

Support for a relationship between demography and modeled habitat suitability is scale dependent for the purple martin *Progne subis*

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Abstract

1. Species distribution models (SDMs) estimate habitat suitability for species in geographic space. They are extensively used in conservation under the assumption that there is a positive relationship between habitat suitability and species success and stability.
2. Given the difficulties in obtaining demographic data across a species' range, this assumption is rarely tested. Here we provide a range-wide test of this relationship for the eastern subspecies of purple martin *Progne subis subis*.
3. We build a well-supported SDM for the breeding range of the purple martin, and pair it with an unparalleled demographic dataset of nest success and local and regional abundance data for the species to test the proposed link between habitat suitability and fecundity and demography.
4. We find a positive relationship between regional abundance and habitat suitability but no relationship between local abundance or fecundity and habitat suitability.
5. Our data suggest that local success is driven largely by biotic and stochastic factors and raise the possibility that purple martins are experiencing a time lag in their distribution. More broadly our results call for caution in how we interpret SDMs and do not support the assumption that areas of high habitat suitability are the best areas for species persistence.

KEYWORDS

abundance, citizen science, demography, extinction debt, MaxEnt, purple martin, species distribution model

1 | INTRODUCTION

Across a species' range, the persistence of a species is, seemingly simply, determined by two demographic parameters—birth and mortality rate. For the ecologists who wish to study them, however, gathering these data can be far from simple (Aizpurua et al., 2017; Brambilla & Ficetola, 2012). Some species have lifetimes longer than the career of the ecologist, some disperse or migrate (making them difficult to track), some have wide distributions (meaning data cannot easily be collected across the entire range) and others are cryptic or

breed cryptically meaning demography is hard to observe. Accurate abundance data can likewise be elusive at the relevant resolutions for conservation purposes (often the extent of the entire range and the grain size of the individual home range; Dallas & Hastings, 2018). Obtaining or estimating this information is nonetheless critical to identify and possibly conserve the environments in which they can persist (Araujo & Williams, 2000; Rodrigues & Brooks, 2007).

Species distribution models (SDMs) estimate the probability of species' occurrence using the relationship between georeferenced records of species occurrence (and sometimes absence) and the

environment at those locations (Elith et al., 2011; Merow et al., 2013). Species distribution models are ubiquitous in conservation biology where they are used to identify and prioritize areas for protection (Guisan et al., 2013) often as part of a structured decision-making process with software such as Marxan (Ball et al., 2009) and Zonation (Moilanen et al., 2009; e.g. Esselman & Allan, 2011; Guisan et al., 2013; Wilson et al., 2005) and, locally, to inform land managers on 'habitat quality' (e.g. Glenz et al., 2001). Compared with demography and abundance, occurrence data are relatively easy to obtain, particularly when absence data are not required (Brambilla & Ficetola, 2012) and when considering charismatic and conspicuous species (Kobori et al., 2015). While conservation decision-making ideally requires data on where a species will 'do best', the output of SDMs is often assumed to provide a useful proxy for underlying demographic parameters and species persistence (Araujo & Williams, 2000; Thuiller et al., 2014).

There both is a theoretical expectation of (Brown et al., 1995; Maguire, 1973), and some empirical support for, a positive correlation between SDM-derived habitat suitability and species abundance. Gutiérrez et al. (2013) demonstrated a stronger link between abundance and SDM-derived habitat suitability than using methods aimed at deriving abundance directly from occupancy data (e.g. He & Gaston, 2000; Hwang & He, 2011; Solow & Smith, 2010; Yin et al., 2014), and SDMs produced from abundance (rather than presence/absence records) can improve explanatory power (Howard et al., 2014). Similarly, multiple studies have supported a positive link between niche centrality and abundance (Martínez-Gutiérrez et al., 2018; Martínez-Meyer et al., 2012; Osorio-Olvera et al., 2020), although this finding is not uncontroversial (Dallas et al., 2017; Santini et al., 2018). The generality of the abundance–suitability relationship is also contested, with a recent meta-analysis showing that the vast majority of studies (416/450) had a positive correlation coefficient (Weber et al., 2017) but Dallas and Hastings (2018) found mostly weak and insignificant correlations in their survey of 246 mammal and 158 tree species.

The robustness of the presumed relationship (Araujo & Williams, 2000; Pulliam, 2000) between habitat suitability and demographic parameters such as fecundity, mortality and population growth rate has gained even less consistent support. Occurrence is not necessarily synonymous with persistence, habitat quality, demographic growth or stability (Bean et al., 2014). Individuals can occur in sink populations with negative population growth (Brawn & Robinson, 1996; Pulliam, 1988), particularly where habitat quality has changed over time for dispersal-limited species (Greiser et al., 2020; Schurr et al., 2007; Thuiller et al., 2014). Species can be absent or rare in their optimum habitats due to competitive exclusion by other species which share their inclusive niche (McGill, 2012). Individuals can be distributed in an ideal free distribution such that population growth is stable across the environment despite fluctuations in habitat quality (Quaintenne et al., 2011).

