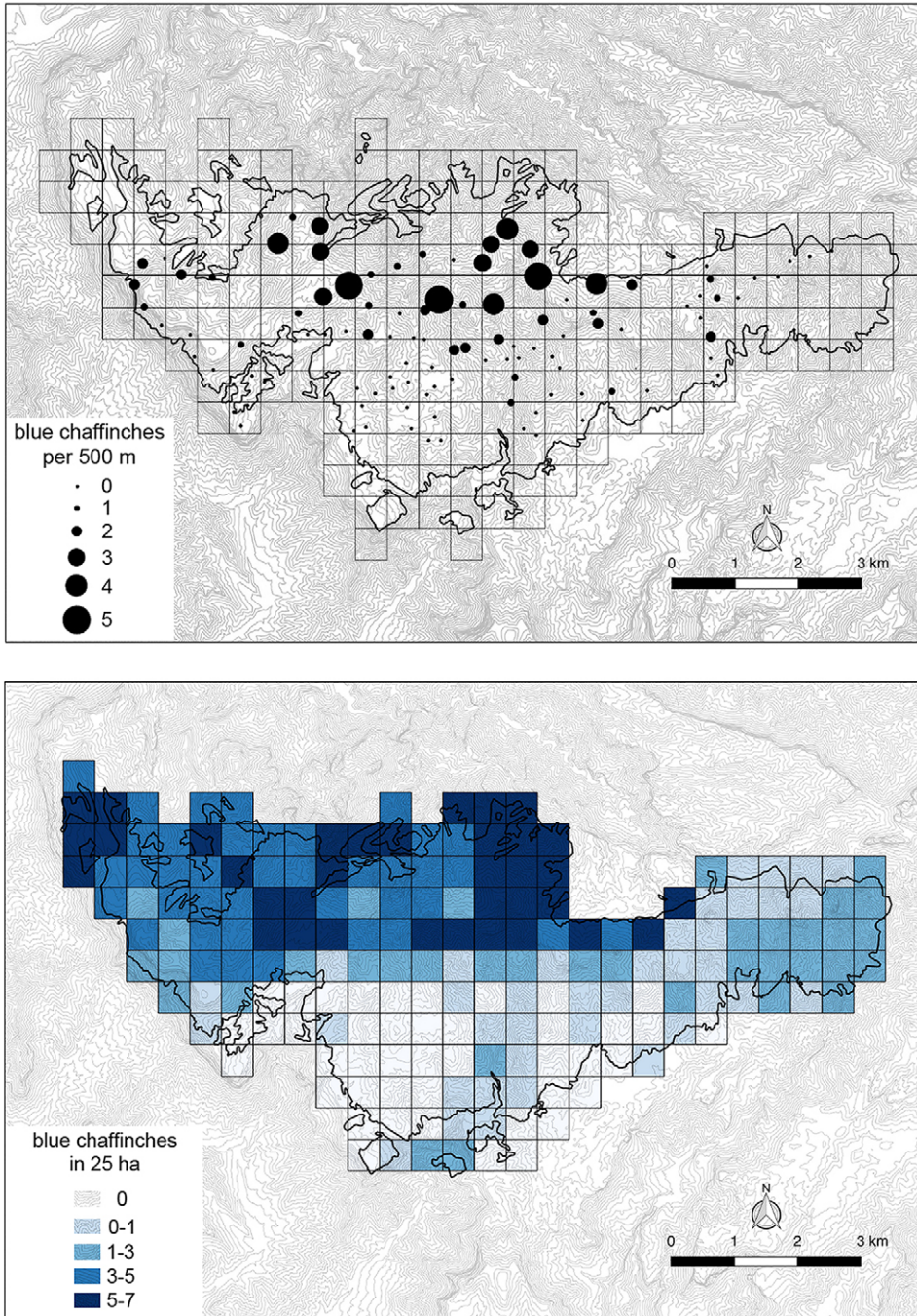
Figure 3. (a) Distribution of the centres of 106 500-m length transects denoting the number of Blue Chaffinches detected in Inagua Nature Reserve. (b) Map of the spatial variation of the abundance of the Blue Chaffinch in UTM grids of 500x500 m² (25 ha) derived from the prediction of the *Random Forest* model analyzing the spatial variation of the bird counts in the sample of 106 transects. The predicted number of Blue Chaffinches per 25 ha has been corrected taking into account the probability of detection of the species (probability obtained by distance sampling = 0.653, SE = 0.063; see the Methods and Results sections).