The suitability–demography relationship has been tested at local to regional scales with high-quality data on breeding success in at least three ornithological studies (Aizpurua et al., 2017; Brambilla & Ficetola, 2012; Pellissier et al., 2013). The authors found positive relationships between habitat suitability and fecundity in red-backed shrikes *Lanius collurio* breeding in Northern Italy, although

with a relatively low explanatory power ($pseudo R^2 = 0.32$; Brambilla & Ficetola, 2012); in one of three wader species studied in one of the three years of a study (Pellissier et al., 2013); and in four or five of 19 passerine species in Catalonia depending on the spatial buffer applied around nests (Aizpurua et al., 2017). Regional scale relationships with habitat suitability and plant functional traits related to growth and vigour were also weak and species-specific (Thuiller et al., 2010). However, none of these studies encompass the entire breeding range of their focal species, some of them rely on proxy values of fecundity (Aizpurua et al., 2017; Thuiller et al., 2010) and some were limited to fecundity measurements on a low number of individuals [19 pairs of red-backed shrikes in (Brambilla & Ficetola, 2012), or <60 individual plants in (Thuiller et al., 2010)].

The same relationship has also gained weak support at the macro-scale, with no clear relationship between population trends and niche centrality in eight widely distributed threatened or endangered birds in North America (Manthey et al., 2015). Furthermore, in a survey of 108 tree species, correlations between the estimated intrinsic rate of increase and habitat suitability were generally negative (Thuiller et al., 2014) despite a positive correlation between abundance and habitat suitability, again supporting the idea that species do not always do best where they are most abundant or where habitat suitability is highest (McGill, 2012).

Given the difficulties in obtaining direct measures of demographic parameters at anything approaching the range-wide scale, many investigations of the putative suitability/demography relationship have relied on estimations of surrogate properties such as tree growth (McGill, 2012) and plant functional traits (Thuiller et al., 2010) or have modelled the intrinsic rate of increase from census data (Thuiller et al., 2014). Other studies have obtained high-quality demographic data, but have been limited to a small subset of the range of the species in question (Aizpurua et al., 2017; Bean et al., 2014; Brambilla & Ficetola, 2012; Pellissier et al., 2013). Even with relatively easily obtained abundance data, there is often a mismatch between the spatial scale at which SDM habitat suitability varies and over which abundance is measured (Manthey et al., 2015; Thuiller et al., 2014). In summary, due primarily to a paucity of adequate data for most species, there is considerable uncertainty about the relationship between demographic success and SDM-estimated habitat suitability.

Purple martins *Progne subis* are migratory cavity-nesting insectivores with regionally declining breeding populations (Tautin et al., 2009). The eastern subspecies (*P. subis subis*) breeds colonially and has an unusually close relationship with humans in which its breeding is completely restricted to man-made structures, generally purpose built nest boxes (Brown & Tarof, 2017). The dependence of this species on humans, means that its breeding distribution may be limited not only by the usual mix of biotic and abiotic factors, but also by human behaviour, which results in potential challenges for modelling. However, this same human association makes the purple martin a conspicuous and easy to monitor species and have led to the creation of unusually rich citizen science data. Like many other North American bird species, the eBird database includes comprehensive occurrence records for the species in its breeding range (Sullivan et al., 2009) and the Breeding Bird Survey

(BBS) has produced maps showing the relative abundance of the species throughout its range (Pardieck et al., 2019). Additionally, the Purple Martin Conservation Association (PMCA) has compiled 'Project MartinWatch' data in which purple martin 'landlords' report parameters related to fecundity such as the number of nests per colony and the number of eggs, nestlings and fledglings per nest. At the time of our study the MartinWatch database encompassed 22 years and included close to 100,000 nest-level records, making it unparalleled as a range-wide single-species demographic dataset, with two orders of magnitude more records available than in any of the previous tests of local fecundity and habitat suitability relationships (Aizpurua et al., 2017; Brambilla & Ficetola, 2012; Pellissier et al., 2013; Thuiller et al., 2010). Colony-level occupancy data (the proportion of nest boxes occupied), colony size and colony longevity data are also available through the PMCA's 'Purple Martin Survey' which provides a finer scale complement to the relative abundance data from the BBS. The combination of these high-quality datasets presents a tantalizing opportunity to evaluate the relationship between occurrence, suitability, demography and abundance using direct measures of demographic parameters at the individual scale and abundance estimates at two spatial scales.

Here we bring together these three citizen science datasets of occurrence (eBird, $N = 39,154$), fecundity (MartinWatch, $N = 87,597$) and abundance (PMCA Survey, $N = 2,304$), together with carefully assembled gridded environmental data, to assess the relationships between fecundity, abundance and habitat suitability from a species distribution model for the eastern subspecies of purple martin throughout its breeding range. We test the hypothesis that purple martins have higher nest-level fecundity and higher colony level and regional abundance in more suitable environments (as estimated by an SDM). The findings of this paper enable a critical examination of the empirical support for a common but little tested applied interpretation of SDMs.

2 | MATERIALS AND METHODS

2.1 | Purple martin breeding range SDM

The eBird database (Cornell Lab of Ornithology, 2018) was filtered to include all breeding occurrence records of purple martins between 1995 and 2016 to match the timeframe that the PMCA MartinWatch data were available. Previous studies have supported the use of eBird records as occurrence data for SDMs, finding their output comparable to models created using satellite tracking occurrence records (Coxen et al., 2017). To reduce sampling bias (Boakes et al., 2010), we thinned the records to separate them by at least 10 km² (Fourcade et al., 2014). This resulted in a final occurrence dataset of 39,154 points.

Species distribution models are best informed by environmental variables selected using expert knowledge of the natural history of the species in question (Merow et al., 2014). Based on this knowledge, we included environmental layers depicting elevation, distance from open water, land cover, tree density, human population density, estimated migration distance and minimum June temperature and Spring mean precipitation between 1994 and 2016 at a 1 km² resolution to

make our 'long-term SDM'. Full details of the rationale behind variable selection are available in Supporting Information Methods.

To allow for the possibility that purple martin occurrence and/or fecundity were more determined by annual weather than by mean climate, we also made a set of 22 'annual SDMs' in parallel with our long-term SDM to represent each year between 1994 and 2016 in which temperature and precipitation climatologies were exchanged for layers depicting annual conditions. Abundance of records in the eBird database increases through time, so we randomly sampled 559 occurrence points for each year from the database to match the minimum number of records available in 1994.

We used MaxEnt version 3.4.1 to create our SDM (Phillips et al., 2006) and the R package ENMEVAL to tune our model by selecting the feature classes and regularization multiplier which minimized AICc (Muscarella et al., 2014) and ran five model crossvalidations (Table S6).

2.2 | SDM evaluation with independent location data

The PMCA MartinWatch dataset consists of citizen science reports collected during the martin breeding season by martin 'landlords' who record egg, hatch and fledge dates and numbers for each nest. After quality filtering (details of which are available in the Supporting Information Methods), the dataset consisted of 87,597 nest records from 594 colony locations collected from 1994 to 2016. We used the locations of these colonies as an independent occurrence dataset with which to test the fit (using the test AUC statistic) and generality our SDM. All locations were used to test the long-term SDM, and we tested the annual SDMs with MartinWatch locations from the relevant years. We used pairwise distance sampling to correct AUC values for spatial sorting bias, and present the calibrated AUC (AUCc) to avoid AUC inflation due to spatial autocorrelation of suitable sites (Hijmans, 2012; Koenig, 2002).

We used the PMCA Survey (with 2,304 records) as an additional source of both successful (housing with at least one purple martin nest with eggs) and unsuccessful (housing has not recorded any purple martin eggs) colony locations; information regarding colony longevity and distance between colonies and colony size (in terms of occupancy percentage and total number of filled nest boxes) in the year 2016. We used *t*-tests to test for a difference in the distance between successful and unsuccessful colonies from their nearest neighbouring colony, under the hypothesis that unsuccessful colonies in suitable areas might have failed to attract birds due to low dispersal of martins from breeding locations.

2.3 | Fecundity and habitat suitability

We checked for relationships between summary fecundity metrics (number of eggs, hatchlings, fledglings, percentage of eggs which fledge and percentage of hatchlings which fledge) and habitat suitability at two levels of biological organization (colony level and nest level), two spatial scales (point locations and zip/postal code) and two temporal

scales (long-term SDM and annual SDMs). This resulted in a total of 228 comparisons. Fecundity metrics were used as dependent variables in linear regressions with habitat suitability metrics. Full details of this procedure are available in Supporting Information Methods.

To compare within-colony variation with within-range variation, we used T-tests to compare the standard deviation in egg number, hatch number, fledge number, egg to fledge percentage and hatch to fledge percentage. We repeated this comparison on the annual scale to compare annual within-site variation with within-range annual variation.

2.4 | Colony level abundance and habitat suitability

Colony abundance is expected to grow over time (Davis & Brown, 1999), so we used colony longevity (number of years that a colony has been established) data from the 2016 PMCA survey to test whether colonies tended to grow over time (in terms of their occupancy percentage or number of nests) using linear regression. We took the residuals from these statistically significant regressions to tests for a relationship between the unexplained variation in colony level abundance and habitat suitability using linear regression. We conducted this analysis using estimates of habitat suitability from both the long-term SDM and the 2016 annual SDM.

2.5 | Regional level abundance and habitat suitability

We used data from the Breeding Bird Survey (BBS) summarizing the relative abundance of purple martins across their breeding range between 2011 and 2015 at a mean grid cell area of 390 km² (max: 479 km², min: 0.4 km², median: 46 km², SD: 158 km²; data are scaled to show relative abundance per unit area; Pardieck et al., 2019). We extracted the mean, minimum, maximum and standard deviation in habitat suitability from the long-term SDM to each of these grid cells and created linear models to test the relationship between relative abundance and habitat suitability at the regional scale. As the data suggested a nonlinear response, we fitted a nonlinear logistic growth model of abundance as a function of the SDM-estimated suitability (Oliver, 1964) using the *nls* function in R. This approach assumes asymptotic increase of abundance as suitability increases.