Table 2. Variable importance of the *Random Forest* describing the spatial variation in the counts of Blue Chaffinches in 106 500-m length transects carried out in Inagua Natural Reserve using 12 predictors. IncMSE: increase in the reduction of the residual variance (mean square error) of the model (using the Out Of Bag sample). IncPurity: contribution to the increase in purity of the nodes. The higher the values of these parameters, the more important these variables are, explaining and predicting the spatial variation of bird counts per census unit. Node depth: average depth of the nodes where the predictor appears defining the branching pattern of the regression tree (1: basal node or first ramification).

|	IncMSE	IncPurity	Node depth
Rainfall July-September	17.90	52.31	1.09
Latitude coordinate	11.74	32.00	1.87
Longitude coordinate	7.45	14.32	3.04
Solar radiation in June	6.35	11.08	2.45
Northern cardinal orientation	7.33	12.41	3.15
Tree (pine) layer cover	6.16	9.06	3.09
Slope of the terrain	5.49	7.70	3.76
Understory cover	3.27	9.11	3.47
Average pine height	3.25	6.26	3.20
Average understorey height	3.04	6.09	4.10
Eastern cardinal orientation	2.02	10.45	3.14
Altitude	0.62	9.05	3.50
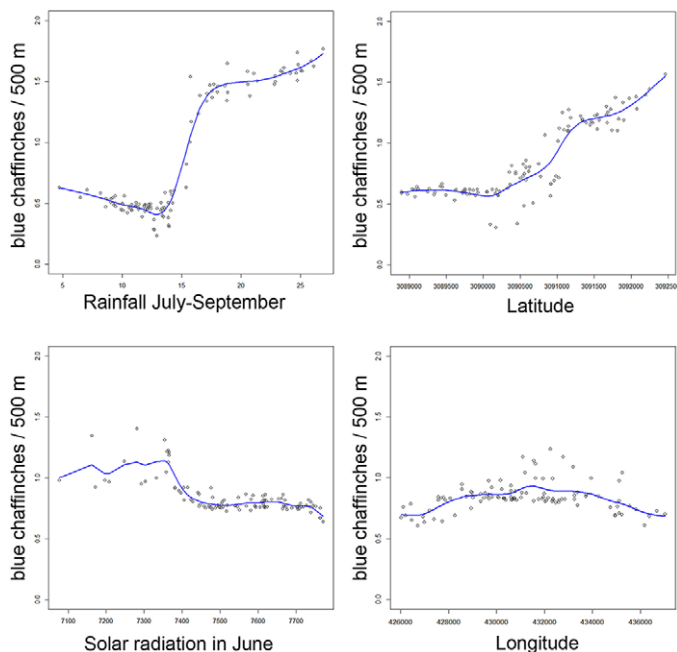
Figure 4. Partial influence plots depicting the relationships between the spatial variation of Blue Chaffinch counts in 106 500-m length transects of Inagua Nature Reserve and the four most important predictors of the *Random Forest* model. Precipitation in mm; geographic WGS84 coordinates of latitude and longitude in metres, and radiation in kWh/m².

Table 3. Out of Bag (OOB) predictive power of four *Random Forest* models carried out with different subsets of predictors (marked with X).

predictors	geographic	orographic	climatic	vegetation
Latitude coordinate	X			
Longitude coordinate	X			
Northern cardinal orientation		X		
Eastern cardinal orientation		X		
Slope of the terrain		X		
Altitude		X		
Rainfall July-September			X	
Solar radiation in June			X	
Tree (pine) layer cover				X
Understorey cover				X
Average pine height				X
Average understorey height				X
OOB % of variance	31.1	8.8	26.2	8.4

Inagua clearly shows that there is a large heterogeneity in the habitat suitability for the species, as one quarter of its area has a density of <2 birds/km², and the density is >10 birds/km² in only 45% of the nature reserve (Figure 3), a very low density for a small woodland bird in the Western Palearctic and the Canary archipelago (Carrascal and Lobo 2003, Estrada *et al.* 2004, Seoane *et al.* 2011). Although the habitat suitability of the pine forests has not yet been estimated in La Cumbre, it is expected that a similar proportion of the area would be suitable for the species (Delgado *et al.* in prep.). Therefore, although the extent of occurrence is about 60 km², the area of occupancy would probably be reduced by half.