Significance of parametric tests was assumed at $p < 0.05$ throughout. Expanded materials and methods are available as Supporting Information.

3 | RESULTS

3.1 | Species distribution model for the breeding range of the purple martin

We built a long-term SDM for the eastern breeding range of the purple martin (Figure 1), based on mean environmental conditions

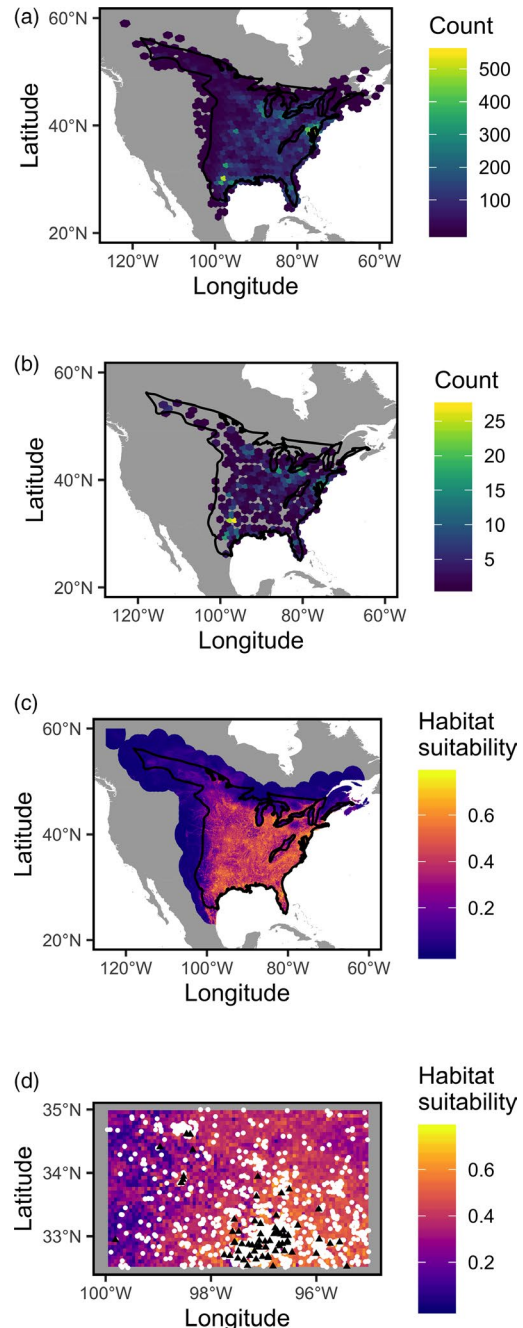


FIGURE 1 (a) Distribution of eBird occurrence points used to train the species distribution model (SDM) after spatial filtering and quality control. Each hexagon covers a 10,000 km² area. (b) Distribution of MartinWatch nest locations used to independently test the SDM after quality control. Each hexagon covers a 10,000 km² area. (c) Habitat suitability throughout the breeding range of the eastern subspecies of purple martin according to our long-term SDM using the logistic transformation. (d) Zoomed region of (c), showing location of eBird occurrence points as white circles, and MartinWatch test locations as black triangles. The colour of each filled hexagon in (a) and (b) indicates the number of occurrence points from the corresponding area. Solid black lines show the extent of the breeding distribution of *P. subis subis* according to the IUCN, where the species is thought to be present across most of the Eastern U.S. (with the exception of the Appalachian region) and the South and East of Canada

between 1994 and 2016 including several climatic and non-climatic variables we developed to capture important aspects of purple martin ecology, and eBird occurrence data collected over the same period. We also built a set of annual SDMs based on weather and occurrences in each of the 22 years in the time period. All models achieved a plausible estimate of habitat suitability, with acceptably high AUC scores even after accounting for spatial sorting bias (Long-term SDM: AUC_c average = 0.80, AUC_c std = 0.0002; Annual SDM: AUC_c = 0.72–0.81; Table S1), and predictions largely in agreement with known natural history of the species and the IUCN distribution estimates (Figures 1 and 2). Further description on the geographic and environmental distribution is available in Supporting Information Results.

3.2 | SDM predictions of independent occurrence data

We used the locations of the PMCA MartinWatch nests as an independent dataset to test the performance of our SDMs. The average $AUC_{c, \text{test}}$ score of 0.799 for our long-term SDM almost equalled the

internal training AUC_c score (Table S1) and implies that the model generalized well and can predict actual breeding sites for purple martins in addition to opportunistic eBird observation locations. Annual SDMs were also highly predictive of occurrence of the MartinWatch sites matched by year with $AUC_{c, \text{test}}$ scores ranging between 0.830 and 0.890 (Table S1).

Examination of habitat characteristics of unsuccessful colony locations did not show any clear contrast between successful and unsuccessful locations (Figure 2), but unsuccessful colonies were situated further from a successful colony than were successful colonies ($T_{149,74} = 3.81$, $p < 0.001$, $\text{mean}_{\text{successful}} = 2.96$ miles, $\text{mean}_{\text{unsuccessful}} = 8.04$ miles).

3.3 | Fecundity and habitat suitability

There was very weak evidence for a positive relationship between habitat suitability in the long-term or annual SDMs and any of the fecundity measurements from the PMCA MartinWatch dataset at either spatial scale considered (point or ZIP code) or at either level of biological organization (colony or nest). Only 10% (23/228) of the

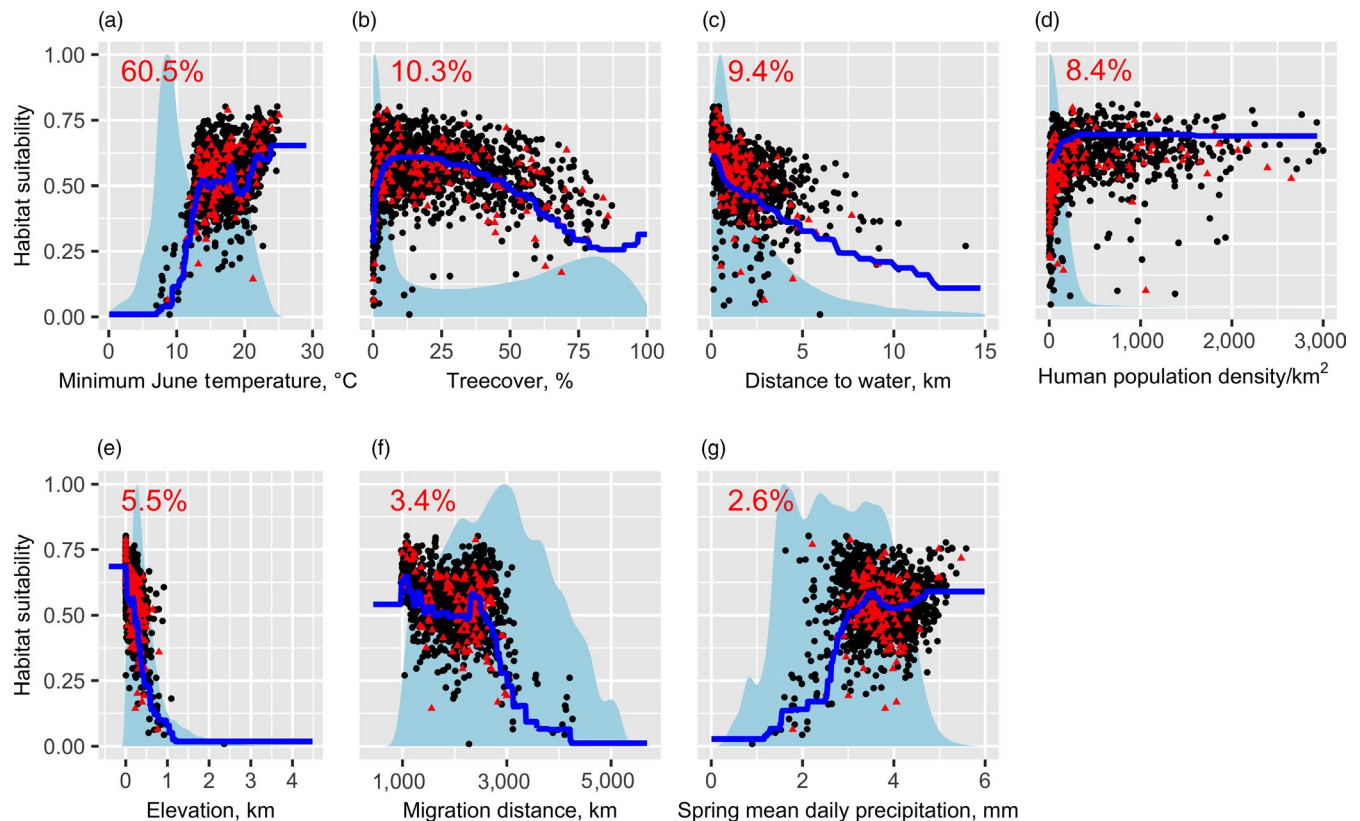


FIGURE 2 Response of habitat suitability to environmental variables in the climatic species distribution model (SDM) estimated using the MaxEnt modelling framework. (a) June minimum temperature (b) tree cover (c) distance from open water (d) human population density (e) elevation (f) migration distance (g) mean daily spring precipitation. Percentages indicate the permutation importance of each variable from MaxEnt. Land cover classification has a predicted permutation importance of 0% and is omitted here. Blue lines show the estimated response curve. Blue shaded areas show the distribution of the environmental variables across the study domain at the background points. Red triangles show the environmental characteristics of sites from the Purple Martin Conservation Association (PMCA) survey which did not attract purple martins and black circles show environmental characteristics of sites which did attract purple martins

regressions resulted in statistically significant results, and those that did, explained an extremely small proportion of the variation (Min $R^2 = 0.0002$, Max $R^2 = 0.03$; Tables S2 and S3).