The Blue Chaffinch population in La Cumbre has increased from two individuals in 2008 to 65-70 birds in 2019. This 34-fold increase has been made possible by a translocation programme that released 173 individuals (mainly juveniles) in September of nine consecutive years from 2010 to 2018, with 111 birds coming from the captive breeding centre of Tafira, and 62 birds from the wild population of Inagua (LIFE+PINZON 2019). This population growth, favoured by an active conservation intervention releasing 7–32 birds per year, is at the upper boundary of the increases recorded for other bird species of conservation concern whose population increases were boosted by translocations, habitat management, or control of invasive predator species (Green and Hirons 1991, Impey *et al.* 2002, Butchart *et al.* 2006, Groombridge *et al.* 2009, Brooke *et al.* 2012, Ghestemme *et al.* 2019). The result of the translocations of Blue Chaffinch in La Cumbre reinforces the success achieved by such conservation programmes in preventing extinctions of endangered species with very low population sizes restricted to only one isolated area (see Williams *et al.* 2012, Luther *et al.* 2016, Withers *et al.* 2019, Bolam *et al.* 2020).

Conversely, the density of the Blue Chaffinch in Inagua has fluctuated between 8.0 and 12.7 birds/km² from 1994 to 2015, except during 2008–2009 when it decreased to 5–6 birds/km² due to the negative impact of a great forest fire (Moreno *et al.* 2018). Therefore, the core population in Inagua can be considered stable in the absence of human intervention, showing a striking resilience after catastrophic events. Moreover, considering that the Blue Chaffinch density in Inagua has remained above those figures from 2016 to 2019 (12.7–17.7 birds/km²), it can be postulated that the removal of 62 juveniles from the source population in four years did not reduce population viability (captures and translocations on September 2015, 2016, 2017 and 2018; LIFE+PINZON 2019). In fact, Rodríguez and Moreno (2008) measured a nesting success of 54.1% and a production of 1.45 fledglings per successful attempt in Inagua, with 33% of the breeding pairs having a second clutch. From these figures an average productivity of a breeding pair is 1.0–1.1 fledglings per year, a very low breeding output for a *Fringilla* species in the Western Palearctic (Perrins 1998). Therefore, 130–180 breeding pairs in Inagua, corresponding to a population of 260-360 adult birds from 2015 to

2019 (see next paragraph), had a probable reproductive output of 135–190 juveniles per year, from which the capture of 12–20 birds per year (or 8–11%) is unlikely to have compromised viability, and yet it contributed to the establishment of a new translocated population in La Cumbre. In fact, a population viability model analysis with VORTEX v.10 (http://www.vortex10.org) showed that the removal of 15-20 juveniles per year did not compromise the survival of the core Blue Chaffinch population in Inagua (Rodríguez 2016).

The fixed network of transects used to carry out population monitoring is limited to the Northern-High and Southern-High sectors of the reserve, which host c.90% of the Blue Chaffinch population restricted to c.56% of the whole area of Inagua pine forests. This current pattern of maximum abundance agrees broadly with the observations made by Thanner (1910) a century before, when he captured 76 Blue Chaffinches at various locations within the two previously mentioned sectors. Thus, it is highly probable that the Blue Chaffinch distribution in Inagua has not changed substantially in the last 100 years.

The sharp decrease of the density of the Blue Chaffinch in 2018 is surprising due to the abrupt change between two consecutive years in which the highest densities were recorded. The monitoring censuses in 2017–2019 were carried out by the same person (Víctor Suárez) using the same census method on the same transects. The causes of the strong fluctuation are unknown, but it is something that can occur in populations of small forest birds. For example, the population trend of *Fringilla teydea* in Tenerife, recorded by the Spanish Ornithological Society in its SACRE monitoring program (SEO/BirdLife 2012), also showed marked fluctuations in the short-term, with changes between 2004 and 2009 as marked as those registered for *Fringilla polatzeki* in 2017–2019 (see also Dierickx *et al.* 2019 for the Raso Lark *Alauda razae*, whose population varied 25-fold from 2004 to 2017 without any conservation intervention). It would be necessary to develop an applied research programme with this endangered species to clarify how the yearly variations in environmental productivity (insects and pine seeds) and reproductive success, probably linked to temperature and precipitation, are determining the observed fluctuations (e.g. see Brooke *et al.* 2012 and Brooke 2018 for the Raso Lark; Benkman 2016 for *Loxia sinesciuris*).