Within colony variation (measured by standard deviation) in egg number ($T_{590} = 72.51$, $p < 0.001$), hatch number ($T_{590} = 86.87$, $p < 0.001$), fledge number ($T_{590} = 96.47$, $p < 0.001$), egg to fledgling percentage ($T_{562} = 76.43$, $p < 0.001$) and hatchling to fledgling percentage ($T_{65} = 4.55$, $p < 0.001$) exceeded that of within-range variation across all years (1994–2016) using one sample T-tests. The same was true when comparing annual variation within sites with annual variation across the range (egg to fledgling percentage: $T_{29,14} = 23.27$, $p < 0.001$; hatchling to fledgling percentage: $T_{31,04} = 1.80$, $p = 0.08$) using 2 sample T-tests. Within colony egg number (0–13), hatchling number (0–13) and fledgling number (0–12) ranges were identical to range-wide variation.

3.4 | Colony level abundance and habitat suitability

Colonies which had been established for a longer period had a larger number of occupied nest boxes ($F_{1,1,346} = 135.50$, Estimate = 0.66, $p < 0.001$, $R^2 = 0.09$) and a higher occupancy percentage ($F_{1,1,346} = 26.2$, Estimate = 0.37, $p < 0.001$, $R^2 = 0.02$; Figure S1). Long-term habitat suitability did not explain the residual variation for occupancy percentage ($F_{1,1,346} = 1.92$, Estimate = 10.13, $p = 0.166$, $R^2 = 0.00$; Figure S2a) and explained very little of the residual variation in the number of occupied nest boxes (and in the opposite direction to our hypothesis; $F_{1,1,346} = 12.48$, Estimate = -19.82, $p < 0.001$, $R^2 = 0.01$; Figure S2b). The same was true of habitat suitability from the 2016 model (Occupancy percentage: $F_{1,1,346} = 2.26$, Estimate = 5.40, $p < 0.132$, $R^2 = 0.00$; Number occupied nest boxes: ($F_{1,1,346} = 20.51$, Estimate = -12.42, $p < 0.001$, $R^2 = 0.01$; Figure S2c,d).

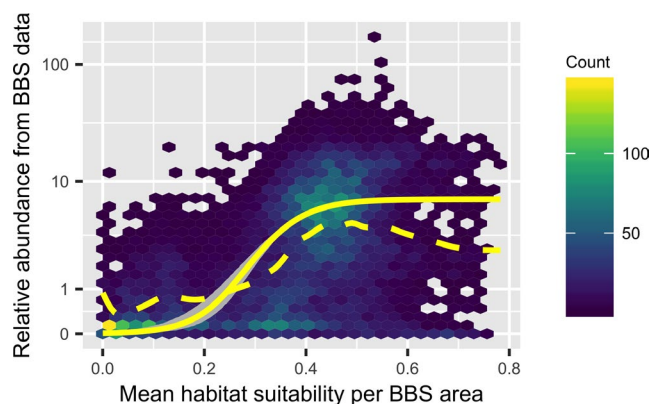


FIGURE 3 Relative abundance of breeding purple martins is constrained in regions of low mean habitat suitability. Note the arc sin transformation on the y-axis. The colour scale of the points shows the number of data points in each hexagonal area. The solid yellow line shows the fit of a logistic growth model, with the grey shaded areas showing the 99% confidence intervals. The dashed yellow line shows a median quantile regression to illustrate a smoothed version of the unmodelled data

3.5 | Regional level abundance and habitat suitability

Linear regression of the mean regional habitat suitability from our long-term SDM and relative abundance from BBS data showed a positive relationship ($F_{1,11,019} = 1717$, Estimate = 13.11, $p < 0.001$, $R^2 = 0.14$). However, visual examination of this relationship suggested a nonlinear relationship in which abundance was constrained below certain habitat suitability. This supported the fit of a logistic growth model (Asymptote: Estimate = 7.02, SE = 0.13, $T_{11018} = 54.35$, $p < 0.001$, Y-intercept: Estimate = -6.52, SE = 0.47, $T_{11018} = -13.78$, $p < 0.001$, Growth rate: Estimate = 18.93, SE = 1.39, $T_{11018} = 13.63$, $p < 0.001$; Figure 3).

Minimum and maximum habitat suitability formed a similar pattern with relative abundance, with noisy positive linear relationships (Minimum: $F_{1,11,019} = 1905$, $p < 0.001$, $R^2 = 0.15$; Maximum: $F_{1,11,019} = 2,644$, $p < 0.001$, $R^2 = 0.19$), nonlinear trends supportive of limited abundance at low habitat suitability and higher (but variable) abundance at high habitat suitability (Figure S3).

4 | DISCUSSION

We built a species distribution model depicting habitat suitability for the eastern subspecies of purple martin across its breeding range. The model was statistically well supported, and met or exceeded the current standards for SDM modelling in all areas (Araujo et al., 2019). While the model was predictive of purple martin occurrence from an independent dataset and regional relative abundance, there was no evidence that higher habitat suitability is reflected in fecundity or abundance at the nest or colony level. While our analysis is limited to a single species, our results provide a rigorous benchmark for important questions surrounding the interpretation of SDMs.

We selected purple martins as our study species due to the unparalleled demographic datasets which have been gathered at extent of the breeding range and the resolution of the nest for this species. However, the same peculiar human-dependence which has facilitated the collection of these data poses a potential confounder in our study. If purple martins are constrained to breeding in man-made nest boxes, then their observed breeding distribution must be somehow affected by where humans position those boxes. One could go so far as to suggest that the modelled quantity is actually the habitat suitability for purple martin enthusiasts, rather than purple martins themselves. We do not believe this is the case in this example for several reasons: (a) Potentially due to our spatial thinning procedure, there is no evident signal of human population patterns in the output from our model. (b) Human population density (included as a way to capture some element of the purple martin's dependence on humans) was not the top predictor in our model, and the relationship was of a threshold type, where there was no expected increase in habitat suitability of purple martins with increasing human population density beyond a low threshold of around 200 people/km². (c) The niche relationships found in the

study were all qualitatively supported by our hypotheses based on knowledge of the natural history of the species (Allen & Nice, 1952; Brown & Tarof, 2017; Root, 1988; Williams & DeLeon, 2020; Winkler et al., 2013). (d) The provision of martin housing does not guarantee its use—purple martin occurrence must therefore be limited by factors other than the availability of martin enthusiasts. Despite these positive indications, however, human population density are not the ideal data from which to estimate the complex relationship between martins and humans. A future refinement of the model may become possible should range-wide martin housing density data become available, or a more complex form of human population density data which takes account the socio-demographic and geographic factors likely found in martin landlords (Raleigh et al., 2019; Ray, 2012).

Despite access to an unparalleled species-specific demographic dataset, we found no evidence of higher fecundity in areas with higher habitat suitability for the purple martin. As a migrant species, we cannot exclude that carry-over effects from migration, or even from previous breeding seasons, are contributing to fecundity in addition to conditions experienced on the breeding grounds (Saino et al., 2017). It is also possible that climate change during the 22-year timespan of this study may be altering the timing of peak food availability and impacting breeding success (Imlay et al., 2018). Either process may disrupt the hypothesized link between habitat quality and fecundity, but are challenging to account for without a large number of individual birds being tracked throughout their whole annual cycle. Despite our best efforts to minimize bias in our occurrence data, it is also possible that the lack of relationship is simply a modelling artefact (Loehle et al., 2015; Yackulic et al., 2013). Our finding does, however, reinforce previous studies that found no link between fecundity and SDM habitat suitability at large scales using proxy values to estimate demographic parameters (Manthey et al., 2015; McGill, 2012; Thuiller et al., 2010, 2014) and those finding an absence of (Bean et al., 2014) or weak and species-specific effects at local and regional scales (Aizpurua et al., 2017; Brambilla & Ficetola, 2012; Pellissier et al., 2013).

It has previously been suggested that purple martin colony size may reflect an ideal free distribution (Davis & Brown, 1999), in which higher abundances of birds cluster in areas of higher habitat quality, leading to equal resource availability in all areas and uniform fecundity across the range (Fretwell & Lucas, 1970). If purple martins formed an ideal free distribution we would predict not only our observed lack of relationship between habitat suitability and fecundity, but also a positive relationship between habitat suitability and abundance, where more martins breed in the areas of highest habitat quality. We did not find support for the latter prediction at the spatial scale at which the fecundity data were gathered (the colony level). Neither colony size (the number of filled nest boxes in a colony) nor the percentage occupancy (the proportion of filled nest boxes within a colony) were related to habitat suitability in either annual or long-term models. These local data are not, however, the perfect data with which to test this hypothesis—both measures are affected by how many nest boxes a 'landlord' has chosen to provide independently of purple martin nesting preferences, and the data

are incomplete in that we have no reliable measure of the abundance of purple martins in the area around our records.

In an example of the often complex scale relationships in macroecology (Blackburn & Gaston, 2002), our analysis of the link between regional scale abundance of purple martins from the Breeding Bird Survey did, however, reveal evidence of a positive nonlinear relationship between habitat suitability from our long-term SDM and relative abundance. This may indicate that purple martins are indeed forming an ideal free distribution, at least at this spatial scale. Martin regional abundance appears to be constrained to low levels in areas of low habitat suitability, but can take a on a wide range of values at higher habitat suitability. This echoes the finding of a 'wedge shaped' relationship between habitat suitability and abundance in 69 Australian rain forest vertebrate species (VanDerWal et al., 2009) and previous descriptions and theory from Hengeveld (1992) and Brown (1995).

Considering the lack of relationship between local fecundity and habitat suitability, and the mismatch in abundance and habitat suitability relationships at two spatial scales, it is possible that the SDM is describing 'good neighbourhoods' which reflect the physiological requirements of purple martins and, as such, its range limits and regional carrying capacity. Whereas, at the colony level, a 'good site' in terms of abundance and nest success, is determined more by biotic and stochastic factors. This idea is supported by our finding that within-colony variability in numbers of eggs, hatchlings and fledglings exceeded the variability across the entire range. In our 'wedge shaped' regional abundance relationship, therefore, low purple martin abundance at low predicted habitat suitability may reflect the distribution of a species at the edge of its abiotic niche, whereas the high variability in regional abundance at high habitat suitability may be caused by the set of complex biotic interactions at local scales.