The importance of abiotic factors in determining the variation in Blue Chaffinch density is supported by the results of the random forest model analysing the spatial variation in abundance during the breeding season in Inagua. Three predictors related to thermal and hydric stress during the breeding season were very important: summer rainfall, solar radiation in June and the latitudinal position in the nature reserve (Table 2 and Figure 4). The abundance of the Blue Chaffinch increases in a non-linear way with the summer rainfall and decreases with the amount of solar radiation in the pine forests of Inagua, which are located at the eastern limit of the Canary forests and are suffering forest dieback as a consequence of global warming (Martín *et al.* 2015). The abundance of the Blue Chaffinch also increases from the southern to the northern part of Inagua, a sector with mature pine forests on steep north-facing slopes where clouds displaced by the north-eastern trade winds accumulate. This area overlaps with the Northern-High sector (Table 1), where the Blue Chaffinch reaches its maximum abundance. The importance of the higher parts of Inagua nature reserve for the Blue Chaffinch is reinforced by its relatively low altitude, with only 9% of its area above 1,300 m and a maximum elevation of 1,575 m. That is to say, there is nowhere to go along Inagua's small altitudinal gradient when confronted with global warming, as species that live near mountaintops may run out of room as a consequence of shifting upslope in response to recent temperature increases (e.g. Forero-Medina *et al.* 2011, Freeman *et al.* 2018). The translocated population in La Cumbre is confronted with less stressful thermal conditions at the higher elevation where it thrives, 250–400 m above the core distribution of the Blue Chaffinch in Inagua.

The large difference between the predictive power of the random forest model in this study, using bird counts in transects, contrasts with that found when modelling the habitat suitability for successful breeding using nest locations (Carrascal *et al.* 2017). The explanation for this marked difference can be found in the very nature of the data. A successful nesting location is a fixed place with environmental characteristics that describe occurrences with demographic relevance. On the

other hand, survey counts at small spatial scales, such as 500-m length transects, may account for the mere routine movements of birds (e.g. exploration of the territory, marking of its limits, interactions with other individuals). Moreover, due to imperfect detection during bird counts there are false negatives in suitable places (only 65% of existing birds are detected up to 175 m away from the observer). Therefore, models based on census data over large areas will always generate "noisy data" with less accurate predictions than those based on occurrences linked to activities that maximise a very relevant aspect of biology of the species.

Habitat suitability obtained from modelling the location of successful breeding attempts was a good surrogate for the observed local abundance during the breeding season, even using data obtained in different years with different methods (Figure 2; 2019 for line transects in this paper, and 2011–2016 for nest locations in Carrascal *et al.* 2017). Thus, in spite of the limitations presented in the previous paragraph regarding census data, this result emphasises and reinforces the direct link between bird numbers and relevant aspects of the biology of the species with demographic consequences, probably mediated through the spatial accumulation of individuals with high performance and fitness (see Van der Wal *et al.* 2009, Lunghi *et al.* 2018). Nevertheless, we did not find perfect, linear association between habitat suitability for successful breeding and Blue Chaffinch local abundance (Figure 2). There was a triangular relationship, showing that while low suitability only led to low abundance, considerable variation in abundance was observed in high suitability habitats, and high abundances were only possible in high suitability places. This pattern suggests that the pine forests of Inagua are not fully occupied by Blue Chaffinches (i.e. not saturated with birds), with some woodland patches of high suitability barely occupied. Therefore, it is possible that the pine forests of Inagua nature reserve, especially those mature patches at higher altitudes, have some potential to host more birds. This possibility might partly explain why, despite the maturity of the trees in Inagua, the Gran Canaria Blue Chaffinch achieves one of the lowest densities in the Western Palearctic for a small woodland bird (e.g. Carrascal and Lobo 2003, Estrada *et al.* 2004), or has a density in the most favourable sectors of Inagua considerably lower than that recorded for *Fringilla teydea* in the pine forests of Tenerife, including coniferous plantations (Carrascal and Palomino 2005, García del Rey *et al.* 2010).

Acknowledgements

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