Purple martins in 'good neighbourhoods' may be prevented from achieving high abundance and fecundity due to interspecific competition from species which may share their inclusive niche (Colwell & Fuentes, 1975; McGill, 2012; Wisheu, 1998) for example through competition for nesting sites or food. The lack of relationship between local abundance or fecundity and habitat suitability may also occur due to a 'bad sites' occurring in 'good neighbourhoods' whereby unfavourable site-level factors limit abundance and nest success. Given the dependence of purple martins on human-provisioned housing, anthropogenic factors such as poor nest box quality can reduce breeding success (Raleigh et al., 2019) and may break down the link between regional habitat suitability and local demography. Alternatively, our discordant local and regional results could be caused by fine-scale habitat heterogeneity where colonies may be situated in very small patches (smaller than the 1 km² resolution of our SDM) of high-quality habitat surrounded by relatively low-quality habitat. These colonies may then achieve high fecundity even in regions of low habitat quality (Denoël & Lehmann, 2006). Future integration of fine-scale space-use data using, for example, GPS tags, may test whether the home ranges of birds support this idea.

Finally, the lack of local abundance relationship may be caused by a historical lag effect in purple martin distribution (Greiser et al., 2020). Purple martins have a relatively high degree of natal

philopatry (Allen & Nice, 1952; Brown & Tarof, 2017; Hill, 2003), so even a small increase in colony fecundity could lead to substantially increased colony level abundance over a few years via positive feedback. In support of this idea, our own data showed a positive link between colony longevity and colony level abundance. Whereas landcover and climate may have changed over time, this philopatry and positive feedback means that birds may return to previous breeding sites, potentially at high abundance, even though habitat quality is no longer high, leading to a potential extinction debt (Cousins & Vanhoenacker, 2011; Frantz et al., 2019; Greiser et al., 2020; Sang et al., 2010). As unsuccessful colonies were more isolated from nearby colonies than were successful colonies, this long-distance migrant may be behaviourally 'dispersal-limited' in its selection of breeding sites (Paradis et al., 1998). New colonies may only be founded through a diffusive process when abundance at nearby colonies exceeds their capacity (Hill, 2003), meaning newly suitable colony locations may not be used.

Although purple martins may appear an unusual species due to their dependence on humans in the breeding season, the species also has traits which may make our findings generalizable to other species. For example, where species meet the conditions of the ideal free distribution (principally an ability to both accurately sample habitat quality at multiple locations to move freely between patches (Fretwell & Lucas, 1970)), or when there is reason to believe that animal perceptions of habitat quality differ at local and regional scales (for example due to local biotic factors) (Johnson, 2005), we suggest that similar patterns may be expected.

How, then, should land managers use this model (or ones like it) for conservation purposes? Given the positive relationship between regional abundance and SDM-derived habitat quality, the SDM is a useful tool for larger scale habitat conservation prioritization. However, there is an inherent mismatch in definitions of breeding habitat quality at different scales, where at very local scales animals and their land managers must seek conditions to maximize individual fecundity, whereas at regional scales, land managers must seek conditions which maximize carrying capacity or abundance (Johnson, 2005). The lack of relationship between local fecundity and the SDM-derived measure of habitat quality limits its utility as a predictive tool at the local level, particularly where species may be following the ideal free distribution. For a land manager seeking priority locations for new purple martin housing, after regions capable of supporting high abundance are identified using the SDM, local potential 'hotspots' might be better identified through a 'diffusive strategy' based on locations of nearby colonies which have a high occupancy and fecundity rate (Hill, 2003).

In summary, we used data from three extensive citizen science initiatives to build an unparalleled demographic dataset across a species' range and found little evidence for a relationship between demography and local abundance and SDM-derived habitat suitability. This is the first time these relationships have been tested across an entire species' range, while using direct measurements of local fecundity; and with access to a fecundity dataset 100 times larger than previous

efforts. This suggests that we need to be careful in our interpretation of SDM output for research and decision-making. In particular, this analysis supports the use of SDMs to delineate species' range boundaries or to estimate regional abundance. However, SDMs parameterized exclusively with abiotic factors (such as the one described here) without consideration of biotic factors including dispersal or interspecific/intraspecific interactions may be limited in their ability to reflect biological realities beyond the edges of distributions and regional scale abundance patterns. Given the findings of this study and others (Bean et al., 2014; Dallas et al., 2017; McGill, 2012; Merow et al., 2014; Thuiller et al., 2010, 2014), there is no strong basis to presume correlations between SDM modelled habitat suitability and local species fecundity or abundance.

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AUTHORS' CONTRIBUTIONS

H.M.W. and A.M.W. designed the research; H.M.W. analysed the data and wrote the manuscript; J.S. collected and curated citizen science data used in the paper; H.M.W. and A.M.W. interpreted results and edited the manuscript. All authors approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.msbcc2fwq> (Williams et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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